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#### EVOLVED STRATEGIES IN NITROGEN ACQUISITION BY PLANTS

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Nitrogen is probably the most studied plant nutrient. It is unique among nutrients in its richness of uptake phenomena. It may enter through leaves or roots, in varied chemical forms. Its environmental concentration commonly varies widely, unlike that of the prime nutrient,  $CO_2$ . Much of its availability to plants is tied to the bacterial decay cycle, the bacteria of which are sharply mismatched to plants regarding limiting factors and time scales of responsiveness. Nitrogen also is a resource that can be "created" via biofixation of atmospheric  $N_2$ , and can in large part be mobilized by uptake demand (but not as well as is phosphorus [Jansson 1971] in a more abiological equilibrium). Its primary internal metabolism varies. For example, nitrate may be reduced in leaves or in roots, by fundamentally different energy supplies. Lastly, N availability appears to limit plant growth over much of the biosphere. (This oft-repeated claim merits critical analysis, expanding a treatment recently given by Button [1978]. I shall address this topic in a later publication.) The limitation by low N certainly is intertwined with limitations by water, with limitations of metabolic flexibility with temperature, and other effects.

All these considerations complicate the construction of a unified picture of N metabolism of the plant and of the whole ecosystem. The survival value of many features is difficult to conceive of at first glance. This holds true despite considerable knowledge in individual fields of research, from enzymatic pathways through molecular biology of biofixation up to large-scale ecosystematic N budgets. To clarify this claim, I will shortly recount a number of gaps in our knowledge. These concern both agronomic practice—such as why plant N metabolism should often run counter to achieving maximal yield up to water/light limits—and also ecological understanding—such as why so little of global photosynthetic energy is budgeted for fixation in an N-stressed world. Considerable new data are demanded, but extant data in many cases allow us to formulate critical questions and to attempt some answers.

I encountered these questions while working on the energetics of N metabolism, a good starting point which may color some of my views. I have conceived a number of principles of evolutionary selection which tie together some quantitative metabolism, some genetics, and some ecological interactions. Such work is not new. For example, Hardy and Holsten (1972) have proposed that generic

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types of N metabolism are evolved responses to challenges evolving in the biosphere: the presence of  $NH_3$ , of  $NO_3^-$ , etc. Bonnier and Brakel (1969) proposed that legume proliferation represents an ecosystem response to looseness in the N cycle. Numerous workers have proposed that N-cycle "tightness" increases during succession. In the current investigation, I hope to contribute to the working set of principles; to re-establish some principles on more sound physiological bases (e.g., to elucidate the competitive risks that are balanced when leguminous N fixation is reduced or eliminated at climax, rather than to propose a direct response of plants to the degree of closure in the N cycle); and to note additional research problems.

As a whole, my proposed view is that the nitrogen-nutrition of plants can be largely reduced to the operation of a reasonable number of strategies that optimize benefits versus costs. The costs and benefits are quantifiable using energetics (as an absolute constraint, but not a complete explanation). The presumed goal is generally to maximize yield under definable ranges of growth conditions. However, ultimate yield may be sacrificed for reducing risks, as in maturation control by day length versus immediate climatic/nutritional favorability. It may also be sacrificed for other competitive measures, as in extensive partitioning of early growth into canopy to the detriment of optimal root: shoot ratio applicable in isolated growth. The utility of the strategic view may be severalfold, beyond that as a learning tool in physiological function. Thus in agricultural breeding to incorporate disparate physiological traits, one might foresee conflicts more easily between strategies (as unified, controlled blocks of physiological activities) than between the individual physiological activities. In ecosystematic studies, it may be easier to predict responses of plant communities to gross environmental changes (such as CO<sub>2</sub> levels in the air; see Revelle and Munk 1977) by means of strategies than with detailed physiological models of species.

# 1. MOTIVATION: SOME PUZZLING PLANT RESPONSES

The basic features of the biospheric N cycle (Burns and Hardy 1975; Delwiche 1970; Svensson and Söderlund 1976; and others) and of the plant N uptake and assimilation through the stage of ammonia (Miller 1931; Street 1949; Spencer 1958; Beevers and Hageman 1969; Pate 1973; Jackson 1978; Lee and Stewart 1978) are well known. For brevity, they are not discussed here. Rather, consider immediately some important aspects of N acquisition by plants in which survival value is hard to discern at first glance.

One large class of problems arises initially in agronomy and other applied plant sciences, wherein the goal crudely stated is to obtain maximal yield of useful plant parts.

1. The counteraction of N fertilization on maturation is a general rule. For a given species and variety of plant, too-high levels of soil N can delay flowering and/or fruiting, even indefinitely in some cases. This effect has long been known (see Miller 1931). In some species maturation can even be reversed (e.g., salvias at the New York Botanical Garden have dropped flowers after excessive manuring [Cronquist, personal communication]). Other species are more resistant to such

potential dominance of N over other maturation controls; soybeans are an example (e.g., Streeter 1978; but see Egli et al. 1978). In complementary fashion, low soil N levels can hasten maturation. Here, however, the N usually shares control with water stress and other variables.

Selective breeding may reveal genetic linkage in such antagonism. Cotton bred for facile N uptake and assimilation eventually has its fruiting ability much compromised (Loomis et al. 1976). Success in separating the linkage has been achieved at considerable effort for only a few crops by the breeding advances in the Green Revolution (Loomis et al. 1976).

There is no reason for this high-N suppression of maturation, inherent in any portion of metabolism. A plant which could capitalize on abundant N in late season while yet maturing would seem intuitively to be at an advantage. Yet it appears that the option has been foreclosed for most species by evolutionary selection. One may ask if this is analogous to genetic fixation of maturation time by day length in temperate species. Unseasonably good weather will not "mislead" a plant into a risky extension of vegetative growth. Nitrogen appears to be unique in overriding many such useful maturation clues. (Where there is no frost risk, as in the tropics, the maturation strategy and N effects upon it should differ notably. I have found no relevant data.)

2. Repression of N fixation by N fertilization in grain legumes is frequent, though variable by cultivar and by strain of *Rhizobium* (Gibson 1976, 1977; Pate and Dart 1961). At high levels of N fertilization, few symbioses show gains in total N nutrition and some (unusual) cultivar/strain choices can even show net losses, that is, an even faster reduction of fixation than gain in nitrate N. This trade-off of  $N_2$  for nitrate occurs in soybeans despite the near equality of energetic costs of assimilation especially if nitrate is reduced in roots, as has been shown for soybeans. (See below, sec. 2*A*). At normal agronomic levels of soil nitrate, fixation tends to be the lesser N source over the whole season (Weber 1966; Hardy and Havelka 1975; 1977). In N-poor soils, it can dominate as expected, as perhaps for alfalfa (Heichel et al. 1978). (With increases of low levels of soil nitrate, the fixation response varies widely as plus or minus by cultivar and strain [Pate and Dart 1961; Gibson 1976, 1977], for complex reasons.)

Ideally, wild legumes that have experienced little or no artificial selection will reflect the evolved strategy more faithfully. Few experiments have been done, as Pate (1976) remarks. Gibson (1976) reports no increased N nutrition for five of six wild leguminous weeds/forages when nitrate is available. If one justifiably presumes that available nitrate is used, then one concludes that fixation has been traded off (reduced). It is unknown whether these wild legumes do nitrate reduction in roots and hence if they, like soybeans, have no energetic basis for the trade-off. (A separate pressing question in agronomy today is whether cereal legumes around the time of anthesis invest suboptimal amounts of photosynthate in  $N_2$  fixation, under any nitrate regime [e.g., Hardy and Havelka 1975]. I argue that, while the evidence cited by these authors is credible and can even be augmented, the generally negative responses of wild legumes to nitrate fertilization [Hardy and Havelka 1975] indicate that it is an artifact of agricultural selection. No insight into evolved strategies can be gleaned from this evidence, but

consideration of which evolved strategies have been imbalanced by breeding can possibly aid diagnosis of the suboptimality in the cultivars.)

3. Soybeans have been characterized as being "self-destructive" of their photosynthetic and N<sub>2</sub>-fixing functions near pod filling (Sinclair and de Wit 1976), despite the potential value of continued function during this time of greatest need for N. Source-sink competition models (Sinclair and de Wit 1976) explain the phenomenon at a mechanistic level but do not assign it any survival value. Indeed, it may be just a cultivated source-sink imbalance of no survival value in the wild (McArthur et al. 1975) in particular cases, but nodules do senesce in all temperate annual legumes at least. That some optimization of senescence time can occur is hinted at by the delay of nodular senescence by unusually favorable conditions for photosynthesis (such as enhanced  $CO_2$  concentration in air, as surveyed by Hardy and Havelka [1977]).

The similar phenomenon of N uptake cutoff toward maturity of nonlegumes is more understandable. The cutoff of photosynthetic source for processing energy is better correlated to this cutoff, and one may argue also that it is better to use up all existing internal N reserves, for which the energy already invested should not be left unused. (The difference in rationalization between N-uptake and N<sub>2</sub>fixation shutoffs admittedly is not vast.)

4. Once taken up from soil, nitrate should in many circumstances be reducible to ammonia with the least drain on yield if it is reduced in leaves rather than roots (see sec. 2A). Yet species vary widely in the fractions of nitrate which they reduce in leaves versus roots (Beevers and Hageman 1969; Pate 1973).

Some of the individual "failings" above may simply indicate hidden costs, perhaps the cost of pH control in nitrate assimilation in leaves. I hypothesize that other apparent failings indicate strategic compromises with other necessary functions (no examples above; see e.g., strategies of reproduction, water relations, temperature adaptation discussed by McComb and Pate [1981]), or strategic sacrifices of yield potential to reduce risks (point 1 above). That is, plants pursue persistence as their ultimate strategy, and this has a moderately direct relation with yield. Still other "failings" may indicate that evolved strategies have been imbalanced by agricultural breeding (point 3 above, or parenthetical note after point 2).

Problems of a second large class arise when one reflects on some ecological or evolutionary studies on wild species and their communities. I will state these problems now, some for the first time and some in new phrasing.

5. In the full nitrogen cycle, recycling of dead organic matter via decay liberates ammonia as an (almost) obligatory intermediate. In many ecosystems (but perhaps infrequently at climax; see below) and in most agricultural fields, the bulk of the ammonia is oxidized to nitrate before plants take it up. The loss of energy is considerable (see sec. 2A). In addition, nitrate is generally very susceptible to mass loss via dentrification and leaching. Loss of N fertilizer applied intensively (hundreds of kg per ha) averages about 50% (Frissel 1977; Huber et al. 1969, 1977), and loss in the global N cycle is estimated directly from figures of Burns and Hardy (1975) as 15%. Ammonia is not susceptible to leaching except on sands where nitrate is also susceptible. (It is volatilized from the soil surface in poten-

tially large amounts, as noted in point 9 below.) Ammonia is, of course, a good alternative nitrogen source to nitrate when provided at low rates to avoid toxicity (Cox and Reisenauer 1973). The generally accepted reason for the tolerance of nitrification (evolutionarily and agriculturally) is that the gain in mobility through soil is very important. (Loomis and Gerakis [1975] add the argument that many crops were domesticated from weedy plants, and are adapted to exploit flushes of nitrogen, particularly nitrate we may assume, that occur upon disturbing the land.) However, ammonia can migrate several millimeters per season even as the predominant form of ammonium. It has a low effective diffusion constant that is still about 0.1 the magnitude of that for nitrate (Nye and Tinker 1977). This enables it to reach the nearest root hair or mycorrhiza in a dense root mat. Grasses in grasslands do have dense roots, and often their uptake of ammonia appears to be sufficiently fast to outcompete the nitrifying bacteria (Ross and Bridger 1978; Purchase 1974). Thus one may explain the apparent absence of nitrification in a number of grasslands (Greenland 1958; Bonnier and Brakel 1969; Woodmansee 1978). Some climax forests also appear to lack significant nitrification (Silvester 1978) and even to suppress nitrification actively by chemical allelopathy (Basaraba 1964; Rice and Pancholy 1972, 1973, 1974; Moleski 1976; Lodhi 1977; 1978a, 1978b; Rice 1979). One must explain why these communities do not do so before climax in order to save energy.

6. In temperate zones, most legumes are herbaceous and evanescent. Herbaceous legumes are often sparse in undisturbed grasslands (Reuss and Innis 1977; Woodmansee 1978; but see Porter 1969). Leguminous trees such as locusts do not form part of typical climax communities. Actinomycete-nodulated plants are also generally pioneering species not persisting to climax (Silvester 1977; Klemmedson 1979). In the heavily productive tropics, the pattern is more irregular; in dry forests, leguminous trees may be a small proportion of the total, while they are common in wet forests (Norris 1969; Lopes 1978). In some cases, leguminous trees are present but may nodulate only seasonally (Norris 1956; Bonnier and Brakel 1969) or never, as apparently is true on some coastal Amazonian regions (de Oliveira and Sylvester-Bradley 1978).

It is puzzling that climax ecosystems often exclude, or reduce the niche for, legumes and other fixers. This occurs even as net primary productivity (NPP) per area rises and so must annual N uptake, even allowing for the tree's ability to scavenge N from senescing leaves (Taylor 1967; Turner 1977). This implies that the N cycle must be tightened substantially during succession. The fractional loss which is tolerable decreases even faster than NPP rises, because of reduction in fixation. Some ecosystems ultimately appear to subsist almost entirely on the abiological input from lightning, ozonization, and fires which is delivered mostly via rainfall (Burns and Hardy 1975).

This frequent demise or reduction of  $N_2$ -fixing species probably in part results from their generally lower competitiveness, which in turn results from the energetic drain of fixation. Also, grain legumes are sometimes loosely characterized as being poorer than average in photosynthetic capacity even when N fertilized (see Zelitch 1971, 1975). Still one might expect the competitiveness of wild legumes to rise as the N cycle tightens. 7. Ever since Hatch and Slack (1966) first outlined the  $C_4$  pathway, building on some pioneering work by Kortschak et al. (1965), its advantages and disadvantages relative to the  $C_3$  path have been investigated and/or speculated upon (e.g., Bishop and Reed 1976; Burris and Black 1976; Baskin and Baskin 1978; Lawlor 1979; Osmond 1980). It seems clear that the  $C_4$  path is useful in warm, arid climes. However, these climes also correlate with poor N reserves in soil (Jenny 1961, and references therein) because of faster decay cycles, more leaching, etc. One might ask why no symbioses or looser associations of  $C_4$  plants with N<sub>2</sub>-fixing microbes have evolved that are as productive as those with  $C_3$  plants, even where  $C_4$  plants dominate and cannot share the  $C_3$  fixation bounty. A partial answer lies in the higher C:N ratio achieved in  $C_4$  plants, allowed in great part by the reduced need for the dominant leaf protein, RuDP CO<sub>2</sub>ase (Brown 1978; Neyra 1978). Nonetheless, a  $C_4$  plant symbiotic with *Rhizobium* or *Actinomycete* organisms, were it to exist, would seem to have considerable competitive advantage.

8. Limitation of plant growth by low availability of soil N is frequently claimed for diverse types of ecosystems. I have estimated in earlier work (1978, 1980) that only 2.5% of global net productivity is invested in fixing N biologically. The biospheric energy budget for acquiring new fixed N certainly should be expandable in the face of such limitation. The benefit of increased yield per unit energy expended for fixation is much larger than unity (see sec. 2A). There should be room for increased standing biomass and for annual productivity; no major ecosystem appears to achieve the potential productivity allowed by solar energy input used at biologically achievable whole-season efficiencies (Cooper 1976; also compare Rodin et al. 1975 with Bassham 1977). One admittedly must expect limitation by some factor, but optimal metabolism occurs when all nutrients are comparably near to causing limitation; N may be far ahead of other factors besides water. Why the biosphere appears to be so notably self-limiting is problematic. (It also may not be as true as generally claimed; again I note that the concept of N limitation needs considerable critical upgrading.) No definite insight has accrued from divergent routes of research, neither those investigating the empirical soil N/climate correlations nor those investigating the mechanistic local N budgets in terms of transfers of N between compartments.

One conceivable origin of limitations to fixation is deficiency of Mo in soils. Molybdenum is an absolute necessity for all N acquisition except of ammonia and is required for very little else metabolically (Ochiai 1978). Limited investigations of Mo availability under agricultural conditions in temperate zones (Karimian and Cox 1979) are inconclusive regarding global patterns. Molybdenum unavailability is a characteristic of acidic soils (Leeper 1978). However, acidic soils can at least retain Mo against leaching as molybdate anion; solubilization by rhizosphere microbial pH shifting or similar mycorrhizal activity (Harley 1978) or by plantderived chelating agents (Lindsay 1974) might sustain plant needs. These routes develop well in the wild if not in agriculture. Much more information is needed on soil Mo. I estimate that it is not the major factor behind low global biofixation; that legumes are commonly present and active early in succession is some evidence.

Walker and Adams (1958, 1959) have hypothesized that phosphorus availability decreases during soil genesis and that nitrogen fixation effectively ceases. Phos-

phorus limitation to ecosystematic productivity, and its possible expression in a nitrogen limitation, is an extensive topic. I must forego its discussion here for lack of space.

9. Ammonia derived almost entirely biologically is present in air at a concentration averaging perhaps one part per billion by volume (Dawson 1977, National Research Council 1979) in the troposphere. Given a mean rainout time of about 10 days, this implies an annual turnover of about 200 Tg (teragrams, million metric tons). This figure is quite uncertain, but most estimates are as high or even higher (Robinson and Robbins 1970; Burns and Hardy 1975; Svensson and Söderlund 1976). Dawson's figure of 50 Tg is most conservative and is most soundly based in soil chemistry and in meteorology, although he did not account for the decrease in the solubility of ammonia in water due to  $CO_2$ , a large effect (Hales and Drewes 1979; National Research Council 1979). In any event, the comparison to estimates of annual biological fixation, about 70 to 180 Tg (Delwiche 1970; Burns and Hardy 1975; Svensson and Söderlund 1976), is striking. This is particularly true in light of the potential for plant yield that this quantity of ammonia represents. The extent to which atmospheric turnover represents net gains and losses by individual ecosystems is almost entirely unknown.

10. On a global scale, bacterial denitrification causes a large loss of fixed N which might otherwise nourish plants. Since the global N cycle is apparently in approximate long-term balance even with anthropogenic input, then dentrification must closely equal in magnitude the sum of biofixation plus the smaller abiological fixation—on the order of 180 Tg/yr (Burns and Hardy 1975). This is about one-sixth of all the N demanded by plants per yr (see sec. 3A). Tolerance of a loss of this size is hard to explain, considering that denitrification is biologically suppressible, at least indirectly by suppressing initial nitrification (see point 5 above).

11. One more metabolic/ecological puzzle concerns the N metabolism of certain bacteria rather than of plants. Species of *Rhizobium* (Rigaud et al. 1973) and of *Azospirillum* (Neyra and Van Berkum 1977; Scott et al. 1979) have been reported to fix  $N_2$  while dissimilating nitrate as a respiratory oxidant source. This uses far more energy and fails to use nitrate as a nitrogen source.

# 2. STRATEGIC BASIS FOR ALLOCATING INTERNAL ENERGY RESOURCES TO ACQUIRE N

# A. Energetics of Assimilation

A disproportionately large share of the gross energy captured photosynthetically by a plant is spent for the 2% or so by weight that is nitrogen (Penning de Vries et al. 1974). Three basic N inputs are available to a plant: (1) atmospheric N<sub>2</sub>, fixed biologically in quantity only in symbioses with *Rhizobia*, actinomycetes, or cyanobacteria. The higher plant bears most of the energetic costs; (2) soil nitrate; (3) soil ammonia/ammonium, the form made available directly by mineralization of decaying organic matter or by asymbiotic N<sub>2</sub> fixers.

The energy cost of symbiotic fixation of  $N_2$  is high, as authors far too numerous to mention have noted. Recent reviews by Phillips (1980) and by Atkins et al.

(1978) are helpful. Generally, 8 to 12 g of glucose are consumed aerobically per g of nitrogen fixed (Minchin and Pate 1973; Herridge and Pate 1977; Atkins et al. 1978; Pate and Herridge 1978; Heytler and Hardy 1979; Pate et al. 1979; Ryle et al. 1979; Layzell et al. 1979; also, more studies on isolated nodules). This reflects the large thermodynamic climb in free energy between  $1/2 N_2$  and  $NH_3$  (fig. 1). The biochemical path, like any other chemical route traversed at usably high rates, uses more energy than the minimum. The biochemistry has been reviewed many times; in this section I will adopt presentations from my own review (1981), which adds a few new concepts.

Necessary reductant is generated from glucose by glycolysis and the tricarboxylic acid (Krebs) cycle, with very high efficiency, above 90% (see review). About 30% of the reductant as a minimum is subsequently lost in an obligatory side reaction producing  $H_2$  gas. Up to 2/3 of the original glucose energy embodied in this  $H_2$ , i.e., 7% of total glucose use, can be recovered by oxidative phosphorylation driven by  $H_2$  to make 2 ATP; ability to so recoup varies with the symbiosis.

Additional energy is required in the form of about 8.5 ATP per N atom reduced (Ljones 1974; my review and reviews by other authors discuss the uncertainties and variations in this number). ATP is expended purely for activation, since  $N_2$  and either NAD(P)H or ferredoxin should react spontaneously to form NH<sub>3</sub>, if very slowly. ATP use accounts for more than half the demand for glucose in fixation, especially if the oxidative phosphorylation that generates it attains P:O ratios less than 3, which is likely. The net thermodynamic free-energy efficiency of fixation is about 28%. This compares well with the 34% efficiency of primary photosynthesis from usable (photosynthetically active) radiation (Thorndike 1976; Bassham 1977). Both N<sub>2</sub> fixation and primary photosynthesis are comparably difficult, refractory to improvements in efficiency, and diluted in efficiency by other demands in whole-plant metabolism.

In converting ATP and reductant demands to glucose use, I assume that 1 mol of glucose can generate 12 mols of reductant (each carrying two hydrogens, denoted as [2H] in fig. 1), or 38 mols of ATP—that is, I assume most efficient aerobic metabolism.

The direct biochemical or "operational" cost of fixation just discussed is inflated by maintenance costs for the (turnover of) nitrogenase enzymes and for nodular tissue and extra root tissue supporting the symbionts. Also, there are "capital" costs for synthesizing these enzymes and tissues initially. These costs are reflected in measurements of carbon use for N<sub>2</sub> fixation in intact legumes. I use the quantitative results of Minchin and Pate (1973) as representative of these total costs in figure 1. Modest, but at times important, variations in costs have been shown in numerous other studies by various authors as referenced at the beginning of this section 2A. These studies are a bit difficult to consolidate and compare because of variations in the degree to which the operational, maintenance, and capital costs are included. In interpreting the results of Minchin and Pate (1973) for figure 1, I assume that a significant fraction (one-half?) of root respiration and growth can be charged to support of N<sub>2</sub> fixation rather than other root functions.

Capital costs amount to roughly 30% of the whole-plant costs of fixation over the whole life cycle (fig. 1). Some of the root and nodular tissue is scavenged at

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FIG. 1.—Energy costs of biological  $N_2$  fixation. Square brackets are used to denote products and reactants without specifying actual stoichiometric coefficients. (A) Reductant use is inflated about 40% over that for  $N_2$  reduction alone, by an obligatory side-reaction that liberates  $H_2$ . The obligatory nature and the stoichiometric coefficient are the subjects of a considerable literature; see reviews of fixation. (B) I assume a stoichiometry of 4 ATP's per reductant [2H] used on  $N_2$  or "wasted" in  $H_2$ -liberation. Again, see reviews for the sizeable literature. (C) In some microbes (symbiotic or free-living), the  $H_2$  can be oxidized to drive phosphorylation. The 1.3  $H_2$ 's evolved per  $N_2$  (minimum) then yield 2 ATP's each, or 2.6 ATP total. For intact legumes, "scav" denotes scavenging of tissue at season's end. Note that 5.2 g of glucose per g of N fixed are used simply as carbon skeletons into which N is incorporated as the amino function (usually). The energy embodied in these carbon compounds is largely conserved; however, as an input requirement to nodules that appear to have restricted rates of total carbon inputs, this temporary tie-up may cause limitation of fixation rates. This idea is currently being discussed informally by researchers. For bacterial fixation, I have critically reviewed (1981) the many literature values for sugar consumption.



FIG. 2.—Energetics of nitrate reduction in higher plants. In the "dark" route of reduction (usually in roots), glucose generates reductants stoichiometrically. The quoted cost excludes the cost of pH rebalancing; see text. This cost lies at the high side of the published estimates. For the direct photosynthetic route used in leaves, GAP = glyceraldehyde phosphate; PGA = phosphoglycerate, pri.; PS = primary photosynthesis (CO<sub>2</sub> fixation). Only the triose-shuttle alternative is shown; Woo et al. (1979) also report tetroses in reductant shuttles.

season's end and should be credited against energy costs. I assume one-half scavenging; recent work by Atkins, Pate, and coworkers (see references at beginning of this sec. 2A) frequently indicates higher fractions. This energy credit is not compounded photosynthetically, however (see sec. 2B on compounding).

The biological fixation of atmospheric  $N_2$  to nitrate, downhill in free energy, is conspicuous by its absence. However, it is also absent in industrial fixation (at competitive costs) and is minimal in natural atmospheric and geological chemistry. The lack of low-energy intermediates in this reaction is extreme (Gutschick 1977, esp. pp. 36–37). Lightning, ozonization, and combustion in air do fix  $N_2$  to pre-nitrate compounds (Burns and Hardy 1975) but the high energy cost of generating the ionic and radical intermediates is supportable only abiologically. Even if an efficient biological process to yield nitrate were to evolve, the high cost of subsequently reducing it to ammonia would make the process unfavorable compared to direct fixation of  $N_2$  to  $NH_3$ .

A large energetic cost of using soil nitrate lies in its reduction, which occurs in two stages, first to nitrate and then to ammonia. The thermodynamically minimal energy for this reduction very nearly equals that for  $N_2$  fixation (fig. 2). One biochemical path is "dark" (nonphotosynthetic) and uses glucose rather copiously. Eight H equivalents or 1/3 of a glucose are required per N atom reduced. From NAD(P)H plus NO<sub>3</sub><sup>-</sup>, the reaction is downhill in free energy. No ATP is used for activation, but neither is any ATP recovered as is possible in dissimilatory nitrate reduction (critique by Haddock and Jones 1977). This cost is less than that of N<sub>2</sub> fixation and is not substantially inflated by capital and maintenance costs. However, there can be large additional costs for maintaining internal pH balance

in the plant. Consider nitrate taken up with any counter-ion, say,  $K^+$ , and then reduced:  $K^+ NO_3^- + 8 [H] \rightarrow K^+ + NH_3 + 2 H_2O + OH^-$ . (The intermediate formation of  $NH_4^+$  is irrelevant, because only neutral derivatives of  $NH_3$  such as amino acids with  $-NH_2$  groups ever accumulate in significant amounts.) The accumulation of hydroxide ions must be countered by synthesis of strong organic acids such as malate or oxalate from pH-neutral precursors such as sugars (Raven and Smith 1976, Davies 1973a, 1973b; deWit et al. 1963). Total retention of the acid anions commits a sizeable amount of carbon, valuable for energy. Loomis and Gerakis (1975) calculate one malate per  $NO_3^-$ ; correcting this to 1/2 malate, because malate is doubly ionized at the neutral pH of cytoplasm (exclusive of vacuoles; Smith and Raven 1979), we obtain an extra cost of 1/3 glucose per N atom. Part of this cost might be discounted because acid anions can be useful for osmotic regulation. However, it is difficult to quantify the fraction. Note that some species (Raven and Smith 1976) restrict investment in organic acid anions. They use them in part only as shuttles for discharging OH<sup>-</sup> equivalents at the roots as  $HCO_{\overline{3}}$  (Ben-Zioni et al. 1970). This may be necessary to avoid accumulating excessive osmotica (Cram 1976); oxalate precipitation (Arnott and Pataud 1970) may help in some species.

A second possible path for nitrate reduction is less costly, perhaps much less so. Photosynthetic reducing power available in leaves may drive reduction directly (fig. 2). The reduction to nitrite uses reducing power shuttled out of the chloroplast via trioses or tetroses (Beevers and Hageman 1969; Klepper et al. 1971; Woo et al. 1980). Slight modifications (energetically speaking) obtain in  $C_4$  plants (Neyra 1978; Neyra and Hageman 1978). This direct shuttling without intermediate formation of glucose saves some small ATP costs, at least. The second step of reduction to ammonia then proceeds inside the chloroplast using directly photogenerated ferredoxin (piecewise discovery is recounted by Losada and Guerrero 1979). The direct cost in carbon compound use can be small, if these two steps are done noncompetitively with photosynthetic CO<sub>2</sub>-fixation. This noncompetitiveness can be achieved two ways. (1) Reduction of nitrate to  $NH_3$  may be done mostly when stomata are closed and  $CO_2$  is depleted toward the compensation point. Empirically, it is seen that amino acids do indeed accumulate during stomatal closure (Barnett and Naylor 1966; Lawlor and Fock 1977, 1978; Lawlor 1979), for minutes or hours until carbon skeletons for incorporating reduced  $NH_3$ are presumably depleted. In barley, even severe carbohydrate depletion does not prevent substantial rates of (leaf plus root) reduction of nitrate (Aslam et al. 1979); in other species, prolonged deprivation of  $CO_2$  does terminate reduction effectively (e.g., Davis 1953; Kessler 1964). (2) Reduction might use excess photosynthetic capacity in parallel with CO<sub>2</sub> fixation, when intercepted light intensity exceeds saturation levels for CO<sub>2</sub> fixation as can occur in C<sub>3</sub> plants. Evidence for this path should be sought. Competition between nitrate and CO<sub>2</sub> at supersaturating intensities is seen in cyanobacteria (simple models of higher plants) in some species and conditions, not in others (Thomas et al. 1976, and references therein).

For either reductive path in leaves, the cost of pH balancing still must be added. Thus, a minimal cost between 1/4 and 1/2 that of  $N_2$  fixation is likely.

Whole-plant measurements of costs of nitrate reduction, especially relative to

 $N_2$  fixation, are a bit inconclusive. Minchin and Pate (1973), Pate et al. (1979), Broughton (1979), and Lambers et al. (1980) by varied means for varied species, estimated a near equality of cost between  $N_2$  and  $NO_3^-$ . Ryle et al. (1979) obtained significantly lower costs for  $NO_3^-$  in several species. Perhaps high levels of nitrate nutrition used by Ryle et al. shifted some of the reduction from roots to leaves, a phenomenon seen by Oghoghorie and Pate (1971). Silsbury (1977) calculated notably lower costs for nitrate, but Broughton (1979) has criticized the method of measuring respiration attributable to assimilations of  $NO_3^-$  and  $N_2$ . Lambers et al. (1980) found lower apparent operational costs for  $N_2$  but higher capital costs, leading to overall equality with costs for  $NO_3^-$ .

Assimilation of ammonia taken up from soil should incur minimal costs, at least under natural conditions of slow availability which obviates toxic effects and equivalent energy losses. No chemical transformation is necessary and, unlike nitrate, active transport up an initial concentration gradient from soil to root interior is probably unnecessary. Free NH<sub>4</sub><sup>+</sup> concentrations in plant tissues are extremely low, roughly commensurate with soil concentrations, except under artificial forcing. Raven and Smith (1976) project a modest energetic expenditure to maintain pH balance (even when  $H^+$  is discharged at the root, this is required). Some overhead costs may be of modest sizes and are incurred only if a plant actively expands the fraction of N acquired as ammonia versus nitrate. Active suppression of nitrifying bacteria, as appears to be exercised by some climax species (see sec. 1, point 5), costs the energy of synthesis of the allelopathic agents. This has not been quantified but is probably modest. If 1% of the plant dry weight were so exuded—a typical total exudate fraction (Mooney 1972; Warembourg and Morrall 1978)—then this cost is still small relative to the gain in yield up to 17% possible by using  $NH_3$  instead of  $NO_3^-$  (see below). A larger cost may be incurred from increased root growth required to access the less mobile ammonium ion. No empirical observations of this yield cost have been made, even where allelopathy has been investigated. In grasslands, where  $NH_4^+$  is often the dominant form of N taken up (see point 5 above), I assume that some of the excess root growth is already present for water uptake. The larger roots proliferate to extract water from a large soil volume; the finer roots proliferate to take up ammonium, which moves only short distances in any volume. These fine roots cost less energy to build than the large roots, as they have less total mass. To confirm this proposal, one requires research on root growth and morphology in response to both water and mineral nutrient needs, along the lines pursued by Drew and Saker (1973, with Ashley; 1975, 1978) for mineral nutrients alone. In sandy soils with little cation-exchange capacity, ammonia is more mobile, and excess root growth would be unnecessary if allelopathy were ever exhibited in such soils.

#### B. Energetic Payoff

The energetic payoff of N acquisition lies in the extra dry matter storable per unit of N acquired. The quantitative payoff is calculable from the cost of acquisition per g of N (c), the fraction of N in plant dry-matter yield (f), and the non-N respiratory costs (r) incurred simultaneously with N costs. These values are not



FIG. 3.—Final yield of dry matter in plant growth as dependent on source of nitrogen. I assume that respiration for biosynthesis exclusive of N metabolism amounts of 30% of final dry matter in both cases.

constants even with one plant, but typical values are c = 12 g sugar/g N, exacted from gross photosynthesis and not net; f = 0.02; and r = 0.3, as a fraction of net yield. Thus, N<sub>2</sub> and NH<sub>3</sub> as sources of N yield the final payoffs in plant dry matter as estimated in figure 3. The benefit: cost ratio for fixing N<sub>2</sub> or assimilating NO<sub>3</sub><sup>-</sup> in roots is 50:12 in mass (sugar vs. average plant matter) and virtually the same in energy. The maximum additional benefit of acquiring N as NH<sub>3</sub> is 8.5/50 = 17% gain in yield; going the other way, it is a 15% drop in yield. This percentage applies before the overhead, if any, for NH<sub>3</sub> uptake is charged. Acquisition of N by reducing nitrate in leaves gives intermediate benefits between NH<sub>3</sub> and rootreduced nitrate.

The inconstancy of c, f, and r complicates matters. I will not present a discussion of their dynamics nor of their coupling to benefit: cost ratios but will merely note the occurrences of inconstancies. In N<sub>2</sub> fixation, the cost, c, varies with maturity of the plant (Atkins et al. 1978; Pate and Herridge 1978; Heytler and Hardy 1979) and with rate of fixation (Heytler and Hardy 1979), dropping sharply as the rate increases, surprisingly. In NO<sub>3</sub> assimilation, the fraction reduced in leaves versus roots may vary with photosynthetic source-sink balances (no data available yet). The fraction, f, adjusts itself to N stress in particular, reducing on a whole-plant average as N stress rises (e.g., Miller 1931), with intriguing dynamics that deserve more research. Genetically fixed schedules of N storage also contribute variations. The respiratory costs of biosynthesis are probably least variable, though the maintenance energy fraction clearly must rise at slow growth rates (Penning de Vries 1975).

The energetic payoff obviously is compoundable. More assimilated N can lead

to more investment in expansion of photosynthetic capacity, hence to further expansion of N assimilation. This compounding may proceed until N uptake becomes limited by depletion of the soil reserves. It also grades off to zero at limits set genetically for phenological development or at limits set by canopy closure, especially by competing species. Note that compounding is possible only for reduced N entering the general metabolic pool; N tied up in N<sub>2</sub>-fixing nodules is not compoundable, as noted earlier.

#### C. Resource Allocation Strategies: Postulates

The strategic elements I propose below can all be given mathematical formulations. The formulations depend upon the level of metabolic detail one wishes to resolve, some peculiarities of each species, etc., so that I leave them for easy derivation.

Some strategic elements are: (1) Prefer nitrate reduction to  $N_2$  fixation, that is, phase out fixation as nitrate becomes available. Only symbiotic fixers have this choice, of course. While nitrate reduction can cost as much as  $N_2$  fixation if done entirely in roots, virtually the full benefit from  $NO_3^-$  reduction is immediately compoundable, while only about 85% of the benefit of  $N_2$  fixation is compoundable (see fig. 1; N investment in nodular and root growth for one particular legume has an extra component of about 1.4 g sugar/g N, recovered only at season's end). These figures admittedly are still close to each other. There may be far more compelling reasons that soybeans prefer to trade from  $N_2$  to  $NO_3^-$ . Some wild legumes do a substantial fraction of leaf reduction of nitrate (Pate 1973); for them, the switch to  $NO_3^-$  might be highly favored.

In cultivated grain legumes, the modest energy savings from switching to  $NO_3^-$  may not persist at high levels of  $NO_3^-$ . Seed yield usually does not increase significantly (Weber 1966; Hanway and Weber 1971; Dart 1973; Hardy et al. 1973; Rachie and Roberts 1974; Olsen et al. 1975; Ham et al. 1976; Havelka and Hardy 1976; Summerfield et al. 1977).

Temperature further restricts  $N_2$  fixation and favors  $NO_3^-$  use, on a nonenergetic basis. The high activation energy remaining in fixation (Hardy et al. 1968) leads to a rapid falloff of rate at low temperatures. For quite nuclear reasons, fixation persists at high temperatures (say, above 40°C) only in a few species, most of them free living and not symbiotic.

2. Prefer reduction of nitrate in leaves versus roots, within one major constraint. Here the cost differentials can be great, as noted earlier. The constraint is that the plants' stomata must be closed for a significant part of the day, preferably in short stretches. (This presumes that the first hypothesis for low-cost reduction applies.) Many cereal grains meet this constraint and appear to do most reduction in leaves and shoots (Huffaker and Rains 1978); potatoes and onions, on the other hand, rarely close their stomata (Sutcliffe 1968). If the second hypothesis for low-cost reduction applies, the constraint is that leaf area index must not be too large and that the plant must have a light-saturation point below the average intensity at the growth site.

Only preliminary surveys of the fraction of  $NO_3^-$  reduction done in leaves versus roots have been made (Beevers and Hageman 1969; Pate 1973), and no correlations to stomatal opening frequency have been made. Surprisingly, no quantitative data appear to exist on trees, which dominate both biomass and productivity

data appear to exist on trees, which dominate both biomass and productivity globally. The variability of the fraction according to plant age, water stress, and other conditions has also not been investigated sufficiently to make any preliminary conclusions.

3. Prefer  $NH_3$  to any other N source, within a few constraints. As already discussed, ammonia supplied at low rates has very low direct energy costs. Even the added cost of ph balancing is perhaps only comparable to that for nitrate reduction. One variable energy cost is significant, however. This is the cost of building the extra density of fine roots necessary to gain access to ammonia that is relatively less mobile than nitrate in soil. Ouantification of this investment in any terms, energy or otherwise, and its control by soil conditions has not been done. Note particularly that it might often be charged against phosphorus uptake and not ammonia, as phosphorus is less mobile than ammonia. Extra root density to get P may be needed, even if the ratio between plant needs and quantity available per unit volume of soil is more favorable for P than for N. In any event, the investment in roots bears risk. The reduction in shoot: root ratio would decrease photosynthetic capacity, hence also the compoundable energy benefit of N acquisition (until N acquisition becomes absolutely limiting at climax of succession; see sec. 3B.1 below). This lessens the competitive advantage of NH<sup>4</sup><sub>4</sub> uptake or even results in temporary disadvantage. The reversal of root-growth investment into shoots, should changing soil conditions merit it, is slow and biosynthetically costly. Note also that mycorrhizae doing similar absorptive work in place of extra root growth probably have similar costliness in plant yield.

The first nonenergetic constraint, that plants get ammonia before it can be nitrified, is hard to guarantee. While plants often can control nitrification actively in climax ecosystems (see earlier discussion), they can exert little control, if any, over the initial mineralization of soil organic nitrogen, hence over the rate of ammonia accumulation. In temperate zones, nitrogen is mineralized in a flush in advance of the peak season for plant photosynthesis. This nitrogen is liberated by bacteria, or even oxidized for energy, rather than assimilated by them because energy and not N typically limits soil bacteria (Clark 1967). If the plants do not take up the liberated  $NH_3$ , the nitrifying bacteria will oxidize much of it. Although nitrifiers are a small population in the soil, they, as other bacteria, can expand their biomass far more rapidly than plants. (It is fortunate for plants' energy budgets at climax that nitrifiers are limited competitors in the soil [Thimann 1963] and that they are also inhibited by ammonia at sufficiently large concentrations [Thimann 1963; Keenan et al. 1979]; thus there is a limit on their initial claim to ammonia.) The alternative for plants, that of sequestering the  $NH_3$  in advance of substantial seasonal C fixation, would require metabolically costly internal detoxification by attaching it to carbon skeletons (Givan 1979). Only a large standing biomass, preferrably of perennials, would have sufficient internal pH-buffering and carbon reserves to do this. Thus we see that a fundamental mismatch can

occur between plants and soil bacteria in the N cycle, regarding their time scales for growth and also their nutrient limitations. One may say that their cooperation in nutrient cycling can be reluctant and mutually limiting.

The second constraint is that pH balance must be maintainable. This point has already been made for nitrate reduction in leaves. It is more serious for plants taking up ammonium at high rates (Mengel 1974), such as might occur during a flush of soil-nitrogen mineralization. Its impact under such natural conditions has not been measured.

4. Exert fast-responding controls over N uptake and assimilation, and also integrative controls that partition photosynthate differentially into growth of shoots, roots, and parts thereof. Much research has elucidated the former type of controls, which include adjustments in roots' specific uptake coefficient, in partition of nitrate taken up between assimilation and vacuolar storage, in the concentration and specific activity of nitrate reductase, etc. A good overview is given by Jackson (1978). Additional information and constraining soil dynamics are discussed by Nye and Tinker (1977). The basic thrust of these responses is to keep a C:N balance, providing a buffering capacity in addition to allow for disparate timings in availabilities of C and N assimilates. Protection against overinvestment in N is important because N is so costly to incorporate. An overinvestment at season's end is a compounded waste of energy and yield.

The second class of controls largely remains a challenge to our quantitative understanding. The controlled allocation of growth, tissue by tissue, determines relative rates of increase of leaf area, root absorbing surface, root:shoot mass ratios, etc. These controls are integrative, because investments in tissue growth are not readily reallocated, yet they determine gross relative capacities to do photosynthesis, nitrate uptake, water uptake, etc. (These capacities are subsequently modulated by the fast feedback controls of the first class.)

Thus, in many species the root:shoot ratio, root morphology, and root placement will vary with growth conditions, particularly soil concentrations of mineral nutrients (e.g., Brouwer and de Wit 1969; Rogers and Head 1969; Troughton 1974; Nye and Tinker 1977; Taylor and Klepper 1978) and more particularly, the latter relative to available light/photosynthetic resource (e.g., Stark 1974). Kuperman (1972) and Caldwell (1979) attempted qualitative formulations of some of the latter balancing responses as optimalities, and Nye et al. (1975) among others have given quantitative formulations (implicitly as optimalities). Pearson (1974) has cautioned about our areas of ignorance, however. Of course, genetic limits exist on the adaptive ranges that can be achieved, and genetic (phenological) programs enforce some long-term tradeoffs. As an example of the latter, consider extension of taproots, which per unit mass are poor for mineral uptake but which can assure late-season availability of water in a predictably drying environment. McComb and Pate (1981) analyze a number of examples.

These adaptive morphological controls operate in complementary fashion with similar controls over water relations (empirically studied especially by Passioura [1972, 1976]) and over purely photosynthetic functions (Cowan and Farquhar 1977; Farquhar 1979). Definitive studies of the quantitative adaptive purposes and their environmental limits are mostly lacking. Also lacking is knowledge of

biochemical mechanisms such as hormones that implement these controls; we have only broad clues.

There are broad opportunities here for detailed strategic studies. The study of the integrative, morphological controls and the optimalities they achieve is a wide-open field. Regarding the fast feedback controls, one might study the pros and cons in luxury storage of unreduced nitrate. Also of interest is the short-term stability of the apparent positive feedback between induction of nitrate reductase by soil nitrate and the enhancement of uptake by nitrate reduction.

5. Allow some flexibility in C:N ratio. Plant growth rates and competitiveness are better served by altering C:N during large changes in C and N availabilities, rather than simply scaling down the whole plant. (The optimalities in the rebalancing of functions, such as photosynthesis vs. nitrogen assimilation, will be the subject of intriguing research.) Proper metabolic function does constrain the flexibility, demanding upper and lower limits to C:N ratios. Below the lower limit, deficiency symptoms appear. Note that seedlings of birch (*Betula verrucosa* Ehrh.) can rapidly adjust net growth rates to restore normal C:N ratios (Ingestad and Lund 1979).

6. For annuals, scavenge N from nonreproductive plants at season's end, even destroying further  $N_{0}$ -fixing abilities. The N invested in parts that will die clearly is best scavenged. The timing relative to senescence of energy-supplying leaves is critical. Nodular senescence in soybean cultivars can be delayed, apparently more than leaf senescence, by high levels of CO<sub>2</sub> in air, as discussed by Hardy and Havelka (1977; and other primary references therein). The apparent nonoptimality in senescence schedules of leaves and of nodules under normal conditions (both too early in pod-filling) may be an artifact of source-sink imbalance bred into the cultivars (McArthur et al. 1975). It may also be only an apparent nonoptimality and not real. More research is needed to define costs and benefits of scavenging. One might consider another aspect, not realized in plants, of scavenging C from leaves to transport to N<sub>2</sub>-fixing nodulated roots and, thus, of scavenging the fixing apparatus last. In the process, one might expect half loss of the C. Thus, such a ploy would be useful only if the seed N: C ratio exceeded the gross plant N:C ratio by more than a factor of two. In the tropics and/or in annuals, scavenging of all nodules at one time is not merited except during water stress, which cuts off energy supplies. Maintenance of energy-intensive nodules then is useless and scavenging begins.

7. In general, compromise the maximal yield to ensure persistence-level yield. This concept was introduced in section 1 after item (4). Both photosynthesis and N acquisition are curtailed at season's end according to environmental cues not related to immediate survival, especially day length. Immediate temperatures and soil moisture levels still might be favorable for growth when curtailment begins. However, the expected stochastic variation in weather is large, and the use of day-length cues reduces the risk of a plant being killed before reproduction. This responsiveness has been selected/evolved, is fixed in genes, and is largely unresponsive to nutritional conditions. However, one nutritional signal can contribute to other maturation controls or even override them. Low soil-nitrate levels can hasten maturation, and excessively high levels can delay it. A simple evolutionary

rationale for the former action, I propose, is that microbially mediated soil-nitrate availability is almost always a single peak in time early in the growing season. The evolutionary experience of temperate-zone plants is that, once soil-nitrate begins to decline, it will get only worse; attempts to extend vegetative growth are futile. The reverse action of high N is probably a freak consequence of the "forward" coupling between low soil N and maturation; it rarely, if ever, occurs in the wild. The reverse coupling does seem to be universal and hard to break in selective breeding programs. The limits of action have not been investigated by phenological stage of development, nor by upper and lower effective  $NO_3^-$  concentration, nor by response time (a week?), etc.

In the wet tropics, N availability can be multimodal in time and erratic (Giambiagi 1978), and temperature/moisture does not cut off safe growing times. A conceivable response to low soil N would be to extend the growing time, to recoup lost nutritional time, providing that a long wait for new soil N peaks is not typical (deleterious to compounding the benefits of N acquisition). I have found no relevant data on this topic.

#### 3. ENERGETICS AND STRATEGY WITHIN AN ECOSYSTEM

## A. Nitrogen and Energy (Carbon) Budgets

Figure 4 outlines the global N cycle and the coupled expenditure of photosynthetic energy that drives it (but not the feedback from the N to C cycles). All these processes occur in any single ecosystem, though not scaled down uniformly nor necessarily achieving steady state locally. For the global N cycle, the values are quoted from Burns and Hardy (1975), who have provided the most recent and detailed estimates but certainly not the only ones (Delwiche 1970; Svensson and Söderlund 1976) nor the final, definitive ones. For photosynthesis, the net figure is adapted from Rodin et al. (1975). The total N demand of 1,050 Tg is my own estimate, based on 70,000 Tg of net primary production, of which one-third is woody tissue containing 0.5% N and two-thirds is leafy or herbaceous tissue containing 2% N.

The annual losses of 180 Tg of N imply that five-sixths of plant organic-N is successfully recycled yearly. Costs of running the N cycle are charged to photosynthesis at three or perhaps four main points: (1) Burns and Hardy (1975) estimated a total of 140 Tg of biofixation of N<sub>2</sub> yearly. Because symbiotic fixation is done at lesser competitive disadvantage than is free-living bacterial fixation, I estimate that four-fifths of all biofixation is done symbiotically. At an average cost of 12 g sugar per g N, the net expenditure of energy is about 1,350 Tg as sugar, or only 1.2% of gross photosynthesis. (2) Free-living fixers, on the average, require considerably more energy, perhaps 50 g sugar per g N (many references; see my review 1981). Thus, they expend about 1,400 Tg of sugar-equilvalent, or 1.3% of gross photosynthesis. However, most such fixers are soil heterotrophs using dead matter (i.e., using the photosynthetic energy storage from previous years and not draining current productivity). (3) Reduction of nitrate inside plants costs perhaps



FIG. 4.—The N cycle and its net photosynthetic drive. (a) The immediate losses from soil are both denitrification and leaching. The leachate is delivered to waters, especially oceans, where most of it ultimately denitrifies. Some is sedimented out in oceans, to be unburied after geologically long times. (b) Schrauzer et al. (1979) have evidence that desert sands containing Fe and Ti may fix as much as 10 Tg of N/yr from atmospheric N and water by an abiological photochemical reaction. (c) Some NH<sub>3</sub> volatilized to air is oxidized by atmospheric trace oxidants such as HO or O<sub>3</sub>. Burns and Hardy (1975) estimate that annually 30 Tg of N meet this fate.

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8 g of sugar per g of N. This assumes that one-half is done half competitively with  $CO_2$  fixation in leaves; thus, this half costs about 2 g of sugar per g of N, plus another 2 g for operating the pH-stat. The other half of nitrate reduction is assumed to be done in roots at an average cost of 12 g of sugar per g of N. These assumptions are risky, given the lack of data, especially for trees. The total cost is thus estimated as  $8 \times 910 = 7,300$  Tg of sugar, or 6.5% of gross photosynthesis. (4) Most abiological fixation arguably is costless to plants (i.e., ozonization and lightning). However, Burns and Hardy (1975) estimate that 20 Tg/yr are fixed by combustion, much of which is natural, especially in forest fires. Such fires cause considerable loss to the photosynthesized biomass but not by metabolic design.

## B. Strategy, and its Limitations and Instabilities

1. At the climax of succession, plants in (most?) ecosystems cannot rely on significant biological fixation; very nearly loss-free nitrogen cycling must be purchased by investing in enlarged absorptive capacity of roots for soil nitrogen. The first part of this proposal is that nitrogen fixation is unstable as a strategy when fixers and nonfixers compete. Nitrogen-fixing higher plants can suffer a competitive disadvantage because of the energetic drain on photosynthesis, unless N stress is quite high on both fixers and nonfixers. (Some leguminous species, especially cultivated varieties, appear to be limited in both photosynthetic capacity [see Loomis and Gerakis 1975; Broughton 1977] and overall competitiveness in their new geographic areas. These limitations are independent of the fixation energy drain. Still, good leguminous competitors exist, say, kudzu [Pueraria *lobata*] and a number of tropical trees.) Nonfixers do not restrain themselves in competition against N<sub>2</sub>-fixers, although they could benefit in the long run from increased availability of soil nitrogen. Thus, on a global scale too small a fraction of photosynthetic energy is invested in fixation for optimal growth of plants as a whole. If worldwide prevalence of nitrogen limitation to growth is indeed the case (as is stated often and usually uncritically), it results from this nonrestraint, which resembles the "tragedy of the commons" in animal husbandry: A resource is overly competed for, to every individual's detriment, but an individual exercising restraint can only worsen his position. Thus, there exists no evolutionarily stable strategy to better the condition of the group. (A secondary competition between fixers and nonfixers may occur locally, in addition to the broad competition for sunlight, water, etc. There can be competition for limited soil molybdenum, which is required for both  $N_2$  fixation and nitrate reduction. However, when nitrification is suppressed in many climax communities, nitrate reduction is not needed and competition ceases for Mo, which has no other known function in plants.)

In some climax communities, nodulated legumes are observed to persist (Norris 1969; Döbereiner and Campelo 1977; Lopes 1978). Quantitatively, one must invoke a trade-off in "principal versus interest." While legumes (or other symbiotic fixers) lose compounding of photosynthetic energy ("interest") because of the energy cost of fixation, they receive a more intensive share of the nitrogen made available (N "principal"), on a running-average basis including all recycling. This balance should be precarious; persistence of fixation should depend on overly large re-

quirement among nonfixers for root investment to gather soil nitrogen, hence upon low soil mobility of mineralized nitrogen in particular.

Apparently, free-living fixers of any type rarely attain the significance of symbiotic fixers, judging from the many field measurements available (e.g., Fogg et al. 1973; Knowles 1977; Reynaud and Roger 1978; Granhall and Lindberg 1978; Todd et al. 1978; Rychert et al. 1978). The lower energy efficiency of free-living versus symbiotic fixation is an extreme penalty in competitions among soil microbes, for which the persistence strategy more closely resembles a striving for maximal yield (Tempest and Neijssel 1978). The predominance of energy limitation over nitrogen limitation for microbes further reduces the role for free-living fixers.

The second part of this proposal is that a dense root mat is required at climax to prevent all but minute amounts of mineralized soil nitrogen from escaping immediate absorption; thus, losses to leaching beyond root zones and/or denitrification are averted. One can calculate that very high annual recycling fractions are required if biological fixation is excluded and only abiological nitrogen inputs can make up small losses. On land, abiological nitrogen inputs may average 5 kg/ha. This estimate is a compromise between (1) some measurements at specific sites (often in temperature zones), some of which are extended by use of atmospheric models (Eriksson 1952; Junge 1958; Wolaver 1972), and (2) an apportioning of the global estimate of Burns and Hardy (1975), two-thirds to land and one-third to ocean (less lightning over oceans, no forest fires). Given a global average demand for N uptake of 80 kg/ha, the recycling ratio would have to be about  $(80 - 5)/80 \times$ 100% = 94%. Specific ecosystems vary, of course. Temperate grasslands (Reuss and Innis 1977; Woodmansee 1978) appear to survive on very low totals of abiological input (0.2-1.0 kg/ha) and biological fixation (0.1-2.5 kg/ha). Their standing biomasses are low, however, and annual N demand may total only 55 ka/ha. The recycling ratio demanded is thus (54.7 to 51.5)/55 = 94%-99%. Similarly, in forest on latosols in the Amazon, nodulated legumes appear to be absent (de Oliveira and Sylvester-Bradley 1978). Prance (personal communication) suggests that abiological fixation here may be larger than the world average, because lightning is more frequent; also, some native cyanobacteria may yet prove to do fixation. The annual N demand is still large, however, due to large net primary production. The recycling ratio might be (300 - 12)/300 = 96%. For some tropical forests on oxosols and spodosols, the operation of a dense root mat for tight recycling has been demonstrated (Stark and Jordan 1978). (In addition, domination of biomass by trees aids recycling, as trees can scavenge much N from leaves before dropping them. This internalized N recycling reduces the net [external] N demand, and thus reduces the required recycling ratio—to perhaps 92% in the last example.) Investment of photosynthate in producing an extensive root mat is not risk free, be it noted. The drain on energy and its compounding by decreased photosynthetic capacity (lower shoot:root ratio) can be risked only when N competition by roots supercedes photosynthetic competition by leaves; indeed, it is probably induced by the latter competition that causes reduction or elimination of symbiotic fixation. The dense root mat that results from the N competition then enables N recycling to be nearly complete, if this rationale is correct. Not only is there an improvement in direct interception of N before losses, but also the loss routes themselves are closed. Soil nitrifying bacteria are outcompeted and the subsequent loss routes of denitrification and leaching are much reduced.

This effectively reformulates Bonnier and Brakel's hypothesis (1969) that legumes nodulate in response to an open (high-loss) N cycle (something they cannot really sense). Basically, symbiotic fixation is a response to low N when photosynthetic competition is low enough. A peripheral indicator that symbiotic fixation is keyed to such joint conditions is that nodulation of herbaceous legumes appears to be more sensitive to nitrate concentrations than to ammonium (Oghoghorie and Pate 1971). Once ammonium ions are predominant, the competition has already shifted beyond N alone, and  $NH_4^+$ -based nodulation controls are not relevant.

Near-sufficient of abiological fixation may prove to be common in climax ecosystems, though perhaps not in a majority. It may have been more common by necessity before symbiotic fixation evolved perhaps 200 million yr ago (Dilworth 1974); however, we know nothing of the competitive status of free-living fixers at such time.

2. Denitrification losses are better than nothing for plant survival, but still not highly beneficial. Denitrification amounting to 1/6 of global N turnover induces a demand for fixation that cannot be filled in full (point 1 above); hence it induces nitrogen limitation. At the same time, however, it helps prevent several other detriments to plant growth: (a) Redox extremes in soil, which exclude plant life but not all microbial life. Board (1977) has noted this role for nitrogen cycling between redox extremes, as well as for S, Fe, Mn, and other elements, on a global scale as well as a local scale. The "set point" of redox level that divides the range for plant life from the range for microbial life is important. Evolutionary extension of the plants' range would cost energy, at least (extra reserves to outlast transient anoxic conditions, e.g.). Reduction of plants' redox range would rapidly increase denitrification losses, hence nitrogen stress. (b) Direct nitrate/nitrite toxicities (rare). (c) Too large a time-lag in soil nitrogen-recycling. As plant litter is decomposed microbially,  $CO_2$  is evolved and the C:N ratio drops. Denitrification in limited soil zones can rebalance C:N to allow maintenance of "useful" rates of microbial decomposition, then mineralization. It is a minor "commission" to microbes for total N recycling.

There is an apparently fortunate balance point in denitrification, which has an undefined stability. If denitrification in oceans were reduced substantially while nitrate runoff to oceans remained at current levels (about 10 Tg per year; Burns and Hardy 1975), oceanic sedimentation of nitrates would deplete atmospheric  $N_2$  in 70 million yr. This time is geologically and evolutionarily brief. In the carbon cycle, the instability is already present: Plant life has buried more than 99% of plant-available carbon as carbonaceous sediments, over 200 million Tg (Hunt 1972). The fraction of plant litter which becomes microbially resistant humus, the "proto-kerogen" as we may call it, is very small, perhaps 0.1% (Kaplan, personal communication), but it suffices to bury carbon effectively. Current plant life suffers a large drop in productivity (about 1/2) because atmospheric CO<sub>2</sub> is low, allowing large competitive photorespiratory losses (Zelitch 1971, 1975).

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#### SUMMARY

Eleven features of nitrogen metabolism in the plant and in the ecosystem are delineated, each appearing to have negative survival value, especially negative effects on yield. These include apparent failures in controls over  $N_{2}$  fixation and over nitrate uptake; preventable energy losses in soil microbial metabolism and in root reduction in nitrate; preventable mass losses of nitrogen via denitrification and ammonia volatilization, and insufficient partitioning of photosynthetic energy to support N<sub>2</sub> fixation in N-limited ecosystems. A quantitative examination of the energetics of metabolizing N<sub>2</sub>, NH<sub>3</sub>, and NO<sub> $\overline{3}$ </sub> reveals behind often high costs some energy inefficiencies required for sufficiently fast kinetics and some compromises with other metabolisms. Cost: benefit ratios can be defined for assimilation of the three forms of N, and each ratio may vary significantly according to other physiological demands, such as pH control at the rhizosphere or stomatal closure for efficient use of water. For the individual plant, I then proposed a number of metabolic principles based on the energetics inside the plant, suitably constrained, and also compromised with the metabolic strategy of soil bacteria. These principles rank-order the preferences for N sources. They also outline complementary roles for normal fast or feedback controls based on immediate environmental variations, integrative controls over relative growth rates of tissues, and nonnutritional controls that schedule maturation. The overall view is that plants in their N-nutrition follow a set of quantifiable strategies, or simple patterns in metabolic adaptations to varied conditions. The goal is to maximize yield over a range of conditions, but at times to sacrifice yield potential for clear requirements such as early competitiveness in canopy expansion. The strategies are heavily conditioned by energetics. Indeed, many are principally patterns of optimally allocating photosynthetic (energy) resources between alternatives such as  $N_2$  versus  $NO_3^-$  assimilation.

I note that agricultural breeding to alter adaptation ranges and to increase yield readily incurs conflicts of desired traits, such as that between ability to use high levels of fertilizer N and ability to mature. I propose that conflicts are easier to foresee between strategies (controlled blocks of biochemical activities, in genetically fixed patterns) than between individual biochemical activities. A second general use of the strategic view may be simpler prediction of overall plant responses to environmental changes (in atmospheric  $CO_2$  levels, soil aeration and acidity, etc.).

When one considers competitive uptake of nitrogen by all the plants in an ecosystem, additional plant responses are seen as necessary. Also, a few inherent instabilities of strategies are seen in  $N_2$  fixation and in denitrification.

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