

MICROBIAL SUCCESSION AS IT RELATES TO PLANT SUCCESSION ON MINE SITES¹

by
Donald A. Klein²

Abstract

Microbe-plant interactions in succession are beginning to be understood on a series of more sophisticated levels. Newer techniques, including molecular approaches, indicate that plant community development is closely linked with the presence and functioning of microbes, including phyllosphere, rhizosphere, mycorrhizal and endophytic types. During succession, a series of plant versus microbial limiting factors, including mineral nitrogen, toxic factors, organic matter and mycorrhizae, can play critical roles at different points in microorganism and plant community succession. The ability to influence plant functioning and community development by better understanding and managing microbes associated with plants will provide a valuable resource for the more effective reclamation of mined lands.

Additional Key Words: bacteria, fungi, mycorrhizal fungi.

Introduction

The problem of plant-soil system development and succession becomes critical when terrestrial ecosystems must be re-constructed (Bradshaw 1983), particularly after a process such as mining. Succession can occur in the plant community and also in the microbial community. These successional processes interact over time as the ecosystem develops in the context of the available nutrients and parent materials (Jenny 1980). When soils are disturbed, mycorrhizal fungi are affected (Allen 1991, Allen and Allen 1990), nutrient cycling is disrupted (Vitousek et al. 1979) and the loss of critical soil invertebrates (Ingham et al. 1986) can occur. No organic matter may be present, and a wide spectrum of initial states of the plant growth environment can occur, ranging from primary to secondary succession, with or without inhibitory materials present.

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2. Professor, Department of Microbiology, Colorado State University, Fort Collins, CO 80523

Our first concern is to draw out generalizations regarding microbe-plant-nutrient interactions in succession, as a framework within which possible similarities and differences with the same problem on mined lands can be developed. A major problem in approaching this question is that our understanding of the characteristics of each of these dynamic components (microbes, plants and nutrients), and how they interact over time and space in succession is changing.

Changing Concepts

The Microbial Community

Our view of the microbial community and its role in terrestrial ecology has changed markedly over the last 10-20 years. In earlier ecosystem studies, the microbial (decomposer) community was considered as an incidental adjunct to the various "higher" consumers (Odum 1971). Since that time, the microbes themselves have been found to be the major consumers of plant-derived organic matter (Prescott et al. 1993). Our understanding of the characteristics of the microbial biomass involved in these processes also has changed. Earlier, the microbial biomass was thought to be primarily bacterial, but today, in most plant-soil systems, the fungi are

recognized as the dominant component (Witkamp 1974). Together with these changes, we now have a better appreciation of the critical role of the microorganism in the rhizosphere. These microbes are now recognized as the critical link between the plant, which requires soluble inorganic nutrients, and the soil organic matter which contains these nutrients, but in complex forms which are not immediately available to plants (Clarholm 1985, Klein 1992). The associative rhizosphere microorganisms also have additional functions in influencing the plant community. These include effects on plant morphology and physiology (Lynch 1990) and modifying plant functioning through the production of ethylene, for example (Arshad and Frankenberger 1992).

More subtle effects which were not even thought of until recently have been found to be important. As noted by Clay (1984), fungal endophyte infection can affect the competitive abilities of plants, particularly through effects on growth, survival, and resistance to herbivory (Cheplick and Clay 1988). These new levels of understanding indicate that microbial contributions to plant-plant interactions must be considered on increasingly more subtle levels.

The techniques available for studying microorganisms in the rhizosphere, and in mycorrhizal and actinorhizal relationships also are now changing rapidly and altering our view of this ecosystem component. Traditional cultural and microscopic procedures have been used in most studies of microbial communities in the plant root environment (Campbell and Greaves 1990). These, however, have been found to be simply inadequate to describe the microbial communities, either in terms of structure, or more critical, in terms of function (Brock 1987).

Today, a wide range of molecular techniques allow us to detect and characterize microbes *in situ* with increasing levels of sensitivity (Ward et al. 1992). Our ability to assess mycorrhizal colonization is also improving with the use of more modern techniques (McGonigle et al. 1990, Wright and Morton 1989). Recently, using molecular techniques, it has been estimated that we only have grown 1% of the microbes present in a soil (Stackebrandt 1992). How can we begin to understand plant-microbe interactions in succession when we have no knowledge of most of the microbes which are present?

The Plant Community

Our understanding of plant competition mechanisms also has been changing, to include a greater consideration of the possible role of microbes in this process. Earlier, plant competition was viewed primarily as a plant-plant matter without considering microbes and their role in mineralization-immobilization processes in a meaningful way (Tilman 1985). Major concerns in this literature were competition for light and space (Chapin et al. 1987), water use efficiency (Firbank and Watkinson 1990) and nutrients, primary nitrogen (Tilman 1987). The use of resources by plants, particularly nitrogen, could be studied using Michaelis-Menton saturation kinetics derived from classical microbial chemostat studies (Herbert et al. 1956). Tilman (1985) used such elementary saturation kinetics to study competition and succession, and based on such studies, he noted that "Succession has two main elements: interspecific competition for resources and the long-term pattern of supply of limiting resources, which I call the resource-supply trajectory." Although some workers in these areas have considered the mycorrhizal fungi as a factor influencing competition and succession between plants (Allen and Allen 1990, Walker and Chapin 1987), below ground processes largely have been disregarded in much of this more plant-oriented ecological literature.

Plant-Microbe Interactions

We now are beginning to view the plants and microbes as interacting system components over time and in space. An important paper which shows this point is by Vitousek and Walker (1989), concerned with biological invasion of an actinorhizal plant into a pioneer community on a lava flow ecosystem. In this study, below ground processes, primarily actinorhizal nitrogen fixation, were beginning to be considered as a critical component in the dynamics of these successional plant community changes.

We are beginning to see additional subtleties in how microbes interact with plants. As noted by Chu-Chou, et al. (1992), fungal endophytes can influence the degree to which mycorrhizal populations can form associations with grasses. The ability to speciate mycorrhizae in soils (Allen et al. 1987) allows the development of a more sensitive understanding of the role

of these mutualistic organisms in the development of the plant-soil system and concerning the dynamics of competition between different mycorrhizal populations in infecting plants. Phyllosphere microbes (Dickinson 1982) are now recognized as having important effects on plant physiology. These have been used to improve nitrogen acquisition by plants (Patti and Chandra 1981), as an example.

We know that plant-microbial interactions in succession are dynamic and evolving over time and space. A critical question is whether the plant or the microbial component might play the controlling role in this process. The earlier view was that the plant controlled the microbial community. As noted by Swift (1976), "increasing vegetation species diversity will lead to increased diversity in the plant symbiotic and resource-specific saprophytic microflora." The opposite view also has been posited. Heal and Dighton (1986) suggested that "the degree and type of change in the decomposer subsystem influence the extent to which secondary succession recapitulates previous succession."

At this point our attempts to understand microbial relationships to plant succession begin to be challenged. The first and most important factor is the level of resolution which is being considered. In more recent analyses, the concept of "fine tuning" of the rhizosphere and associated microbes (Chanway et al. 1991) is evident and this sheds a somewhat different light on this problem. We now perceive that more subtle mutualistic interactions occur in the rhizosphere microbial community, and that the microorganisms, through these indirect interactions, can influence plant competition (Turkington et al. 1988, Chanway et al. 1990, Thompson et al. 1990). Microbial interactions with available nutrients and abiotic factors may therefore be a determining factor in the plant community development, and ultimately influence the outcome of the succession process.

Nitrogen Effects

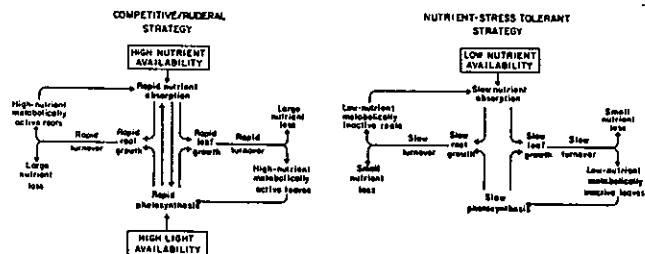
Nitrogen is one of the most critical links between plant and microbial succession on disturbed or intentionally managed sites. Independent of the plant, mineral nitrogen has an overwhelming effect on the terrestrial microbial community and the processing of organic matter. Nitrogen will cause a shift to a more bacterial versus fungal

dominated system, as discussed by Klein et al. (1989) and Turner and Newman (1984).

These shifts controlled by nitrogen also occur in managed plant-soil systems, as described by Inouye, et al. (1987), Parrish and Bazzaz (1982) and Tilman (1982). Nitrogen availability has been found to have major effects on the course of succession in both mesic sites (Carson and Pickett 1990, Vitousek 1990); and in semi-arid systems (McLendon and Redente 1992). Nitrogen (McLendon and Redente 1991), or added nitrogen immobilizing materials such as carbohydrates (McLendon and Redente 1992), through their effects on the microbial community, will retard or accelerate succession, respectively.

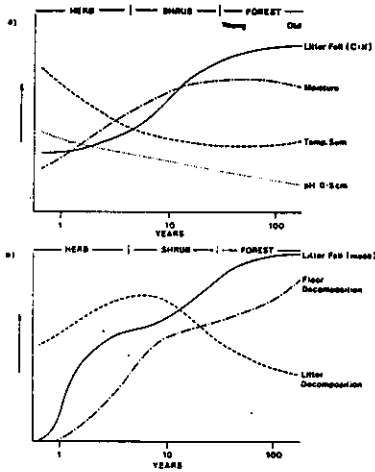
These nitrogen effects can be observed in disturbed natural plant communities. In abandoned old fields, higher levels of mineral nitrogen are present due to removal of the primary producers, and subsequent organic matter mineralization (Vitousek et al. 1979). Species which are dominant early in the plant community development process are most commonly rapid-growing non-mycorrhizal annuals which will rapidly deplete these mineral nitrogen pools. Later in the successional process, slower-growing perennial plants become dominant. The characteristics of these two markedly different types of plants are noted in figure 1 (Chapin 1980). These two plant types also can be considered as nitrophilic and non-nitrophilic (Fichtner and Schulze 1992) and as non mycorrhizal and mycorrhizal, respectively (Allen and Allen 1984).

Figure 1. Comparison between early and late successional plants: carbon processing and litter dynamics.



Litter decomposition is a critical controlling factor in ecosystem function and succession which also is linked to nitrogen availability (Melillo et al. 1989). Early successional plants have relatively high tissue nitrogen concentrations (McLendon and Redente 1992, Woodwell et al. 1975) which is reflected in the nitrogen contents of their litter. The retention of this nitrogen in the litter of early successional plants will lead to increased rates of replacement by more nitrogen-stress tolerant later successional plants. These shifts in resource characteristics over time (figure 2), are critical in analysis of plant community development on mined sites.

Figure 2. Changes in litter characteristics and decomposition in the course of succession.



In contrast, later successional plants will have lower tissue nitrogen concentrations and have more recalcitrant litter with lower nitrogen levels (McLendon and Redente 1992). With the accumulation of this more recalcitrant litter, increases in the fungal component will occur, due to increased substrate heterogeneity and distribution between the litter and the underlying soil (Holland and Coleman 1987, Paustian and Schnurer 1987).

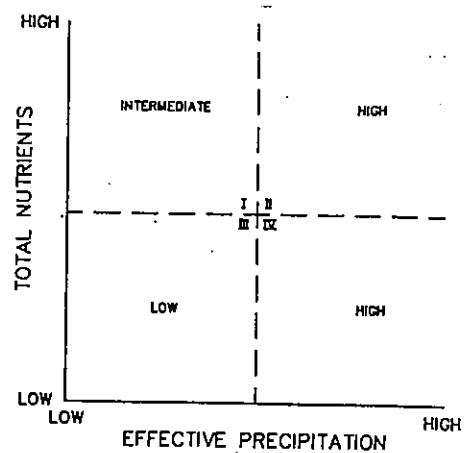
Mycorrhizal Effects

Mycorrhizal propagule levels also can influence the course of succession. As discussed by Allen and Allen (1990), with lower initial levels of mycorrhizal propagules, the development of mycorrhizal-dependent later successional plants can be delayed. This is

particularly critical in situations where soils will be stored, or where surface soil mixing and/ or use of subsurface materials can decrease mycorrhizal propagule levels.

A series of factors can control the environment-mycorrhizal interactions, as noted by Allen and Allen (1990) in figure 3. A critical point is that the mycorrhizae are more important in regulating competition in higher precipitation biomes, and at higher available levels of nutrients.

Figure 3. The importance of mycorrhizae in regulation competition in seral biomass of varying nutrients and precipitation.



It is interesting to note that plants from low precipitation areas are considered to be facultative for mycorrhizal fungi (Reeves et al. 1979). An important point is that the mycorrhizal fungal population structure can change with seral chronosequences. Because different mycorrhizal fungi cause different plant physiological responses, including changes in plant growth, and also in nutrient and water uptake processes, these can also influence the rate and course of succession (Chu-Chou et al. 1992). There is also an increased interest in the effects of mycorrhizae as components of tripartite (Subba Roa and Krishna 1988) and tetrapartite systems (Shatarpaul et al. 1989), where the plant will develop relationships with two or three microbial components, respectively, in the process of plant community development. As an example, these interactions have been found to be important in the reclamation of desertified ecosystems (Herrera et al. 1993).

Successional Interactions

With this information available, it is possible to consider the differences between classic primary and secondary successions and the range of alternative development paths which can occur between microbes, plants and nutrients in mined lands.

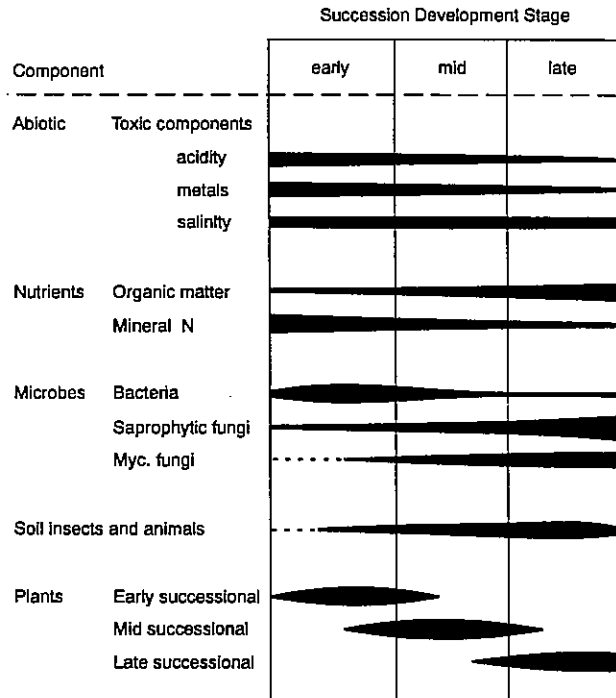
Mined land systems can have a wide variety of initial states. The critical role of microbes as possible controlling factors of the development of the various alternate system paths and final points must be considered. Major factors are nitrogen, organic matter, saprophytic and mycorrhizal fungi, together with soil insects and animals.

The type of disturbance is critical in terms of subsequent system responses. If soil organic matter is still present, physical disturbance can increase organic matter lability to microbially mediated decomposition. In tropical areas where rates of decomposition and organic matter formation are not in equilibrium (Mohr et al. 1972), if plants are removed, soil organic matter is rapidly lost. In other disturbed sites, even if organic matter is retained, critical components of the microbial community can be damaged (Perry et al. 1989). These include the particular lability of the saprophytic and mycorrhizal fungal communities, due to top physical disturbance, and loss of critical substrates. Changes in litter characteristics and microbial communities, as can occur particularly with soils from forest regions, can limit the ability of the plant community to be re-established (Amaranthus and Perry 1989). Without organic matter, the possibility of re-establishing plant communities approximating the original communities is even further diminished.

Metals such as tin, nickel and copper are of major concern. If present in materials on which plant and microbial communities must be developed, these can lead to decreases in nitrogen cycling, specifically in nitrification (Rother et al. 1982). Increases in leachable materials such as soluble salts from mine spoils also can affect biogeochemical cycling (Fresquez and Lindemann 1982). Successional control factors can be critical either initially, in the mid-point of a succession, or towards the end of the successional process, as noted in figure 4.

A useful management approach is to recognize the nature of the potentially limiting plant vs. microbial factor, such as nitrogen, organic matter, metals or salinity, at various points in the

Figure 4. The times of maximum effect/influence of abiotic, nutrient and biotic factors in the course of succession.



succession process. For many early successional plants, the absence of a microbial component critical in the later stages of the succession will not play a role, such as with mycorrhizae. In comparison, with other components, such as toxic metals, the materials may not have as great an effect later in the successional process due to the increased presence of organic matter and soil development, leading to binding and inactivation of the metals, or more metal-tolerant microbial and plant communities. However, if the plant community cannot develop beyond these critical first stages (organic matter accretion and acquisition of toxic metal tolerance), succession may not proceed.

Nitrogen, added either in organic or mineral forms, can have major effects on plant community succession (McLendon and Redente 1991, 1992), and on the functioning and characteristics of the microbial community. When added without sufficient organic matter, or without a functioning plant community, it may result in a retardation or reversal of plant and microbial community development. World-wide, nitrogen loading of ecosystems through industrial pollution, urban atmospheric deposition, and agricultural runoff with subsequent microbial nitrification, denitrification and atmospheric deposition has increased

the nitrogen burden on terrestrial ecosystems (Mosier et al. 1991, Rastetter et al. 1991). This is having major effects on the fungal components of terrestrial ecosystems (Cherfas 1991).

Management Implications

In managing mined land reclamation, the decision to apply nitrogen at the beginning of a program, particularly to achieve visible effects within the time required to have release of reclamation bonds, can have significant negative effects on longer-term plant community development. In a like manner, mycorrhizae added to a potential plant growth environment without plants and/or organic matter can lose viability by the time the system develops to where the mycorrhizae would be required by later successional plants.

A major temptation is to apply all factors at the time of initial reclamation, and to then assume that the system will develop normally. This, however, can lead to the interruption of microbial community-plant community development at a certain point in the succession process, or even preclude succession.

A critical concept is that of meshing of plant and microbial community development as the successional process proceeds. Plants from specific later successional seres can be used initially in establishing a plant community, providing that a more fungal-dominated microbial community has already developed on a particular site. To more quickly create conditions where later successional plants can become dominant, higher C/N ratio materials such as carbohydrates or particularly lignified plant materials can be added to stored soil organic matter to draw down mineral nitrogen levels, and allow a more rapid development of the plant community, as suggested by studies of McLendon and Redente (1992).

If topsoiling and mineral nitrogen immobilization cannot be used to accelerate microbial community development and to assist the successional process, biologically processed organic materials, primarily composts, can be used. Although these have been used in many countries (Miller 1993), they have been used to a minimal extent in mined land reclamation in North America. With the increased need to recycle organic matter, and to manage

the coupling of plant and microbial systems, composts can and should play a more significant role in mined land reclamation. Major efforts are being given to this technology in Hungary and other European countries. Composted materials have distinct advantages over mulches, as mulches do not provide a fully developed microbial community, biogeochemical cycling, or the stabilized organic matter needed to accelerate and facilitate succession.

A variety of commercial companies are developing proprietary inocula which can be used to facilitate microbial community development in composts and in mulch-compost mixtures. Inoculation with microbes, such as associative nitrogen fixing microbes, rhizosphere competent microbes, or possibly mycorrhizal or actinorhizal components also is being used.

A critical need is to create microbial niches and the diverse functions related to effective biogeochemical cycling to allow a more diverse and productive plant community to be maintained. This will require a more dynamic and integrated view of below ground organisms and the plant community as the system develops over time than has been used to the present.

The plant sees the below ground world through the cloud of microbes surrounding the roots (Klein 1992) and these microbes can play vital roles in plant physiology and competition (Lynch 1990). The major goal which we have as reclamation specialists is to be able to identify the potential plant vs. microbial community limiting factors at various points in the successional process (mineral nitrogen, organic matter, metals, saline materials, etc.), and to work most effectively to manage these complementary processes in the reclamation environment. The subtleties of these interactions, and the potential for their management are becoming more fully appreciated. Increased knowledge will provide increased opportunities and challenges.

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