

# Perennial crops and endogenous nutrient supplies

T.E. Crews\*

Environmental Studies Program, Prescott College, 220 Grove Ave, Prescott, AZ 86301 USA.

\*Corresponding author: tcrews@prescott.edu

Accepted 29 November 2004

Research Paper

## Abstract

Perennial cropping systems may achieve significant improvement over annual systems in the synchrony between crop nutrient demands and nutrient supplies. Improvements in nutrient synchrony would result in the reduction of nutrient losses and their associated environmental impacts. A perennial system with high levels of synchrony would also require fewer nutrient inputs, such that it may be possible to develop an agriculture that functions mostly, if not entirely, on nutrient inputs from endogenous sources (i.e., weathering of primary and secondary minerals and biological nitrogen fixation). In this paper I describe three realms of research that will inform the development of relatively high-yielding grain production systems grown on endogenous nutrient supplies: (1) improvement of nutrient synchrony through the development of perennial crops; (2) identification of soils that are in a high nutrient release phase of pedogenesis, which could balance the export of rock-derived nutrients in crop harvests; and (3) optimization of legume density, harvest index and percent nitrogen derived from the atmosphere (%Ndfa) to achieve adequate nitrogen inputs through biological fixation.

**Key words:** legume, lithophilic nutrients, nitrogen, nitrogen fixation, pedogenesis, phosphorus, sustainability, synchrony, weathering

## Introduction

It is often surprising for students of agriculture to learn that some of the most productive terrestrial ecosystems on Earth—the tropical rainforests—often grow from the most highly weathered and thus least fertile soils<sup>1,2</sup>. How is this possible? Simply put, a wide array of nutrient cycling mechanisms<sup>3,4</sup> prevent nutrient losses from exceeding what are often very low levels of nutrient inputs, thus allowing for high levels of photosynthesis to take place. When tropical rainforests that exist on highly weathered soils are cleared and burned for annual crop production, it is common for farmers who do not rely on fertilizer inputs to obtain only one or two years of harvests before soil nutrient deficiencies profoundly limit crop growth<sup>5</sup>. Crop productivity cannot be sustained primarily because the annual crops lack the extensive and morphologically diverse root systems and associated organisms that prevent the perennial tropical forest vegetation from leaking nutrients. Moreover, nutrients are exported from the annually cropped ecosystem in the harvest and are usually not returned in human manure.

The same eventual limitation of crop productivity caused by excess nutrient loss via leaching, runoff, gas fluxes and harvests was also commonplace in traditional agricultures

of regions with less weathered soils<sup>6,7</sup>. In less-weathered temperate soils, gradual mineralization of nutrient-rich soil organic matter was responsible for longer lags between the initiation of annual crop production and the appearance of intense nutrient limitation. Once soil microbial respiration approached equilibrium with net primary production (NPP) in crop residues, however, nutrient losses (via harvests, leaching, runoff and/or denitrification) from annually cropped systems typically exceeded the relatively low background rates of natural nutrient regeneration.

In response to nutrient limitation encountered in annual cropping systems, traditional farmers of many cultures developed sophisticated, site-specific management strategies that effectively concentrated nutrients in time and/or space. An example of a farming system that concentrates nutrients in time would be a fallow rotation where nutrients are taken up and stored in fallow vegetation. When the fallow site is once again used for crops, the one or more years of 'banked' nutrients in the fallow vegetation are released through decomposition and made available to crops. An example of traditional farmers concentrating nutrients in space can be found in floodplain agriculture, such as that which occurred in the Nile River valley before the Aswan Dam<sup>8</sup>. Essentially, nutrients and nutrient-rich particles of silt, clay or organic matter are transported from

large watersheds via leaching or runoff, into relatively small plots of land in the floodplain below.

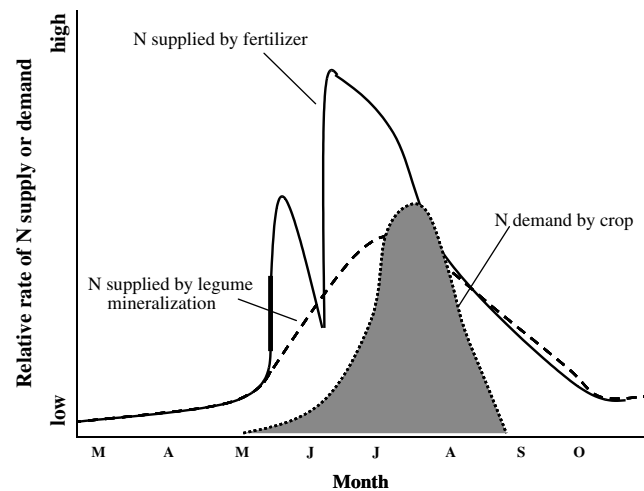
During the twentieth century, traditional fertility management strategies in many cultures gave way to the modern practice of applying highly concentrated forms of essential crop nutrients. While highly successful at addressing nutrient limitation, synthetic fertilizers, particularly nitrogen (N), have now come under considerable scrutiny because of the detrimental ecological consequences of nutrient losses from agriculture; these include stratospheric ozone destruction, greenhouse gas production, freshwater and marine eutrophication and, in some cases, hypoxia, as well as threats to human health<sup>9–11</sup>. Moreover, N fertilizers, in particular, are very energy expensive to produce, usually comprising the greatest commercial energy input into modern production agriculture<sup>12</sup>. While annual grain-producing agroecosystems developed over the past 50 years have been highly successful at raising food productivity, dependence on non-renewable resources, and ecological impacts, cast serious doubt on their long-term sustainability.

In spite of its shortcomings, there exist few viable alternatives to annual crop production in general, and grain production in particular. One alternative—a perennial grain-producing polyculture—has been investigated by researchers at the Land Institute in Salina, Kansas. They have based their design of a perennial polyculture on taxonomic and functional groups that they observed in the native tallgrass prairie of central and eastern Kansas. The polyculture consists of a warm-season grass, a cool-season grass, a sunflower and a legume<sup>13</sup>. While it has been the goal of the Land Institute to develop a cropping system that, like the prairie, maintains productivity on inputs from atmospheric deposition, biological N fixation and soil mineral weathering, the question remains: Is it possible for a grain-producing agroecosystem to be both high yielding and continuously productive while relying on endogenous nutrient supplies? In this paper, I present a framework, based in part on research conducted in native ecosystems, to begin to address this question. I describe three considerations, and ultimately research directions, that I believe to be cardinal for a grain-producing agroecosystem to approach or achieve continuous high yields while relying on endogenous nutrient supplies:

- 1) Improvement in synchrony between rates of nutrient availability and crop demand.
- 2) Identification of soils that are in a ‘high nutrient release’ phase of pedogenesis or soil development.
- 3) Optimization of legume density, harvest and %N derived from the atmosphere (%Ndfa).

### Improvements in Nutrient Synchrony

Nutrient synchrony is defined as the matching of crop demands for nutrients with nutrient supplies, either from organic or inorganic sources<sup>14</sup>. Annual, high-input



**Figure 1.** Asynchrony of crop demand (...) for nitrogen (N) and N supply via a split application of fertilizer (—) and legume residue mineralization (---) in a hypothetical north temperate annual cropping system<sup>16,17</sup>.

agriculture currently achieves low levels of nutrient synchrony, with only 30–50% of applied N fertilizer and 45% of applied phosphorus (P) fertilizer actually being taken up by crops<sup>15</sup>. This striking and important asynchrony can be largely explained by the absence of a proportionate sink or demand for fertilizer-supplied nutrients during most of the year. The high concentrations of nutrients that are applied as fertilizers at the beginning of a cropping cycle are susceptible to leaching, runoff and, in the case of N, denitrification and ammonia volatilization (Fig. 1)<sup>16,17</sup>. Nutrients remaining after a cropping cycle or mineralized from crop residues during fall or winter, are also susceptible to loss. While there is some evidence that under conventional management practices N supplied to crops via legume residues may be less vulnerable to leaching or gaseous loss than fertilizer N<sup>18</sup>, rarely do either legume-based or fertilizer-based annual agricultural systems exceed levels of N synchrony greater than 60%, even when best management practices are employed<sup>17</sup>.

Many innovative technologies and management strategies have been developed in an attempt to reduce the leakiness of annual cropping systems; they include adjustment of the timing and frequency of fertilizer application, adjustment of planting dates, application of nitrification or urease inhibitors, and planting of cover crops<sup>19,20</sup>. While these efforts are extremely important, it is arguable that attempts to modify annual agriculture have reached a stage of diminishing returns—technological advances have resulted in improved recovery of applied N, but the costs of technology, skilled labor and management are likely to be much greater for N recovery levels higher than 50%.

In contrast to modern annual agroecosystems, most native ecosystems maintain high levels of nutrient synchrony, particularly for limiting nutrients. For example, as

**Table 1.** Examples of net primary production (NPP), biomass-nitrogen (-N) and leached-N from perennial native vegetation, annual crops and perennial crops from temperate regions.

Ecosystem	Location	NPP (dry biomass)	Plant biomass-N	Leached-N	Leached-N/ biomass-N	Sources
		----- kg ha <sup>-1</sup> yr <sup>-1</sup> -----			%	
Native systems						
Temperate deciduous forest	New Hampshire, USA	10,400	523	4	<1	21
Tallgrass prairie	Kansas, USA	4170 <sup>1</sup>	140 <sup>2</sup>	<1 <sup>2</sup>	<1	22, 23
Annual agroecosystems						
Barley fertilized 120 kg yr <sup>-1</sup>	South-central Sweden	9630	183	10	6	24, 25
Corn fertilized 187 kg yr <sup>-1</sup>	Iowa, USA	20,000 <sup>3</sup>	201 <sup>3</sup>	60	60	26
Perennial agroecosystems						
Perennial fescue fertilized 200 kg yr <sup>-1</sup>	South-central Sweden	14,640	380	1	<1	24, 25
Alfalfa	Minnesota, USA	11,315 <sup>1</sup>	343 <sup>4</sup>	2	<1	27

<sup>1</sup> Above-ground net primary production (ANPP) only.

<sup>2</sup> Median values for prairie watersheds with fire frequencies ranging from 1 to 20 years (includes roots and shoots).

<sup>3</sup> Estimated ANPP and biomass-N based on extrapolations from reported grain yield of 10 MT ha<sup>-1</sup>.

<sup>4</sup> Plant biomass-N for above-ground biomass only.

a percentage of N contained in live plant biomass, native ecosystems commonly lose one to two orders of magnitude less N to leaching than do annual agroecosystems (Table 1)<sup>21–27</sup>. High retention of N and other essential nutrients in most native ecosystems is, in many respects, attributable to the predominance of perennial vegetation. Perennial plants retain nutrients in two important ways: (1) through retranslocation within plants before tissue senescence; and (2) by maintaining extensive root systems that can capture nutrients in broad windows of time and space. When multiple perennial species grow together, the efficiency of nutrient capture increases further. For example, native perennial grasses maintain different tissue qualities, root:shoot ratios and, in turn, nutrient mineralization rates<sup>28</sup>. Variation in these and other species-specific attributes leads to spatial and/or temporal partitioning of nutrient resources<sup>29,30</sup> and ultimately reduces the likelihood of large pools of available nutrients accumulating in soils and then being lost through leaching or denitrification.

Levels of nutrient synchrony that approach those of native systems have been achieved in perennial pasture and forage cropping systems<sup>17</sup>. In the Kjettslinge farm study in Sweden, researchers measured leaching outputs of only 1 kg N ha<sup>-1</sup> yr<sup>-1</sup> from a perennial fescue (*Festuca pratensis*) ley that received 200 kg N ha<sup>-1</sup> yr<sup>-1</sup> as fertilizer<sup>24,25</sup> (Table 1). In tile-drained plots in Minnesota, Randall and colleagues<sup>27</sup> reported that plots of alfalfa leached 37 times less nitrate than annual continuous corn or corn–soybean rotations. These findings and others<sup>31–33</sup> suggest that herbaceous perennials have the potential to maintain high NPP, biomass harvests and high levels of nutrient synchrony. With every kilogram of nutrient that is retained in a perennial cropping system, one less kilogram of nutrient input is required to support high yields.

## Balancing Nutrient Losses with Endogenous Nutrient Inputs

It is widely accepted that plants require 14 elements other than oxygen, hydrogen and carbon, which they directly obtain from air and water<sup>34</sup>. These 14 elements or nutrients are N, P, K, Ca, Mg, S, Mn, B, Zn, Cu, Ni, Cl, Mo and Fe. Several other elements—Co, Na, Si—are essential to particular plants, or at least enhance their growth<sup>34</sup>. Of all the essential nutrients required by plants, only N originates almost entirely from the atmosphere and is ‘fixed’ or made available to the biota by organisms<sup>35</sup>. All other essential nutrients originate from the dissolution of primary and secondary minerals, or in other words, the weathering of rocks and soils. In this paper, I refer to these as ‘lithophilic’ (rock-loving) nutrients, to identify them as elements that cycle on a geological time scale. For a nutrient to be lithophilic does not imply that it was recently weathered from a rock mineral, simply that the origin of the nutrient can ultimately be traced back to the dissolution of rock minerals. In ecosystems with young to middle-aged soils, N is the nutrient that most commonly limits NPP of native and unfertilized agroecosystems<sup>36</sup>. In ecosystems developed on older, highly weathered soils, the low biotic availability of P or another lithophilic element often becomes the most limiting nutrient to productivity<sup>37,38</sup>.

### *N limitation as a lithophilic nutrient limitation in disguise*

The reasons why N limitation develops and persists in young to moderately developed ecosystems are complex and not entirely understood. Broadly speaking, there are numerous pathways for N loss to occur in most

ecosystems<sup>36,39</sup>, and rates of loss through these pathways are imperfectly matched by rates of N inputs via atmospheric deposition and biological N fixation. In ecosystems where N limitation is chronic, one would expect organisms with the capacity to fix N to have a competitive advantage over organisms having to compete for limited soil N<sup>36</sup>. Occasionally this is what is found, but often in temperate regions, potentially competitive N fixing species, such as woody legumes, are absent from the flora of N-limited ecosystems<sup>40</sup>. Alternatively, when legumes are present in the flora, the activity of N fixers is frequently constrained by one or more of the following ecological factors: the energetic costs of fixing N, preferential herbivory of N-rich legumes, sensitivity of N fixers to fire, extreme soil pH, drought or low availability of lithophilic nutrients<sup>35,36,41</sup>.

Many of the factors that prevent legumes from eliminating N-limitation in native systems are effectively addressed through management practices in legume-based agroecosystems (e.g., adjustment of legume density and spacing, rhizobial inoculation, irrigation, control measures for weed competition and herbivory). However, it is difficult to increase the availability of lithophilic nutrients that affect N fixers through farm management practices. The activities of symbiotic N-fixing bacteria can be affected directly or indirectly (*vis-à-vis* host vitality) by a range of lithophilic nutrients, including K, Ca and Mo<sup>42-44</sup>. However, the availability of P stands out as a nutrient that has been shown to affect N fixation rates of rhizobia in legumes<sup>43,45-49</sup>, as well as free-living bacteria, both heterotrophic<sup>50</sup> and autotrophic<sup>51</sup>.

The requirement for key lithophilic nutrients by N-fixing symbioses led Vitousek and Howarth<sup>36</sup> to suggest that N limitation in some ecosystems is actually 'limitation by some other nutrient in disguise'. Certainly, in agroecosystems where legume densities can be adjusted, N availability might be best characterized as a proximate limiting factor, with the availability of lithophilic nutrients required by N fixers being an ultimate limiting factor. Crews<sup>52</sup> illustrated this in research on a traditional farming system that is found in different physiographic regions of south-central Mexico. Farmers grew maize and alfalfa—the alfalfa was fed to livestock whose manure was used to fertilize the maize. N fixation by alfalfa, and thus N supplies to the maize via manure, was regulated in part by the availability of native soil P.

### *Weathering rates of essential lithophilic nutrients*

An adequate supply of lithophilic nutrients is essential for crop growth and for N fixation. As with N, farmers have increasingly addressed crop limitations caused by inadequate supplies of lithophilic nutrients by applying mineral fertilizers. Also as with N, the prospect of improving the synchrony of crop demand with nutrient supply could substantially decrease the need to use exogenous nutrients to balance losses. But the question remains, is it possible for soils alone to continuously supply adequate levels of

lithophilic nutrients to crops, especially when they are being removed continuously in harvests? The experience of most annual agriculture suggests that the answer to this question is no, at least not when yields are great<sup>8</sup>. However, if nutrient synchrony can be substantially increased with perennials, then continuous production based solely on endogenous nutrient supplies may be possible on some soils in certain climates (Fig. 2). To understand where these soils might be found, I will describe three soil-related attributes that broadly determine rates of lithophilic nutrient release from weathering; namely, original parent material structure and composition, stage of soil development and current climate.

### *Original parent material structure and composition*

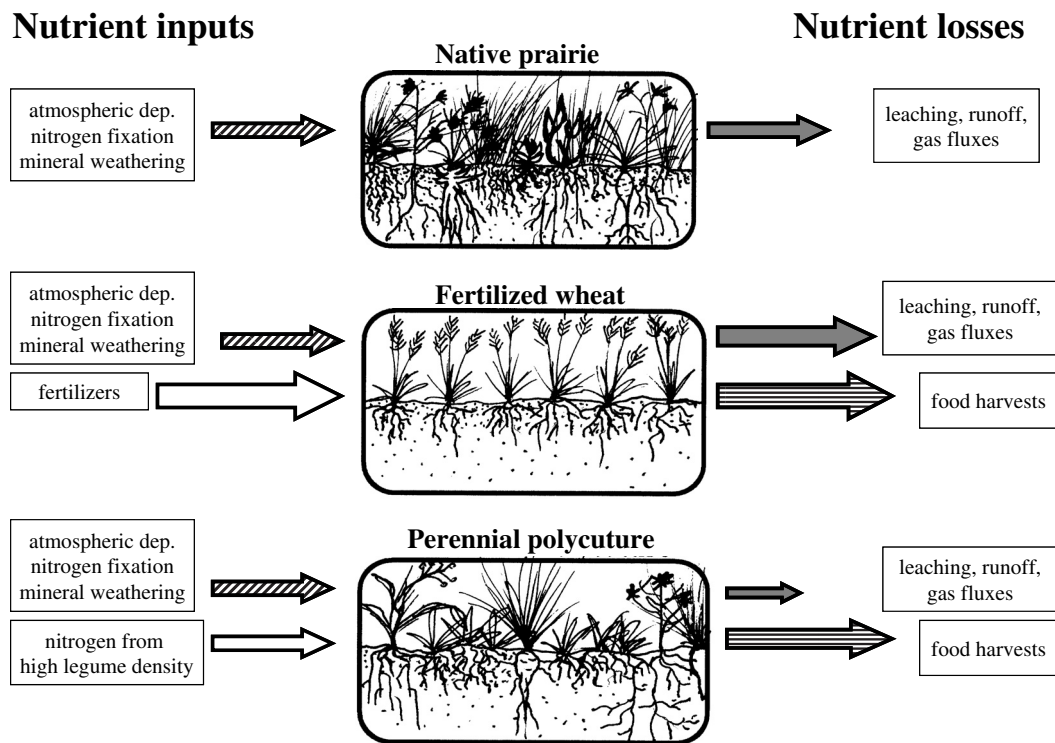
Soil parent material refers to the original rock or deposited material (alluvial, colluvial, eolian) from which a soil develops. Rock-forming magmas in the Earth's mantle vary considerably in their lithophilic nutrient concentrations, and these variations are reflected in the constituent minerals that comprise rocks at the Earth's surface<sup>53</sup>. Moreover, variation in cooling and depositional processes can affect nutrient concentrations of rocks and minerals. For example, the P concentration of the constituent minerals of a typical granite is 0.05%, compared to a typical basalt, which is 0.15%<sup>54</sup>.

Equally important as the lithophilic nutrient content of rock and mineral parent materials is their stability under Earth surface conditions. Geomorphologists utilize numerous elemental ratios to evaluate the susceptibility of different geological substrates to weathering reactions<sup>55</sup>. Reiche's weathering potential index (WPI)<sup>56</sup> relates the mole percentage of the sum of alkalis and alkaline earth elements (the most mobile ions in the weathering process) minus combined water (an indication of the extent of hydrolysis already taken place) to the total moles present in the mineral exclusive of water (see Eqn 1).

Reiche's WPI is intended to reflect: (1) the stability of the crystalline structure of a mineral; and (2) the extent to which a mineral has already been weathered<sup>56,57</sup>. Substrates with high WPI values are considered less stable and thus more weatherable (Table 2). While very qualitative, the WPI values, coupled with lithophilic nutrient concentrations, illustrate which parent materials have the propensity to weather relatively quickly and, in the process, release essential nutrients.

### *Stage of soil development and lithophilic nutrient availability*

In the past several decades, biogeochemical theory has developed suggesting that nutrient availability of a soil is not simply a unique property reflecting complex local circumstances but, rather, is understandable within a broad framework of biogeochemical changes that occur during long-term soil development<sup>37,39,58</sup>. For example, Walker



**Figure 2.** Relative avenues of nutrient inputs and losses for native prairie, annual wheat and a perennial polyculture; dep.; deposition.

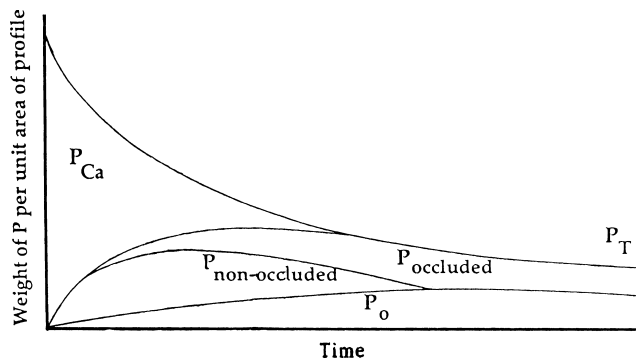
$$\frac{100 \times \text{moles}(\text{K}_2\text{O} + \text{Na}_2\text{O} + \text{CaO} + \text{MgO} - \text{H}_2\text{O})}{\text{moles}(\text{SiO}_2 + \text{TiO}_2 + \text{Al}_2\text{O}_3 + \text{Fe}_2\text{O}_3 + \text{Cr}_2\text{O}_3 + \text{K}_2\text{O} + \text{Na}_2\text{O} + \text{CaO} + \text{MgO} - \text{H}_2\text{O})} \quad (1)$$

and Syers<sup>37</sup> proposed a model of how forms of soil P change over the course of long-term soil development (Fig. 3). They suggested that at the onset of primary succession, when a new parent material is exposed for colonization by the biota, all P is held in primary minerals, the most common being apatites ( $P_{Ca}$ ; calcium phosphates containing varying quantities of carbonate, fluoride, sulfate, hydroxide and several cations). Since apatites are generally

contained in rocks or large particles of primary minerals, P availability at very early stages of soil development tends to be low. Through the action of weathering, the primary mineral-P dissolves, and the labile phosphate is either taken

**Table 2.** Examples of calculated weathering potential index (WPI) values<sup>56</sup> and percentages of calcium (%Ca) and phosphorus (%P) for selected parent materials<sup>54</sup>.

Rock type	WPI	%Ca	%P
Rhyolite	2.5	0.81	0.03
Granite	7	1.31	0.05
Gneiss	7	0.09	0.04
Schist	7	0.81	0.04
Diorite	13	4.67	0.13
Andesite	14	4.82	0.09
Basalt	18	6.72	0.15
Gabbro	22	6.80	0.11



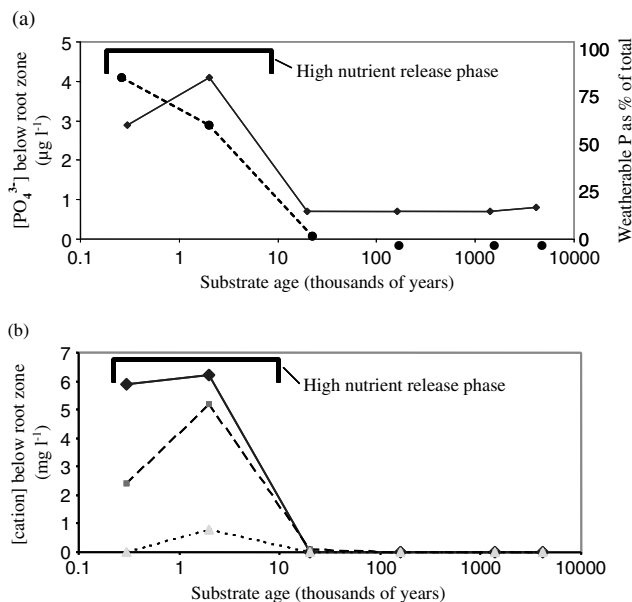
**Figure 3.** Walker and Syers' model<sup>37</sup> of changes in forms of soil phosphorus through time.  $P_T$  = total soil P,  $P_{Ca}$  = primary mineral calcium phosphates (largely apatite minerals),  $P_o$  = organically bound P,  $P_{non-occluded}$  = relatively labile P that could potentially be available to the biota,  $P_{occluded}$  = sparingly soluble P, largely associated with oxides of Fe and Al and mostly unavailable to the biota.

up by organisms, thus entering the organic P pool ( $P_o$ ), or sorbed onto charged sites of secondary minerals—especially hydrated forms of Fe or Al oxides (referred to as the non-occluded  $P_i$  pool).

At some intermediate stages of soil development, Walker and Syers<sup>37</sup> predicted that biologically available P would be greatest, as much of the  $P_o$  and  $P_i$  fractions are relatively labile. As soils develop further, silicate clay minerals give way to dominance by Fe and Al hydrous oxides, and P associated with these minerals becomes increasingly occluded and unavailable. In addition, the soil organic matter pools become increasingly recalcitrant, rendering P in the  $P_o$  pool less biologically active as well. Soils of temperate regions do not generally reach this later stage of soil development, as glaciation has periodically reset the clock of soil development to initial stages. The Ultisols and Oxisols of the tropics, on the other hand, are representative of highly weathered soils dominated by Al and Fe secondary minerals.

The model of Walker and Syers<sup>37</sup> was tested on a soil age-gradient spanning early to late stages of soil development under native rainforest across the Hawaiian archipelago<sup>59</sup>. While there were some interesting differences between Walker and Syers' model and results from the Hawaiian archipelago, overall, P changes across the Hawaiian chronosequence agreed to a large extent with model predictions (Fig. 3). In Hawaii, primary mineral P declined in the first 20,000 years of soil development, causing an increase in non-occluded P and  $P_o$ . In later stages of ecosystem development non-occluded  $P_i$  and  $P_o$  decreased as percentages of total P, and occluded P increased. The testing of the Walker and Syers' model is relevant to sustainable agriculture because current nutrient availability in Hawaii was found to be directly related to long-term changes in soil biogeochemistry<sup>39,59,60</sup>. Soil available P on the Hawaii soil age-gradient increased in the first 20,000 years of soil development, and then began to fall, as primary apatite minerals became exhausted (Fig. 4a). The availability of base-forming cations exhibited similar trends (Fig. 4b)<sup>39</sup>.

As discussed above, the original parent material of a soil can have an important influence on its ability to supply lithophilic nutrients to the biota. Equally important is where a parent material and soil are in the context of long-term development. The findings from the Hawaiian study suggest that there is a high lithophilic nutrient release stage of soil development (Fig. 4a,b). Lithophilic nutrients from weathering are substantially exceeding biological uptake during this stage. In a native ecosystem this nutrient excess exits the ecosystem through leaching and into rivers, but in an agroecosystem with high nutrient retention, it could sustain food harvest exports (Fig. 2). This stage is likely to begin when sufficient primary minerals have broken down or undergone dissolution to release lithophilic nutrients which are essential to the growth of vegetation as well as the activities of symbiotic or asymbiotic bacteria<sup>50,58</sup>. The stage appears to end when most primary minerals in the



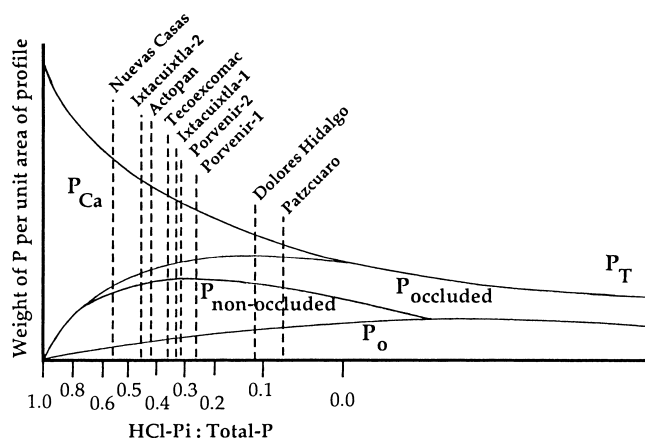
**Figure 4.** Changes in lithophilic nutrients with soil development across a 4.1 million year chronosequence in Hawaii: (a) Changes in % weatherable phosphorus (P) from primary minerals (dashed line) and concentrations of labile P below the rooting zone (solid line); (b) changes in concentrations of labile base cation nutrients below the rooting zone:  $Ca^{2+}$  (solid line),  $Mg^{2+}$  (long dash),  $K^+$  (short dash). Note log scale on x-axis. (Modified from Hedin and colleagues<sup>39</sup>.)

rooting zone have been exhausted through weathering, and the soils become acidic, with low cation exchange capacity.

Crews<sup>61</sup> characterized the forms of soil P in soils sampled from numerous never-fertilized traditional farms in south-central Mexico that had been cultivated continuously for a minimum of 200 years. All soils contained ratios of primary mineral P to total P between 0.08 and 0.57<sup>61</sup> (Fig. 5). All of these soils fall within the high lithophilic nutrient release phase described in the Hawaiian study (Figs. 4a,b). Other researchers have found that the cultivation of previously unplowed soils often results in substantial net mineralization of organic P, which can support crop requirements for 10–100 years<sup>62,63</sup>. However, in much older agroecosystems, average net ecosystem production should approach zero, at which time P is sequestered in newly formed organic matter as fast as it is mineralized. Thus Crews<sup>61</sup> concluded that for older, unfertilized and continuously cultivated agroecosystems to be viable, net P exports in harvests must be made up by dissolution of primary P-bearing minerals.

### Current climate

The timing and duration of a particular soil's nutrient release stage will vary depending, to a large extent, on parent material and climate. The stage occurred fairly quickly in the Hawaiian soil age-gradient (when depicted on a non-log scale) because the basalt parent material has a

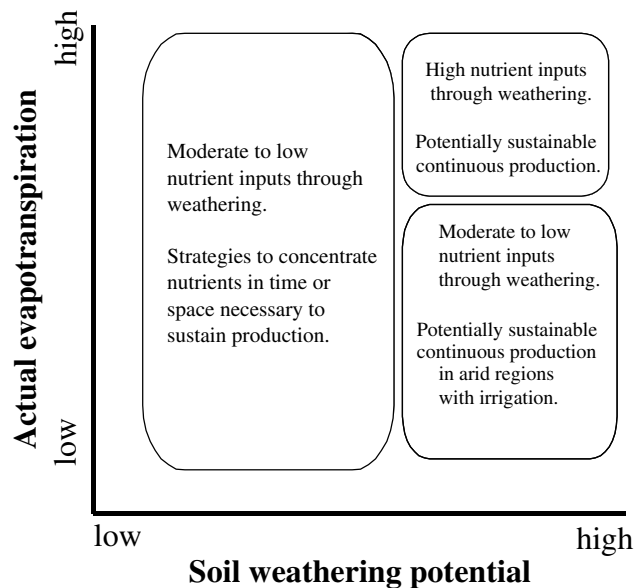


**Figure 5.** Placement of continuously productive traditional farming sites in Mexico on the Walker and Syers<sup>37</sup> model of changes in soil phosphorus (P) forms with time. Soils were sampled from 3-year-old alfalfa stands and sites were situated on the model using HCl-Pi ( $P_{ca}$ ): $P_T$  (primary mineral P to total P) ratios. Farms were reported to have been in production for >200 years<sup>61</sup>.

high weathering potential (Table 2), and the climate is favorable for weathering reactions, with a mean annual temperature of 16°C and annual precipitation of 2500 mm. More moderate levels of nutrient release are likely in ecosystems where the climate is either drier or colder, or the parent materials have a lower WPI.

Figure 6 depicts a simple conceptual model that combines substrate WPI (soil + parent material) and climate (actual evapotranspiration or AET) to indicate where nutrient release might be sufficient to balance harvest losses in a perennial polyculture. Actual evapotranspiration (AET) is a measure of transpired and evaporated water loss from an ecosystem. It is a useful surrogate for the simultaneous availability of water and solar energy in an environment during a defined period of time<sup>64</sup>. Several authors have suggested the utility of using AET to predict mineral weathering rates<sup>65,66</sup>. In addition to the direct effects of AET on mineral dissolution, temperature and precipitation are also primary drivers of the biological processes associated with NPP and decomposition which have been shown to affect mineral weathering rates profoundly<sup>64,67–69</sup>.

Empirical studies that have attempted to estimate actual lithophilic nutrient release through weathering have proven challenging, particularly for P, due to our inability to distinguish between newly weathered P (an input) and P that has been mineralized from organic matter (cycling P). In an impressive review of the subject, Newman<sup>70</sup> found direct estimates of P release by weathering to range between 0.05 and 1.0 kg P ha<sup>-1</sup> yr<sup>-1</sup>; however, these estimates largely came from soils that were significantly weathered and not likely to have high apatite contents. Using indirect evidence (Si dissolution measurements), Newman<sup>70</sup> estimated that P dissolution rates of 5 kg ha<sup>-1</sup> yr<sup>-1</sup> were



**Figure 6.** A conceptual model showing where high rates of lithophilic nutrient release might sustain an agroecosystem with high synchrony. Potential nutrient release is presented as a function of weathering potential of soil and rock minerals and the combined influence of temperature and precipitation (actual evapotranspiration).

possible. This indirect estimate could sustain harvest exports of 1500 kg wheat grain ha<sup>-1</sup> yr<sup>-1</sup><sup>18</sup>. While Newman considered 5 kg ha<sup>-1</sup> yr<sup>-1</sup> to be at the high end of probable P weathering rates, there has simply not been enough work to constrain this value accurately. Variation in parent material, rooting depths and rhizosphere effects are tremendous<sup>53,68,71,72</sup> and little understood in terms of quantitative effects on weathering rates. That said, there clearly exist upper limits to lithophilic weathering rates. To increase agricultural production beyond what the upper limit will allow, it would be necessary for farmers to employ a strategy of concentrating nutrients in time or space, to recycle nutrients in human manure back into agroecosystems, or to apply exogenous fertilizers.

### Optimizing legume density, harvest and disturbance regimes

Of all the essential nutrients, N limitation should be the easiest to address, given our ability to overcome N deficits through biological N fixation. However, using legumes to meet the N requirements of a perennial polyculture will involve considerable attention to crop species selection, breeding and cropping systems design. Moreover, numerous management strategies must be considered to maximize the transfer of N fixed by legumes to non-fixing crops<sup>17,18</sup>. Here I will describe three important aspects of legume-based polycultures that will require optimization to sustain appreciable yields: they are the legume harvest index, cropping density and %N derived from the atmosphere.

### Legume harvest index

The legume component of the perennial polyculture assemblage has potential as a source of protein-rich food for human or livestock consumption. However, this role of the legume as a food crop may conflict with its role as N supplier to the other members of the perennial polyculture. As with many plants, seed production in legumes constitutes a substantial N sink, and if this sink requires too much of the total N fixed by the legume, it will fail to supply adequate N for non-fixing species of the polyculture. The net N contribution of a legume crop to the agroecosystem can be determined using equations 2–4<sup>73</sup>.

$$N_{\text{contribution}} = N_f - N_{\text{ls}} \quad (2)$$

$$N_f = (P_{\text{fix}} \times N_{\text{I}}) \quad (3)$$

$$N_{\text{ls}} = (\text{NHI} \times N_{\text{I}}) \quad (4)$$

where:  $N_{\text{contribution}}$  = net legume N contribution to the polyculture;

$N_f$  = N in legume from N fixation;

$N_{\text{ls}}$  = the amount of total legume N allocated to seed;

$P_{\text{fix}}$  = proportion of N in legume from N fixation;

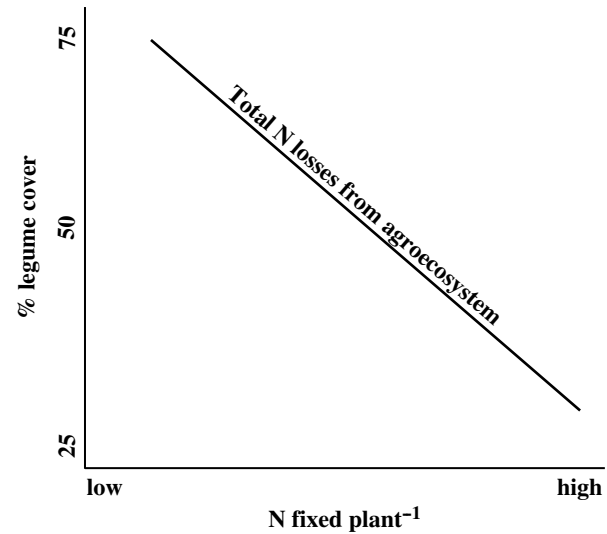
$N_{\text{I}}$  = total N in legume; and

$\text{NHI}$  = N harvest index—the proportion of N allocated to seed.

The extent to which legume N is allocated to non-legumes in the cropping system versus a seed crop is mainly a function of the legume's N harvest index (NHI)—that is, the percentage of the total plant N that is allocated to the seed—and the proportion of N in the legume that originated from fixation versus soil recovery ( $P_{\text{fix}}$ ). Simply put, for the polyculture legume to make a net N contribution to other non-fixing members of the community,  $P_{\text{fix}}$  must be greater than NHI<sup>73</sup>. The greater  $P_{\text{fix}}$  is relative to NHI, the more N will be available to non-fixers. Obviously, if no seed N is harvested, then all of the N that is fixed in the legume will become available to the biota. Recent improvements in estimating below-ground N contributions by legume species have effectively increased estimates of total legume N ( $N_{\text{I}}$ ), often by about 40%<sup>74,75</sup>. Given these revised total N budgets, it appears more possible than previously thought that the legume component of a polyculture could be managed to simultaneously produce a crop and maintain soil N fertility.

### Legume cropping density

In order to meet the N requirements of the non-legume crop species, the density or % cover of legume in the polyculture will have to be optimized (Fig. 7). Essentially, the N contribution of the legume from N fixation has to equal, on a mass balance, the sum of N losses from the agroecosystem, which includes all grain harvests (including any harvested legume seed), as well as N that escapes via denitrification, ammonia volatilization, runoff and leaching (Eqns 5 and 6).



**Figure 7.** The relationship between nitrogen (N) fixed per legume plant and the % cover of legumes needed in a perennial cropping system to balance N losses. The N loss curve represents one set rate of N losses from the agroecosystem in harvests, denitrification, ammonia volatilization, leaching and runoff.

$$L_{\text{density}} = N_{\text{losses}} / N_{\text{f-plant}} / 1000 \quad (5)$$

$$N_{\text{losses}} = \text{NLC}_{\text{harvest}} + N_{\text{ls}} + N_{\text{escape}} \quad (6)$$

where:  $L_{\text{density}}$  = legume plants  $\text{ha}^{-1}$  required to balance N losses from the agroecosystem;

$N_{\text{f-plant}}$  = N fixed per legume plant ( $\text{g yr}^{-1}$ );

$\text{NLC}_{\text{harvest}}$  = N in non-legume crop ( $\text{kg ha}^{-1} \text{yr}^{-1}$ );

$N_{\text{ls}}$  = N in legume seed ( $\text{kg ha}^{-1} \text{yr}^{-1}$ ); and

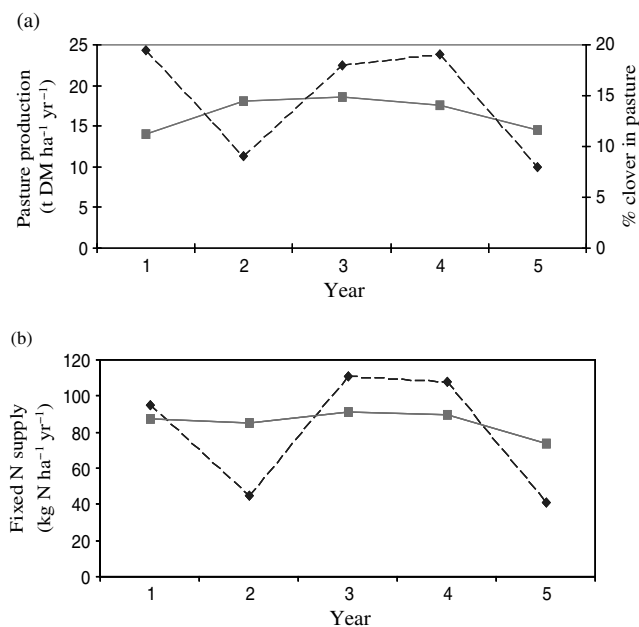
$N_{\text{escape}}$  = total N that escapes from the agroecosystem via ammonia volatilization, denitrification, leaching and runoff ( $\text{kg ha}^{-1} \text{yr}^{-1}$ ).

It is possible that a polyculture of perennial plants with diverse N acquisition strategies might self-optimize legume density in response to polyculture N demands. Ledgard<sup>76</sup> reported findings from a non-fertilized pasture where, over 5 years, clover densities and contributions from N fixation varied as a function of soil N availability, climate and pest/disease cycles (Fig. 8a,b).

### Percent N derived from the atmosphere (%Nd<sub>fa</sub>)

As illustrated in Equation 3, the proportion, or percentage, of N that a legume acquires from the atmosphere through N fixation ( $P_{\text{fix}}$ ) is a critical variable in determining whether legumes that are harvested for food can also make a net contribution to the N economy of other crops. When multiplied by 100,  $P_{\text{fix}}$  can be converted to the term 'N derived from the atmosphere', or %Nd<sub>fa</sub>, which can vary substantially from 0 to 98%<sup>77</sup>. In considering the N-supplying role of the legume in a perennial polyculture, it is critical to explore ecosystem dynamics that maintain high %Nd<sub>fa</sub> values, regardless of whether the legume is eventually harvested for grain. Soil N availability is a





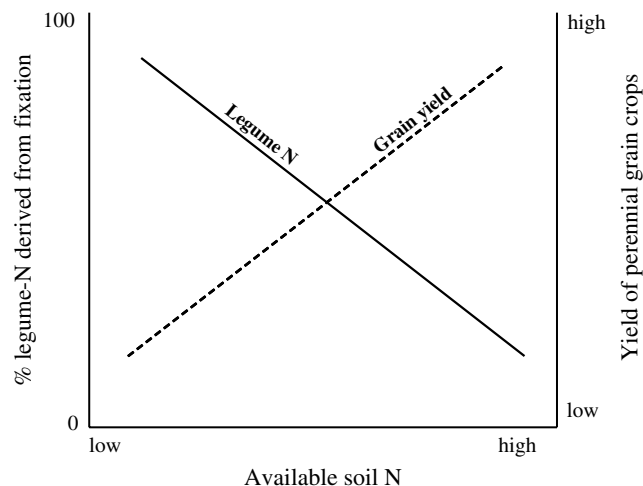
**Figure 8.** Relationships between legume and grass abundance in a pasture community as a function of N fixation and soil N availability over a 5-year study: (a) annual changes in total pasture production (solid line) and % clover cover (dashed line); (b) clover fixed N supply (dashed line) and modeled estimates of annual N availability from legume residues (solid line). (From Ledgard<sup>76</sup>.)

major determinant of N fixation by legumes<sup>35,73,76</sup>. The metabolic costs of taking up  $\text{NH}_4^+$  or  $\text{NO}_3^-$  from the soil typically requires less plant energy than N fixation, at least when nitrate reduction is carried out in leaves<sup>34,35</sup>.

There may exist a tension between the simultaneous requirements of maintaining high rates of N supply to maximize grain yields, and maintaining high %Ndfa in the legume crop to supply future crops with N (Fig. 9). Traditional farmers who relied on legumes to supply grain crops with N generally avoided this tension by separating the N-fixing legumes from the crop in time or space. For example, in a traditional Mexican agroecosystem, monocropped plots of alfalfa were intensively harvested to supply forage to animals and ultimately manure to maize plots; in this way, plant available N was minimized in the rhizosphere of the N fixer, and maintained at a high level in the rooting zone of the grain crop.

As with the optimization of legume cover in the pasture community described by Ledgard<sup>76</sup> (Fig. 8a,b), it is possible that the %Ndfa of legumes will, to some extent, self-optimize in relation to the diverse spatial and temporal N uptake patterns of a polyculture. That said, there are numerous avenues of research that could potentially increase the %Ndfa of perennial legumes grown in polyculture.

**Selection or breeding for nitrate tolerance.** The extent to which nitrate negatively affects rates of N fixation varies considerably from species to species. Harper and Gibson<sup>78</sup> found the threshold concentrations of  $\text{NO}_3^-$  for complete



**Figure 9.** Potential trade-offs in a perennial polyculture between legume N-fixing efficiency (%Ndfa) and potential grain yield, resulting from shifting supplies of available soil N.

suppression of N fixation to range from 2 to 20 mM (about 10.5–105 mg nitrate-N kg<sup>-1</sup> soil). These findings suggest that legumes might be bred or selected to fix in the face of relatively high nitrate concentrations<sup>79,80</sup>. However, Ledgard<sup>76</sup> warns that breeding for nitrate tolerance could force the legumes in a mixed stand to be out-competed, due to the greater energetic costs incurred by the N fixers.

**Breeding for the ability to switch rapidly between fixing N<sub>2</sub> and taking up soil N.** In theory, legume competitiveness with grasses might be increased if legumes were able to respond to short-term changes in soil N status by quickly shifting their C allocation patterns between N fixation and growth<sup>76</sup>.

**Favoring the uptake of ammonium over nitrate.** While ammonium has been shown to reduce N fixation in numerous actinorrhizal species<sup>81</sup>, and many researchers acknowledge a negative effect of  $\text{NH}_4^+$  on legume N fixation<sup>34</sup>, its effect is not nearly as well documented as that of nitrate. Some researches have actually found legumes either to have no response, or a positive response, to the presence of ammonium in soils<sup>82,83</sup>. Gutschick<sup>84</sup> reported that N is taken up by plants in some grasslands at a sufficient rate to out-compete nitrifying bacteria. If little  $\text{NO}_3^-$  is allowed to accumulate, and  $\text{NO}_3^-$  is the form of soil-N responsible for inhibiting N fixation, then it is possible that fixers in these ecosystems will continue to fix even when substantial combined N (in the form of  $\text{NH}_4^+$ ) is mineralized through the growing season<sup>40</sup>. Mycorrhizal fungal symbioses in the grass and sunflower components of the polyculture may play a key role in scavenging ammonium (or even forms of organic N) from the legume rhizosphere<sup>85</sup>. Like selecting or breeding for nitrate tolerance, this approach could result in non-fixers out-competing legumes.

**Selectively cutting the legume to cause concurrent N release.** Selectively cutting the legume in the polyculture might function to induce root and nodule senescence and N

release. If a cutting were timed according to the uptake requirements of the non-fixing crops, mineralized N from the legume roots would be scavenged and greater legume N fixation would eventually be promoted. Alternatively, if the grass components of the perennial polyculture are shown to exhibit some degree of compensatory growth<sup>86,87</sup>, then mowing or grazing the entire polyculture at an early or middle stage of the growing season may stimulate both N transfer and greater grass productivity.

**Temporal separation of N fixation and high grain yields.** A temporal separation of N fixation and the grain-producing stage of the cropping cycle might involve a 2-year rotation of grazing and harvesting—in the harvest year, the polyculture takes advantage of high soil N availability from the previous fallow year. During the grazing year, N fixers have a high  $P_{fix}$  because harvests in the previous year have drawn soil N levels down.

**Spatial separation of legume and grass roots.** Deep tap roots are common to prairie legumes. To the extent that N is transferred from the legume to non-fixing associated species via decomposing shoot residues, it is possible that the legume roots may occupy a zone of the soil profile that is relatively low in combined N compared to the surface horizons which are commonly more exploited by grass species.

## Conclusion

Smil<sup>88</sup> has estimated that over 40% of humans alive today owe their existence to the Haber–Bosch industrial process of synthesizing ammonia. However, this estimate is based on an agriculture that leaks between 40 and 70% of applied N. If 40% more N was taken up by crops, then much less N would need to be fixed to achieve the same level of crop productivity. In other words, Smil's estimation of humanity's dependence on synthetic N might be accurate for annual agriculture, but if farming systems with greatly improved synchrony were developed, then the human dependence on industrial N sources would be reduced accordingly.

The development of perennial polycultures comprises one promising approach to improving N synchrony while maintaining relatively high yields. Increasing synchrony is an extremely important goal regardless of whether nutrient inputs originate from fertilizers or endogenous sources. However, synthetic fertilizers are ultimately not sustainable in the long term, as they are extremely energy intensive to produce, in the case of N, or finite and non-renewable, in the case of P and other lithophilic nutrients. If agroecosystems can be designed to maintain high rates of productivity while relying to the greatest extent possible on endogenous nutrient supplies, then the environmental impacts caused by excessive nutrient enrichment of the biosphere, as well as human dependence on non-renewable resources, will be lessened.

In this paper I have framed what I believe to be the most important considerations and challenges facing the initial

development of grain-producing perennial polycultures with regard to endogenous nutrient acquisition. Some of the issues I raise may be resolved through currently unpredictable dynamics of interacting perennial functional groups (N fixer, warm-season grass, cool-season grass). However, there exist differences between the native prairie and a perennial polyculture, not the least of which is the likelihood of annual nutrient removal in harvests (Fig. 2). These losses could be matched, or at least greatly offset, by nutrient inputs from the weathering of soils that are in a high nutrient release phase of soil development, and through management of legume N fixation.

**Acknowledgements.** I would like to thank the following people who knowingly, or unknowingly, contributed in some fashion to the ideas underlying this paper or practical aspects of producing the manuscript: Sarah, Ruby and Claire Crews, Kenny Cook, Stan Cox, Lee DeHaan, Jerry Glover, Meghan Gould, Bob Howarth, Wes Jackson, Alex Muro, Mark Peoples, Ron Regina, Wayne Regina, David Van Tassel, and Peter Vitousek.

## References

- 1 Whittaker, R.H. 1975. *Communities and Ecosystems*. 2nd ed. Macmillan, New York, USA.
- 2 Van Wambeke, A. 1992. *Soils of the Tropics*. McGraw-Hill, New York, USA.
- 3 Herrera, R., Merida, T., Stark, N., and Jordan, C.F. 1978. Direct phosphorus transfer from leaf litter to roots. *Naturwissenschaften* 65:208–209.
- 4 Sanford, R.S. Jr. 1987. Apogeotropic roots in an Amazon rain forest. *Science* 235:1062–1064.
- 5 Harlan, J.R. 1995. *The Living Fields: Our Agricultural Heritage*. Cambridge University Press, Cambridge, UK.
- 6 Rowley-Conwy, P. 1981. Slash and burn in the temperate European neolithic. In R. Mercer (ed.). *Farming Practice in British Prehistory*. Edinburgh University Press, Edinburgh, UK. p. 85–96.
- 7 Hurt, R.D. 1987. *Indian Agriculture in America*. University of Kansas Press, Lawrence, Kansas, USA.
- 8 Newman, E.I. 1997. Phosphorus balance of contrasting farming systems, past and present. Can food production be sustainable. *Journal of Applied Ecology* 34:1334–1347.
- 9 Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H., and Tilman, D.G. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7:737–750.
- 10 Turner, R.E. and Rabalais, N.N. 2003. Linking landscape and water quality in the Mississippi River basin for 200 years. *Bioscience* 53:563–572.
- 11 Townsend, A.R., Howarth, R.W., Bazzaz, F.A., Booth, M.S., Cleveland, C.C., Collinge, S.K., Dobson, A.P., Epstein, P.R., Holland, E.A., Keeney, D.R., Mallin, M.M., Rogers, C.A., Wayne, P., and Wolfe, A.H. 2003. Human health effects of a changing global nitrogen cycle. *Frontiers in Ecology and the Environment* 1:240–246.
- 12 Mudahar, M.S. and Hignett, T.P. 1987. Fertilizer and energy use. In Z.R. Hinsel (ed.). *Energy in Plant Nutrition and Pest Control*. Elsevier, Amsterdam, The Netherlands. p. 25–62.

- 13 Jackson, W. and Jackson, L.L. 1999. Developing high seed yielding perennial polycultures as a mimic of mid-grass prairie. In E.C. Lefroy, R.J. Hobbs, M.H. O'Connor, and J.S. Pate (eds). *Agriculture as a Mimic of Natural Ecosystems*. Kluwer Academic Publishers, Dordrecht, The Netherlands. p. 1–37.
- 14 Myers, R.J.K., van Noordwijk, M., and Vityakon, P. 1997. Synchrony of nutrient release and plant demand: Plant litter quality, soil environment and farmer management options. In G. Cadisch and K.E. Giller (eds). *Driven by Nature*. CAB International, Wallingford, UK. p. 215–229.
- 15 Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., and Polasky, S. 2002. Agricultural sustainability and intensive production practices. *Nature* 418:671–677.
- 16 Robertson, G.P. 1997. Nitrogen use efficiency in row-crop agriculture: Crop nitrogen use and soil nitrogen loss. In L. Jackson (ed.). *Ecology in Agriculture*. Academic Press, San Diego, California, USA. p. 347–365.
- 17 Crews, T.E. and Peoples, M.B. 2005. Can the synchrony of nitrogen supply and crop demand be improved in legume and fertilizer-based agroecosystems? A review. *Nutrient Cycling in Agroecosystems*, in press.
- 18 Crews, T.E. and Peoples, M.B. 2004. Legume versus fertilizer sources of nitrogen: Ecological tradeoffs and human needs. *Agriculture, Ecosystems and Environment* 102:279–297.
- 19 Dinnes, D.L., Karlen, D.L., Jaynes, D.B., Kaspar, T.C., Hatfield, J.L., Colvin, T.S., and Cambardella, C.A. 2002. Nitrogen management strategies to reduce nitrate leaching in tile-drained Midwestern soils. *Agronomy Journal* 94:153–171.
- 20 Cassman, K.G., Dobermann, A., and Walters, D.T. 2002. Agroecosystems, nitrogen-use efficiency and nitrogen management. *Ambio* 31:132–140.
- 21 Likens, G.E., Bormann, F.H., Pierce, R.S., Eaton, J.S., and Johnson, N.M. 1977. *Biogeochemistry of a Forested Ecosystem*. Springer-Verlag, New York, USA.
- 22 Knapp, A.K., Briggs, J.M., Blair, J.M., and Turner, C.L. 1998. Patterns and controls of above ground net primary production in tallgrass prairie. In A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins (eds). *Grassland Dynamics*. Oxford University Press, New York, USA. p. 193–221.
- 23 Blair, J.M., Seastedt, T.R., Rice, C.W., and Ramundo, R.A. 1998. Terrestrial nutrient cycling in tallgrass prairie. In A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins (eds). *Grassland Dynamics*. Oxford University Press, New York, USA. p. 222–243.
- 24 Andrén, O., Lindberg, U., Boström, U., Clarholm, M., Hansson, A.C., Johansson, G., Lagerlöf, J., Paustian, K., Persson, J., Pettersson, R., Schnürer, J., Sohlenius, B., and Wivstad, M. 1990. Organic carbon and nitrogen flows. *Ecological Bulletins* 40:85–126.
- 25 Paustian, K., Bergström, L., Jansson, P., and Johnsson, H. 1990. Ecosystem dynamics. *Ecological Bulletins* 40: 153–180.
- 26 Jaynes, D.B., Colvin, T.S., Karlen, D.L., Cambardella, C.A., and Meek, D.W. 2001. Nitrate loss in subsurface drainage as affected by nitrogen fertilizer rate. *Journal of Environmental Quality* 30:1305–1314.
- 27 Randall, G.W., Huggins, D.R., Russelle, M.P., Fuchs, D.J., Nelson, W.W., and Anderson, J.L. 1997. Nitrate losses through subsurface tile drainage in conservation reserve program, alfalfa, and row crop systems. *Journal of Environmental Quality* 26:1240–1247.
- 28 Wedin, D.A. and Tilman, D. 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* 84:433–441.
- 29 McKane, R.B., Grigal, D.F., and Russelle, M.P. 1990. Spatiotemporal differences in <sup>15</sup>N uptake and the organization of an old-field plant community. *Ecology* 71:1126–1132.
- 30 Van Der Krift, T.A.J. and Berendse, F. 2001. The effect of plant species on soil nitrogen mineralisation. *Journal of Ecology* 89:555–561.
- 31 Mathers, A.C., Stewart, B.A., and Blair, B. 1975. Nitrate-nitrogen removal from soil profiles by alfalfa. *Journal of Environmental Quality* 4:403–405.
- 32 Bergström, L. 1987. Nitrate leaching and drainage from annual and perennial crops in tile-drained plots and lysimeters. *Journal of Environmental Quality* 16:11–18.
- 33 Huggins, D.R., Randall, G.W., and Russelle, M.P. 2001. Subsurface drain losses of water and nitrate following conversion of perennials to row crops. *Agronomy Journal* 93:477–486.
- 34 Marschner, H. 1995. *Mineral Nutrition of Higher Plants*. 2nd ed. Academic Press, New York, USA.
- 35 Vitousek, P.M., Cassman, K., Cleveland, C., Crews, T., Field, C.B., Grimm, N., Howarth, R.W., Marino, R., Martinelli, L., Rastetter, E., and Sprent, J.I. 2002. Towards an ecological understanding of biological nitrogen fixation. *Biogeochemistry* 57/58:1–45.
- 36 Vitousek, P.M. and Howarth, R.W. 1991. Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* 13:87–115.
- 37 Walker, T.W. and Syers, J.K. 1976. The fate of phosphorus during pedogenesis. *Geoderma* 15:1–19.
- 38 Vitousek, P.M. and Farrington, H. 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. *Biogeochemistry* 37:63–75.
- 39 Hedin, L.O., Vitousek, P.M., and Matson, P.A. 2003. Nutrient losses over four million years of tropical forest development. *Ecology* 84:2231–2255.
- 40 Crews, T.E. 1999. The presence of nitrogen fixing legumes in terrestrial communities: Evolutionary vs. ecological considerations. *Biogeochemistry* 46:233–246.
- 41 Bordeleau, L.M. and Prévost, D. 1994. Nodulation and nitrogen fixation in extreme environments. *Plant and Soil* 161:115–125.
- 42 Robson, A.D. and Bottomley, P.J. 1991. Limitations in the use of legumes in agriculture and forestry. In M.J. Dilworth and A.R. Glenn (eds). *Biology and Biochemistry of Nitrogen Fixation*. Elsevier, Amsterdam, The Netherlands. p. 320–349.
- 43 Cadisch, G., Sylvester-Bradley, R., Boller, B.C., and Nösberger, J. 1993. Effects of phosphorus and potassium on N<sub>2</sub> fixation (<sup>15</sup>N-dilution) of field-grown *Centrosema acutifolium* and *C. macrocarpum*. *Field Crops Research* 31:329–340.
- 44 Crews, T.E., Kurina, L.M., and Vitousek, P.M. 2001. Organic matter and nitrogen accumulation and nitrogen fixation during early ecosystem development in Hawaii. *Biogeochemistry* 52:259–279.
- 45 Gates, C.T. 1974. Nodule and plant development in *Stylosanthes humilis* H.B.K.: Symbiotic response to phosphorus and sulphur. *Australian Journal of Botany* 22:45–55.

- 46 Israel, D.W. 1987. Investigation of the role of phosphorus in symbiotic dinitrogen fixation. *Plant Physiology* 84: 835–840.
- 47 Pereira, P.A.A. and Bliss, F.A. 1987. Nitrogen fixation and plant growth of common bean (*Phaseolus vulgaris* L.) at different levels of phosphorus availability. *Plant and Soil* 104:79–84.
- 48 Davis, M.R. 1991. The comparative phosphorus requirements of some temperate perennial legumes. *Plant and Soil* 133:17–30.
- 49 Peoples, M.B., Lilley, D.V., Burnett, V.F., Ridley, A.M., and Garden, D.L. 1995. Effects of surface application of lime and superphosphate to acid soils on growth and N<sub>2</sub> fixation by subterranean clover in mixed pasture swards. *Soil Biology and Biochemistry* 27:663–671.
- 50 Crews, T.E., Farrington, H., and Vitousek, P.M. 2000. Changes in asymbiotic, heterotrophic nitrogen fixation on leaf litter of *Metrosideros polymorpha* with long-term ecosystem development in Hawaii. *Ecosystems* 3:386–395.
- 51 Eisele, K.A., Schimel, D.S., Kapustka, L.A., and Parton, W.J. 1989. Effects of available P and N:P ratios on non-symbiotic dinitrogen fixation in tallgrass prairie soils. *Oecologia* 79:471–474.
- 52 Crews, T.E. 1993. Phosphorus regulation of nitrogen fixation in a traditional Mexican agroecosystem. *Biogeochemistry* 21:141–166.
- 53 Harley, A.D. and Gilkes, R.J. 2000. Factors influencing the release of plant nutrient elements from silicate rock powders: a geochemical overview. *Nutrient Cycling in Agroecosystems* 56:11–36.
- 54 LeMaitre, R.W. 1976. The chemical variability of some common igneous rocks. *Journal of Petrology* 17:589–637.
- 55 Ritter, D.F., Kochel, R.C., and Miller, J.R. 2001. *Process Geomorphology*. McGraw-Hill, New York.
- 56 Reiche, P. 1950. A survey of weathering processes and products. University of New Mexico Publications in Geology, no. 3. The University of New Mexico Press, Albuquerque, New Mexico.
- 57 Carroll, D. 1970. *Rock Weathering*. Plenum Press, New York, USA.
- 58 Vitousek, P.M., Chadwick, O.A., Crews, T.E., Fownes, J.H., Hendricks, D.M., and Herbert, D. 1997. Soil and ecosystem development across the Hawaiian islands. *GSA Today* 7:1–8.
- 59 Crews, T.E., Kitayama, K., Fownes, J.H., Riley, R.H., Herbert, D.A., Mueller-Dombois, D., and Vitousek, P.M. 1995. Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology* 76:1407–1424.
- 60 Vitousek, P.M., Turner, D.R., and Kitayama, K. 1995. Foliar nutrients during long-term soil development in Hawaiian montane rain forest. *Ecology* 76:712–720.
- 61 Crews, T.E. 1996. The supply of phosphorus from native, inorganic phosphorus pools in continuously cultivated Mexican agroecosystems. *Agriculture, Ecosystems and Environment* 57:197–208.
- 62 Haas, H.J., Grunes, D.L., and Reichman, G.A. 1961. Phosphorus changes in Great Plains soils as influenced by cropping and manure applications. *Soil Science Society of America Proceedings* 25:214–218.
- 63 Tiessen, H., Stewart, J.W.B., and Bettany, J.R. 1982. Cultivation effects on the amounts and concentration of carbon, nitrogen and phosphorus in grassland soils. *Agronomy Journal* 74:831–835.
- 64 Rosenweig, M.L. 1968. Net primary productivity of terrestrial communities: prediction from climatological data. *The American Naturalist* 102:67–74.
- 65 Gorham, E., Vitousek, P.M., and Reiners, W.A. 1979. The regulation of chemical budgets over the course of terrestrial ecosystem succession. *Annual Review of Ecology and Systematics* 10:53–84.
- 66 Stephenson, N.L. 1990. Climatic control of vegetation distribution: The role of the water balance. *The American Naturalist* 135:649–670.
- 67 Meetemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* 59:465–472.
- 68 Bormann, B.T., Wang, D., Bormann, F.H., Benoit, G., April, R., and Synder, M.C. 1998. Rapid, plant-induced weathering in an aggrading experimental ecosystem. *Biogeochemistry* 43:129–155.
- 69 Moorhead, D.L., Currie, W.S., Rastetter, E.B., Parton, W.J., and Harmon, M.E. 1999. Climate and litter quality controls on decomposition: An analysis of modeling approaches. *Global Biogeochemical Cycles* 13:575–589.
- 70 Newman, E.I. 1995. Phosphorus inputs to terrestrial ecosystems. *Journal of Ecology* 83:713–726.
- 71 Crowley, D.E. and Rengel, Z. 1999. Biology and chemistry of nutrient availability in the rhizosphere. In Z. Rengel (ed.). *Mineral Nutrition of Crops*. Food Products Press, New York, USA. p. 1–40.
- 72 Ryan, P.R., Delhaize, E., and Jones, D.L. 2001. Function and mechanism of organic anion exudation from plant roots. *Annual Review of Plant Physiology and Plant Molecular Biology* 52:527–560.
- 73 Peoples, M.B. and Craswell, E.T. 1992. Biological nitrogen fixation: Investments, expectations and actual contributions to agriculture. *Plant and Soil* 141:13–39.
- 74 McNeill, A.M., Zhu, C., and Fillery, I.R.P. 1997. Use of in situ <sup>15</sup>N-labelling to estimate the total below-ground nitrogen of pasture legumes in intact soil-plant systems. *Australian Journal of Agricultural Research* 48:295–304.
- 75 Khan, D.F., Peoples, M.B., Chalk, P.M., and Herridge, D.F. 2002. Quantifying below-ground nitrogen of legumes. 2. A comparison of <sup>15</sup>N and non isotopic methods. *Plant and Soil* 239:277–289.
- 76 Ledgard, S.F. 2001. Nitrogen cycling in low input legume-based agriculture, with emphasis on legume/grass pastures. *Plant and Soil* 228:43–59.
- 77 Peoples, M.B., Herridge, D.F., and Ladha, J.K. 1995. Biological nitrogen fixation: An efficient source of nitrogen for sustainable agricultural production? *Plant and Soil* 174:3–28.
- 78 Harper, J.E. and Gibson, A.H. 1984. Differential nodulation tolerance to nitrate among legume species. *Crop Science* 24:797–801.
- 79 Gresshoff, P.M. 1990. The importance of biological nitrogen fixation to new crop development. In J. Janick and J.E. Simon (eds). *Advances in New Crops*. Timber Press, Portland, Oregon, USA. p. 113–119.
- 80 Herridge, D.F. and Danso, S.K.A. 1995. Enhancing legume N<sub>2</sub> fixation through selection and breeding. *Plant and Soil* 174:51–82.
- 81 Wheeler, C.T. and McLaughlin, M.E. 1978. Environmental regulation of nitrogen fixation in actinomycete nodulated plants. In J.C. Gordon, C.T. Wheeler, and D.A. Perry (eds).

- Symbiotic Nitrogen Fixation in the Management of Temperate Forests. School of Forestry, Oregon State University, Corvallis, Oregon, USA. p. 124–142.
- 82 Waterer, J.G., Vessey, J.K., and Raper, D.C. 1992. Stimulation of nodulation in field peas (*Pisum sativum*) by low concentration of ammonium in hydroponic culture. *Plant Physiology* 86:215–220.
- 83 Goi, S.R., Sprent, J.I., Games, E.L., and Jacob-Neto, J. 1992. Influence of nitrogen forms and concentration on the nitrogen fixation of *Acacia auriculiformis*. *Symbiosis* 14:115–122.
- 84 Gutschick, V.P. 1981. Evolved strategies in nitrogen acquisition by plants. *The American Naturalist* 118:607–637.
- 85 Attiwill, P.M. and Adams, M.A. 1993. Nutrient cycling in forests. *New Phytologist* 124:561–582.
- 86 McNaughton, S.J. 1984. Grazing lawns: Animals in herds, plant form, and coevolution. *The American Naturalist* 124:863–886.
- 87 Dyer, M.I., Turner, C.L., and Seastedt, T.R. 1993. Herbivory and its consequences. *Ecological Applications* 3:10–16.
- 88 Smil, V. 2001. *Enriching the Earth*. MIT Press, Cambridge, Massachusetts, USA.