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The presence of nitrogen fixing legumes in terrestrial communities: Evolutionary vs ecological considerations

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Abstract. Nitrogen is often a limiting factor to net primary productivity (NPP) and other processes in terrestrial ecosystems. In most temperate freshwater ecosystems, when nitrogen becomes limiting to NPP, populations of N-fixing cyanobacteria experience a competitive advantage, and begin to grow and fix nitrogen until the next most limiting resource is encountered; typically phosphorus or light. Why is it that N-fixing plants do not generally function to overcome N limitation in terrestrial ecosystems in the same way that cyanobacteria function in aquatic ecosystems? To address this question in a particular ecosystem, one must first know whether the flora includes a potential set of nitrogen fixers. I suggest that the presence or absence of N-fixing plant symbioses is foremost an evolutionary consideration, determined to a large extent by constraints on the geographical radiation of woody members of the family Fabaceae. Ecological factors such as competition, nutrient deficiencies, grazing and fire are useful to explain the success of N-fixing plants only when considered against the geographical distribution of potential N-fixers.

Introduction

Plants are predominantly made up of carbon, oxygen and hydrogen which are supplied by air and water. Beyond these three elements, nitrogen is required in the greatest quantity. Although almost 80% of the atmosphere is comprised of nitrogen, which occurs in the gaseous form N_2, it cannot be directly accessed by plants.

The transformation, or 'fixation' of nitrogen from the unavailable gaseous form in the atmosphere to forms that plants and other organisms can use (either NH_4^+ or NO_3^-) is mediated by (1) bacteria in symbiotic relationships with vascular plants, (2) symbioses between cyanobacteria and fungi (lichens) or plants, (3) free living heterotrophic or autotrophic bacteria that are typically associated with soil or detritus, and (4) abiotic reactions in the atmosphere associated with lightening (Sprent & Sprent 1990). Although the latter three sources of fixation are more global in occurrence, the bacteria/vascular plant symbioses usually sustain the highest rates of nitrogen fixation per unit area where they occur (Boring et al. 1988). For the rest of the paper, vascular plants that have the capacity to host symbiotic relationships with N-fixing bacteria will be referred to as 'nitrogen fixing plants' or simply 'nitrogen fixers.' In addition, 'legumes' will be used interchangeably with members of the Fabaceae family.

Why nitrogen limitation commonly develops on land has perplexed ecologists for some time. Nitrogen is the sole nutrient whose rate of input is largely controlled by the biota. The input rates of all other essential nutrients can be influenced by the biota, but are ultimately constrained by abiotic factors that drive soil and rock dissolution (Gorham et al. 1979). Presumably, the organisms that are capable of fixing nitrogen should experience a competitive advantage when nitrogen is limiting, making N limitation a transient condition (Vitousek & Howarth 1991). Working to understand why N-fixers are present in some communities and stages of succession while not in others is important in answering more basic questions about the occurrence of nitrogen limitation in terrestrial ecosystems.

A number of ecological explanations have been suggested to help understand why nitrogen fixing plants are often *not* favored over non-fixing plants when N is limiting (Vitousek & Howarth 1991). Probably the most broadly applied explanation focuses on the relative energetic costs of supporting nitrogen fixation versus producing roots to appropriate soil nitrogen (Gutschick 1980, 1981; Vitousek & Field, this volume). Calculations and models suggest that it is energetically advantageous (i.e., requires less of a plant's photosynthate) to grow roots and take up soil N than to fix N when soil N is available (Gutschick 1981; Vitousek & Field, this volume). The implication of this energetic tradeoff is that when light becomes limiting during succession, N-fixing plants are outcompeted by non-fixing plants that are able to put relatively more energy into aboveground growth; thus nitrogen fixing plants are eliminated from the community before adequate N is fixed to attain maximum rates of NPP (Vitousek & Howarth 1991).

Ecological constraints that may limit the success of N-fixing plants other than the energetic cost of N fixation include the availability of soil nutrients other than N (especially P or Mo) (Robson & Bottomley 1991; Smith 1992; Crews 1993), the existence of poor edaphic conditions such as high acidity, alkalinity or aridity (Alexander 1984; Bordeleau & Prévost 1994), removal of N-fixing species by preferential grazing (Hulme 1994, 1996), and removal of woody dicots (including woody legumes) by fire (Bahre 1995).

I argue here that before ecological explanations for the success of N-fixing plants can be considered, it is essential to first evaluate the abundance or paucity of potential nitrogen fixing species – particularly woody legume species – for a given ecosystem. Some terrestrial ecosystems may be nitrogen limited simply because they are outside of the center of legume diversity. In ecosystems where nitrogen limitation exists even when potential fixers are in the flora, then ecological explanations for understanding the colonization and activity of N-fixers are appropriate and useful. Below I will review how the geographic radiation of the Fabaceae has resulted in the domination of the tropics by this group of plants and the comparative paucity of legumes in the floras of temperate regions.

Legume diversity and biogeography

The tropics

The family Fabaceae (Leguminosae) is by far the most diverse and widespread group of plants that have the capacity to host N-fixing bacteria. Ranking behind only the Asteraceae and Orchidaceae in size, the Fabaceae is the third largest family of flowering plants with about 650 genera and 18,000 species (Polhill et al. 1981; Sprent 1995). Although there is some debate as to how the Fabaceae should be broken up into sub-families, the predominant view is that there are three: the Caesalpinioideae, the Mimosoideae and the Papilioniodeae (Polhill et al. 1981; Sprent 1995). The Caesalpinioideae and Mimosoidae mainly consist of woody shrubs and trees (and woody vines in the case of Mimosoidae) that are largely confined to tropical and subtropical regions (NAS 1979). The Papilionoideae is made up of woody shrubs and trees as well as perennial and annual herbs; this sub-family is distributed worldwide with the woody members being largely concentrated in the tropics and sub-tropics (Allen & Allen 1981).

Only around 20% of all legume species and about half of legume genera have been examined for nodulation (Sprent 1994a; de Faria et al. 1989) and far less have been actually tested for nitrogen fixing activity (Virginia et al. 1989; Boring et al. 1988). Members of the three sub-families have been found to have different capacities to support nodulation. Of the species examined, 97% of the Papilionoideae, 90% of the Mimosoideae and 23% of the Caesalpinoideae have been found to nodulate (Allen & Allen 1981, de Faria et al. 1989). The N-fixing bacteria that infect the roots of Fabaceae belong to one of two genera, *Rhizobium* or *Bradyrhizobium* (Sprent 1994b).

It is generally accepted that legumes evolved in the humid tropics (Herendeen et al. 1992). They are well-represented in successional to mature, full-statured communities ranging from wet, lowland rainforests, to tropical deciduous forests, thorn scrub forests, deserts and savannas. Although it is

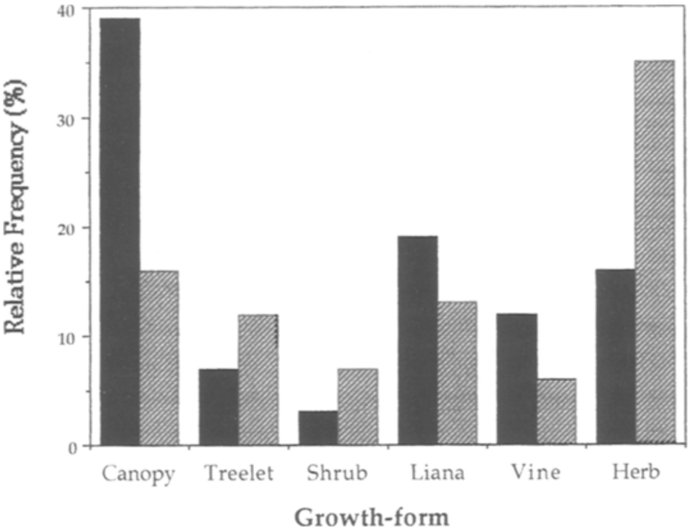

Figure 1. Relative frequency distribution of growth-forms for legumes (solid bars) and the total flora (hatched bars) on Barro Colorado Island, Panama. From Rundel (1989), data from Croat (1978).

clear that not all legumes can support nodulation and thus N fixation, the geographical extent of potential fixers is nevertheless ubiquitous in the tropics (Allen & Allen 1981; de Faria et al. 1989; Moreira de Souza et al. 1992).

Legumes comprise an important component of canopy trees in lowland mesic and wet tropical forests throughout the world (Rundel 1989). In lowland Neotropical rainforests, there are generally more legume tree species than any other family (Hammel 1990; Foster & Hubbell 1990; Foster 1990). Moreover, Moreira de Souza and colleagues (1992) report that in the Brazilian Amazon, the Fabaceae has the greatest diversity of all plant families. In measuring ecological success as a function of density, it is also clear that legumes are extremely successful in the wet tropics. Reports of legume densities range from 2–8% from the Africa and Asia (Rundel 1989). In the Neotropics, legumes commonly make up 12–15% of total tree stems (Rundel 1989) with reports exceeding 50% (Allen & Allen 1981). It should be re-emphasized that not only do legumes comprise a significant percentage of the floras and stand densities of lowland tropical forests, but that they are fully represented and in many cases dominant in the canopy, such as at Barro Colorado Island in Panama (Figure 1) (Croat 1978; Rundel 1989).

Legumes have also been extremely successful in drier tropical ecosystems. In dense stands of tropical deciduous forest at Chamela, Mexico, legumes are the most diverse family, making up about 14% of the overall flora (Martínez-

Yrízar et al. in press). In the drier tropical thorn-scrub ecosystems of Mexico, Gentry (1942) found legumes to be overwhelmingly dominant, with some communities having up to 90% coverage. Species of the legume genus *Acacia* are common to dominant in tropical thorn scrub communities in both Africa and Australia (see Rundel 1989).

Desert communities that evolved from tropical floristic elements, tend to have a significant legume presence. The Sonoran desert of the S.W. United States and N.W. Mexico is an example of a tropically-derived desert flora (Brown 1994), with a strong legume (herbaceous and woody) component (Turner et al. 1995; Eskew & Ting 1978). The two deserts adjacent to the Sonoran – the Chihuahuan and Mojave – are both derived from temperate floristic elements and, with the exception of *Acacia greggii* in the Chihuahuan, have considerably lower legume diversity and abundance (Rundel & Gibson 1996; Brown 1994).

Legumes are well represented in many, although not all, tropical savanna ecosystems. From the standpoint of diversity, Solbig (1996) reported that the Fabaceae has more common tree species in American savannas than any other plant family. In terms of abundance, Medina and Bilbao (1991) found that percent relative cover of legumes in Trachypogon-savanna sites in Venezuela ranged between 6–56%. Others have found low coverage by legumes despite the fact that on a per area basis, legume species richness was higher than that of grasses (Blydenstein 1967; Velasquez 1965 as cited in Medina & Bilbao 1991).

Overall, the rule in lowland American tropics and many tropical ecosystems on other continents, is that potentially nodulating, woody legumes are common and often dominant. This is true from open-canopied arid ecosystems to dense-canopied rainforests, from ecosystems with alkaline, base saturated soils to acid, P deficient soils.

In considering the evolutionary pathways that led to the incredible diversity and dominance of legumes in the tropics, McKey (1994) postulated that nitrogen fixing symbioses between legumes and rhizobia originally evolved in a nitrogen rich environment of mesic tropical forests. He offers evidence suggesting that in general, members of the Fabaceae are nitrogen-demanding plants that maintain high levels of N in leaf tissue in order to maximize photosynthetic rates per unit leaf area. This, in turn, allows the legumes to amortize the carbon costs of leaf construction, and thus have the ability to produce and drop leaves quickly in response to changing resource availability. McKey (1994) contends that this 'N-rich lifestyle' pre-dated the evolution of N-fixing symbioses; in fact, he suggests that it was specifically this N-demanding strategy that provided the selective pressure for the evolution of N-fixing symbioses. Once such symbioses in legumes evolved, the plants were then able to move into other environments with greater resource constraints – environments that would not have supported the pre-symbiosis, N-demanding lifestyle. McKey's hypothesis contrasts with the 'conventional wisdom' recently articulated by Sprent (1994a) who contends that N-fixing symbioses along with mycorrhizal symbioses and cluster roots evolved in legumes under conditions of extreme N limitation. These structures provided legumes with an arsenal of strategies for exploiting combined N when it was available, and the ability to fix N when it was not (Sprent 1994a).

The temperate regions

With few exceptions (e.g., species of *Robinia*, *Gleditsia*, *Cercis*, *Gymnocladus*), only annual and perennial herbaceous legumes, and some low-stature woody legumes have successfully colonized ecosystems in temperate latitudes (Rundel 1989).

In contrast to lowland tropical ecosystems where legumes are typically present through most seral stages, legumes tend to be important components of temperate communities following disturbances. In the prairies of North America, legumes are generally not abundant except following fire (Woodmansee et al. 1981); however, examples exist where legumes persist in mature grassland communities (Paul et al. 1971; Becker and Crockett 1976; Turkington et al. 1977). In temperate deciduous forests of Eastern North America herbaceous legumes are present after logging, blow-down, and during old field succession, but they are lost from the communities as the woody canopy closes (Greller 1988). Herbaceous legumes are significant in the early successional floras of most other temperate communities including pinyon/juniper and ponderosa woodland, interior chaparral, temperate coniferous, prairie, alpine, boreal and tundra ecosystems (Boring et al. 1988; Bordeleau & Prévost 1994; Brown 1994).

It is clear that tropical ecosystems contain a tremendous variety of potentially fixing legume species; their presence in tropical ecological communities, especially the Neotropics, is the rule and their absence is the exception. The floras of temperate regions, on the other hand, have good representation of many early successional legumes, but legumes in late seral stages and woody legumes in general are notably absent.

The presence and absence of N-fixers

In a seminal paper that explored the evidence for and causes of nitrogen limitation in aquatic and terrestrial ecosystems, Vitousek and Howarth (1991) described three mechanisms that could prevent nitrogen fixing plants from reversing terrestrial N limitation where it occurs. The mechanisms were

1. Energetic constraints on the colonization or activity of nitrogen fixers.
2. Limitation of nitrogen fixers or fixation by another nutrient which would then represent the ultimate factor limiting NPP.
3. Other physical and ecological mechanisms (such as grazing).

(Vitousek & Howarth 1991)

As indicated, the proposed mechanisms are intended to explain both the presence and absence of fixers as well as the extent to which N-fixers are fixing N compared to their potential. I suggest that the first two mechanisms are useful primarily to explain rates of N fixation achieved by fixers in a community and only occasionally the presence or absence of the N-fixers themselves; for this I suggest that one needs to consider the biogeographic context of the community. The other mechanisms listed in #3 are fully appropriate for addressing both N fixation as well as the presence or absence of N-fixers.

Energetic constraints on N-fixers

Numerous authors have used energetics to frame the discussion of the ecological success of N-fixers (Högberg & Alexander 1995; Gutschick 1987). The rationale for invoking energetics to explain the absence or gradual disappearance of either legume or actinorhizal species from communities, is that there is a high cost associated with supporting symbiotic N fixation, and that paying this cost is thought to be only advantageous under conditions of low soil N availability. When adequate soil N is available, even if only for a brief time, then nonfixers should enjoy higher relative growth rates (RGR) assuming that they can invest more in aboveground, photosynthetic structures and less in belowground, N-acquiring structures (Vitousek & Howarth 1991; Vitousek & Field, this volume; Gutschick 1981, 1987).

I suggest that an energetic explanation for the presence or absence of N-fixers is not applicable to most ecosystems for two reasons; the first being that mature plant communities with insignificant representation of nitrogen fixers, often have few, if any, tall-statured, woody legume species in their floras. Examples of such communities are found in temperate ecosystems ranging from deciduous forests of the Northeast, U.S. (Likens et al. 1977), to coniferous forests in Southern Chile (Hedin et al. 1995). I suggest that the absence of potential N-fixing species in late successional temperate ecosystems can at least in part be attributed to the evolutionary success of woody legumes being almost entirely restricted to the tropics and subtropics.

The second reason why an energetic explanation for the presence or absence of N-fixers is not applicable to most ecosystems is that attributing the low relative growth rates of N-fixing species to the cost of N fixation per se may not be justifiable. There is little question that at some level of soil N, the metabolic cost of sustaining N fixation should be higher than using available soil NH_4^+ or NO_3^-; at least when nitrate reductase is carried out in the leaves (Beevers & Hageman 1969; Ryle et al. 1979). McKey (1994) has argued, however, that the energetic cost of symbiotic nitrogen fixation has been overemphasized, while the possible benefits of a nitrogen-intensive strategy have gone under-recognized. These benefits include the production of thin, protein-rich leaves that allow for high photosynthetic rates and rapid turnover of photosynthetic parts in response to shifting water, light and even nitrogen resource conditions (McKey 1994).

Acknowledging the possibility that N fixation may pay for itself energetically at higher soil-N levels than were previously thought, there will still be a threshold at which point it is less expensive for a fixer to invest in roots to acquire combined N than to sponsor N fixation. If fixed-N was the only source of N available to legumes, then it would follow that the high cost of fixation would allow non-fixers to outcompete them when soil-N was available. However, it is widely known that legumes can regulate the extent to which they rely on fixed-N versus soil-N (Peoples & Craswell 1992), especially when soil-N is in the form of nitrate (Marschner 1995). When intermediate levels of soil N are available, legumes rely on a combination of fixed and soil N (Neyra 1978; Virginia et al. 1989), and at high levels of soil nitrate, N fixation in many legumes largely ceases (Marschner 1995). Indeed, McKey (1994) suggests that the ability to adjust investment in symbiosis in response to the fluctuating availability of combined N is an important feature in the success of many contemporary and probably ancestral legumes.

In some legumes, the presence of available NH_4^+ in soils has been shown to stimulate nodulation and fixation (Waterer et al. 1992; Goi et al. 1992). This circumstance may provide an interesting exception to the ability of legumes to adjust fixation in relation to levels of combined soil-N. According to Gutschick (1981) N is taken up by plants in some ecosystems such as grasslands at a sufficient rate to outcompete nitrifying bacteria. If little NO_3^- is allowed to accumulate, and NO_3^- is the form of soil-N responsible for inhibiting N fixation (Marschner 1995), then it is possible that fixers in these ecosystems will continue to fix in the face of an aggrading soil N pool. Such a scenario could easily result in N-fixers being outcompeted due to the energetic costs of uninhibited fixation.

That legumes have an overwhelming presence in the canopies of many tropical forest communities – many of which sustain at least seasonally high levels of soil N (Vitousek 1982) – is the best evidence that legumes are not inherently at an energetic disadvantage under conditions of intensive competition for light. Why is it that legumes do not experience a disadvantage? One possibility is that they do not actively fix nitrogen (or even nodulate) in the face of abundant combined N, and thus do not experience any cost greater than a nonfixer. In this case, it is arguable that the *potential* for a legume to host N fixing symbioses does not translate into low relative growth rates (i.e., legumes only experience a cost when fixing). Alternatively, legumes may continue to support N fixation even at moderate levels of soil N because the cost of fixation is more than accounted for by the benefits of high photosynthetic rates (McKey 1994).

This is not to imply that there are not legumes with low relative growth rates. As with other early successional species, pioneer legumes may trade off high RGRs for the ability to persist under unpredictable, nutrient or water stressed conditions (Chapin 1980). It cannot be assumed, however, that low RGRs in such cases are related to the capacity to fix N.

McKey (1994) proposed that once N-demanding members of the Fabaceae had evolved the capacity for symbiotic N fixation, they were equiped to move into a broad array of habitats and take advantage of brief resource-rich (warm or wet) periods. They did succeed in colonizing almost every terrestrial habitat type in the tropics and subtropics; why then have woody legumes gone underrepresented in the floras of most temperate ecosystems? This is clearly a question worthy of further investigation. Temperature fluctuations, light intensity and timing of soil resource dynamics are but three factors that may be involved in limiting woody legume distribution in temperate regions.

N-fixers and soil conditions

As with the topic of energetics and N fixation, a discussion of how soil resources may affect the abundance of nitrogen fixing plants is only germane to geographic regions that have N-fixing plants in their floras. For example, legume abundance in tropical savannas varies widely, and in some cases, extreme soil conditions have been identified among the factors limiting the establishment or persistence of legumes (Medina & Bilbao 1991). In general, however, legumes seem to persist quite well on highly weathered, P-deficient and often acid soil conditions of many tropical rainforests (Leigh & Wright 1990; Foster & Hubbell 1990; Lovejoy & Bierregaard 1990). Given the widespread success of legumes in tropical regions, it appears that edaphic conditions are more likely to affect nodulation and N fixation in legumes (Bordeleau & Prévost 1994; Vitousek & Sanford 1986) than the establishment and persistence of legumes themselves.

Table 1. Dichotomous key to explaining the presence or absence of legumes in ecological communities.

1 (A) Legumes are uncommon or absent in the flora. (2-A)
(B) Legumes are common in the flora.

2 (A) The ecosystem is outside of the center of diversity of the Fabaceae.
(B) Ecological limiting factors prohibit the successful colonization or persistence of legumes (e.g. herbivory, fire, competition by nonfixers and/or extreme edaphic conditions such as low P or Mo, high soluble aluminum, alkalinity, etc.)

Table 2. Dichotomous key to explaining the nitrogen fixing activities by legumes in plant communities.

1 (A) The N-fixing plant/bacterial symbioses are fixing nitrogen at rates far below their potential. (2-A)
(B) The N-fixing plant/bacterial symbioses are fixing nitrogen near their potential.

2 (A) The cost of acquiring soil-N (production of roots, nitrate reductase) is less than the cost of N fixation (*energetic cost of fixation*).[1]
(B) One (or more) critical soil resources such as P, Mo, Ca, Co or water is in short supply and thus limiting N fixation rates (*N limitation by another nutrient in disguise*).[1]

[1] After Vitousek and Howarth (1991).

Conceptual keys to understanding the presence or absence of legumes and N fixation

Using a dichotomous key, I suggest an approach to interpreting the presence or absence of legumes in terrestrial plant communities (Table 1). In Table 2, I use a similar key to describe how nitrogen fixation may be regulated by ecological mechanisms; while Vitousek and Howarth (1991) invoked these mechanisms to explain the activity *and* colonization by N-fixers, I restrict them to only explaining the activity of N-fixers.

Conclusion

That woody legumes have evolved as one of the most successful plant groups in tropical and subtropical regions, and are virtually absent from more temperate regions has profound ecological implications. In as much as nitrogen limitation may be reversed by N-fixing plants, it is reasonable to suggest that N-limitation in temperate, terrestrial ecosystems is first a function of the potential flora of N-fixing plants and secondly a function of ecological limitations inherent to N-fixers compared to nonfixers.

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