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Plant–soil interactions: ecological aspects and evolutionary implications

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Abstract. Building on the concept of plants as ecosystem engineers, and on published information on effects of particular plant species on soils, we review the evidence that such effects can provide a positive feedback to such plants. Based on case studies involving dune formation by Marram grass, N supply by N₂-fixing plants, depression of N availability by ericaceous plants, 'islands of fertility' in deserts, mull- and mor-forming temperate forest trees, and formation of peatbogs, as well as similar other cases, we conclude that there is strong evidence for plant–soil feedbacks in a variety of ecosystems. We argue, moreover, that these feedbacks could have played a role in the evolution of the plant species in question. These ideas are based mainly on correlative observations, and need further testing.

Introduction

Jones et al. (1984) defined *ecosystem engineers* as organisms that directly or indirectly modulate the availability of resources to other species by changing the physical state of biotic or abiotic materials leading to the modification, maintenance, or creation of habitats. They defined autogenic engineers as organisms that change the environment via their own physical structures, i.e. their living and dead tissues, and allogenic engineers as those which transform living or non-living materials from one physical state to another. Jones et al. (1994) suggested that the results of ecosystem engineering often feed back to the fitness of the engineers and in that case can be considered as 'extended phenotypes' subject to natural selection (Dawkins 1982).

The chemical and physical properties of soils are influenced by soil dwelling biota, larger animals and plants (Hole 1982; van Breemen 1993) and soils are therefore the products of ecosystem engineering. Many of the soil properties influenced by plants (e.g. acidity and nutrient availability) are

community until finally a stable state, or climax, was reached (Kingsland 1991). By the mid 1950s, Clements's theory had been largely discredited but components of the organismal view of plant communities and succession had been adopted by several ecologists in an attempt to bridge evolutionary biology with systems ecology. For example, Patten and Odum (1981) and Odum and Biever (1984) argued that evolution would provide mutual adaptation of species to form functionally integrated systems (Loehle & Pechmann 1988). The idea of group selection inherent in this work was criticised (cf. Williams 1966) because one could argue that the properties of systems (e.g. net primary production) arose as a consequence of natural selection of individual species, and the individualistic distributions of species and their interaction with the environment (Loehle & Pechmann 1988).

Soil physical and chemical properties change during the course of succession and the effects of plants on these changes dominate, particularly during primary succession. The three models of autogenic plant succession proposed by Connell and Slatyer (1977) are a convenient framework for a discussion of the effects of succession on the evolution of plant effects on soils. In all three models, both early and late successional species colonise at the same time. In their 'facilitation' model, the growth of the late successional species depends on the presence of early successional species which alter resource availability (above- and/or below ground) in a manner which increases the survivorship of later successional species. In the 'tolerance' model, all species grow to maturity in the presence of early successional species because they can ultimately outcompete early successional species because they can tolerate the decrease in resource availability during succession. In the 'inhibition model' all species resist invasion by competitors. The first occupant of a site excludes or inhibits later colonists until the former die or are damaged, thus releasing resources allowing later colonist to thrive and mature. In reviewing 150 published studies of primary succession, Connell and Slatyer (1977) concluded that there was considerable evidence for the 'inhibition model', that some cases of succession conformed to the 'facilitation model', but that there was little evidence for the 'tolerance model'.

The work of Grime (1977) serves another framework to examine effects of plants on soils. Grime (1977) distinguished three primary plant growth 'strategies' in response to the intensity of stress (shortages in resources, extreme temperatures and water regimes, growth-inhibiting substances), and disturbance (floods, windstorms, fires, herbivores, plowing, mowing). According to Grime (1977), plants adopt a 'competitive' strategy on relatively fertile, undisturbed sites where intra- and interspecific interactions for light, water, and nutrients regulate the distribution and abundance of plants. In stressed environments, the adoption of a 'stress tolerant' plant strategy is

associated with conservative utilisation of water, nutrients and photosynthates (stress tolerant strategy), and on disturbed, productive habitats the 'ruderal' plant strategy is associated with rapid growth, short life span and the production of a large quantity of seeds. An integrated screening programme of 43 common British plants for 67 traits (Grime et al. 1997) found broad support for the existence of the three plant strategies. Three different multivariate methods identified a primary axis with soil nutrient availability separating the ruderals and competitors from the stress-tolerant species. Principal component analysis yielded a tertiary axis separating ruderals from competitors.

We will return to the succession and primary plant strategy models later to discuss them in relation to the case studies we present below.

Effects of plant species on soils

We ask the question of whether the effects of plant species on soil chemical and physical properties influence plant fitness. By focusing on the effects of individual species within a community, this approach implicitly assumes that the evolutionary process occurs at the level of the individual. We will consider a number of cases, some of which are dealt with more extensively later in this volume. They were selected on the basis of specific plant species or of species belonging to a certain functional group of plants with a strong effect on soil properties. In the discussion session we will review the six cases, examine other ecosystems for comparable examples, and see if we can draw general conclusions about the possible evolutionary significance of soil-plant feedbacks. The case studies are: (1) dune formation by Marram grass (Van der Putten 1993), (2) increasing N supply by N_2 -fixing plants, (3) depression of N availability by ericaceous plants (Berendse, this volume), (4) 'islands of fertility' in deserts (Schlesinger and Pilmanis, this volume), (5) mull- and mor forming temperate forest trees (Finzi et al.^{a,b}, in press), and (6) formation of bogs by peatmoss (van Breemen 1995).

Marram grass as a dune former

Ammophila species such as Marram grass and American beachgrass are perennial plants of coastal foredunes. Both species enhance sand deposition by decreasing the wind speed around tillers and tolerate burial up to 1 m per year (Ranwell 1958). Both species are vigorous if buried regularly, but degenerate after sand deposition ceases. Van der Putten et al. (1993) resolved the long standing debate surrounding the mechanisms of *Ammophila* success following sand burial (e.g. Huiskens 1979) by showing that soil pathogens were a major cause of death in Marram grass when sand dunes stabilized. However,

with roots constantly colonising recently deposited, windblown sand Marram grass escapes the pathogens. Better ability to increase sedimentation rates surrounding Marram grass plants could increase Marram grass fitness by providing a substrate free of pathogens, increasing plant vigour and reproductive output.

N₂-fixing plants

Symbiotic nitrogen fixation converts unreactive dinitrogen (N₂) in the atmosphere to a reactive plant-available form. Because N is a major mineral nutrient in soils and is essentially absent in soil parent material, N₂-fixation has a potentially important effect on plant growth and ecosystem development. Yet, Walker (1993) who reviewed 150 published primary successional seres found that, while N₂ fixing species were present in all seres, there was no correlation between the presence of N₂ fixers and total N accumulation in surface soils. Moreover, while nitrogen fixers apparently facilitated the growth of some non-N₂ fixing plant species, they often inhibited the growth of other species by competing successfully for other limiting resources.

Depression of N availability by ericaceous plants

Berendse (1994, this volume) argued that the rate of litter decomposition is an important component of plant fitness in heathland ecosystems subject to high rates of annual N deposition. Following sod removal, the early successional species *Erica tetralix*, could slow down the rate of succession by producing litter which decomposed slowly and depressed nutrient (N) availability as a result of inherently high nutrient-use efficiency. Berendse (1994) showed that *Erica*, by decreasing N availability, transiently increased its fitness by increasing offspring survivorship. Over time however, soil N accumulation facilitated the replacement of *Erica* by the later successional grass species *Molinia caerulea*. He argued that the later successional species *Molinia* replaced *Erica* by producing litter that decomposed more rapidly leading to enhanced nutrient (N) availability required by this fast growing species with lower inherent nutrient-use efficiency. Thus with increasing N availability, *Molinia* outcompeted *Erica* leading to the development of a quasi-stable state until disturbance (sod removal) reset the heathland system to an early stage of succession.

Islands of fertility in the Southwestern USA

Shrubs concentrate soil nutrients (e.g. N, P, K) in 'islands of fertility' that are localised beneath their canopies, while adjacent barren intershrub spaces are

here. Nevertheless, these questions need to be highlighted and addressed if we are to begin linking ecological studies to broader questions of evolution especially with recent concerns over rapid environmental changes associated with human activity.

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