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SOIL DISTURBANCE AND THE MINERAL NUTRITION OF NATIVE PLANTS

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INTRODUCTION

Among plants there is a large variety of ways in which mineral nutrition can be managed. Plants that are native to impoverished soils use nutrients very efficiently, although at a cost in growth and reproductive rates. Plants of richer soils may use nutrients more extravagantly, but grow and reproduce in those habitats at rates otherwise unattainable (Chapin, 1980). The use of nutrients and their physiological effects on both target and weedy vegetation has a fundamental relevance in land restoration. The differences between them, and the exploitation of those differences, is the subject of this paper.

NUTRIENTS AND PLANT GROWTH

Plants can deal with nutrient-poor soils by effective uptake of nutrients or by economical use of nutrients within the plant. Most native species depend on mycorrhizal symbionts to help them effectively take up phosphorus from the soil (Hayman, 1978). Roots also selectively exploit locally rich microsites in the soil, and the plant can be said to be effectively rooted in a medium that is richer than the bulk soil (St. John et al., 1983). Most plants, under nutrient stress, can allocate a larger portion of their growth to the root system and less of it above ground (Mooney, 1973).

Plants of nutrient-poor soils not only take up nutrients effectively, they often possess specific mechanisms to conserve nutrients. Among these are evergreenness and slow turnover of leaves (Monk, 1966; Small, 1972). However, old leaves are photosynthetically less efficient than new leaves, and evergreen plants tend to grow slowly (Chapin, 1980).

The slow growth rate in itself is probably the most important single difference between plants of nutrient-rich and nutrient-poor sites (Chapin, 1980, 1983). The photosynthetic rates of plants span two orders of magnitude (Mooney and Guimon, 1979) and the maximum rates at which plants can grow under ideal circumstances (R_{max}) differ by a factor of twelve (Grime and Hunt, 1975). The fastest-growing plants retain their leaves only a short time, since young leaves have the highest photosynthetic rate and are less likely to be shaded by older leaves (Chapin, 1983). Rapid turnover of leaves carries a heavy cost in mineral nutrients, however. While a portion of the nutrient supply is transported to newer leaves at senescence, half or more of the nutrient stock of each leaf is lost with the leaf. Thus uptake per unit time must be rapid, a condition obtainable only in relatively rich soil. Plants capable of the fastest growth rates are usually ruderals, a term used by Grime (1978) to indicate species that invade highly disturbed but potentially productive habitats. It is interesting that most of our fast-growing crop plants were derived from ruderal ancestors (Chapin, 1980).

There are consistent differences in morphology and chemistry that tend to make late successional, perennial species grow more slowly that early successional, weedy species. Rates of photosynthesis generally tend to decline with successional stage (Bazzaz, 1979). In a study of root systems, early successional plants had as little as 20% of their biomass allocated to the root system. Mid and late-successional species had up to 37% of their biomass in the roots (Parrish and Bazzaz, 1982). Perennials may allocate a significant fraction of their photosynthate to storage, for use in the next growing season (Mooney, 1973). Perennials may extend large amounts of photosynthate on defenses against herbivory. As much as 15% of current photosynthesis was used in production of defensive phenolic compounds by the chaparral shrub *Heteromeles arbutifolia* (Mooney, 1978). Slow growers in general tend to allocate much more of their photosynthate to defensive compounds, defending themselves against herbivores at the cost of tissue production (Coley et al., 1985).

Plants with adaptations that allow them to survive periods of drought may necessarily sacrifice growth rate (Jones, 1983). To conserve water it is often necessary to retard the rate of CO_2 exchange at the same time, as happens when stomata close during drought stress. Species with crassulacean acid metabolism (CAM) are perhaps the most suited to drought of all plants (Walter, 1984). However they are so disadvantaged in competition for CO_2 that they are virtually excluded from closed canopy vegetation (Mooney, 1973).

Many of our desirable native species are among the slow growing species with low R_{max} values, called "stress tolerators" by Grime (1978). In an undisturbed natural community these stress-tolerators are able to grow slowly and reproduce continuously, where demanding ruderal species cannot. In a potentially productive soil, however, the ruderal strategy is clearly superior. I will show in the next section that mechanical disturbance at least temporarily creates an environment in which the desirable natives are hopelessly out-matched in growth and reproductive rates by ruderals.

MECHANICAL DISTURBANCE AND PLANT-AVAILABLE NUTRIENTS

It is critically important to restoration efforts that disturbed soils tend to be richer in available forms of nutrients than undisturbed soils. The changes brought about by disturbance create a favorable environment for ruderals. These changes are mediated by loss of the nutrient sink (uptake by plants), addition of organic matter, and stimulation of the microflora.

In undisturbed vegetation, nutrient ions are absorbed rapidly as they are solubilized. One of the key reasons for greater availability in disturbed soils is the loss of this rapid uptake. Bormann and Likens (1979) reported that clear-cutting a northeastern forest ecosystem caused the loss of about 400 kg/ha of N over a period of three years. The loss was thought due to the lack of uptake by vegetation, and to the loss of exchange surfaces that accompanied decomposition of soil organic matter. The importance of uptake in reducing nutrient availability was also emphasized by Walker and Chapin (1986), who showed that trenching to cut the roots of alder trees significantly increased the availability of nitrogen in the soil, and its concentration in the tissues of plants growing inside the trenched plot.

A second important disturbance-related process is the addition of nutrient-bearing organic matter to the soil. Initially microbial activity may immobilize nitrogen and other elements, but as the carbon is respired away these nutrients become available.

Several disturbance-related processes are stimulatory to the microflora. Aeration, higher soil temperature and increased soil moisture that usually accompany destruction of the natural vegetation, all bring about favorable conditions for microbial activity. Nitrification, the conversion of ammonium nitrogen to nitrate, is a microbial process that may accelerate dramatically under disturbance. Mature vegetation is thought by researchers to inhibit nitrification (Vitousek et al., 1982), and the change in rate results from the removal of this inhibition. Bormann and Likens (1979) reported up to an eleven-fold increase in nitrification rate.

All of these processes shift soil nutrients from unavailable organic forms to readily available forms. No new quantities of nutrients are brought into the ecosystem by disturbance, but the location and availability of the nutrients is shifted dramatically.

Disturbance Destroys Symbiont Propagules

Most late-successional natives depend on mycorrhizae, but the symbiotic organisms are often destroyed by the disturbance. Vesicular-arbuscular mycorrhizae can maintain propagule populations only in the presence of suitable host plants (Mosse et al., 1981). With the vegetation removed, or with only non-host species on the site, the populations drop off quickly to very low levels. Ruderals are often independent of symbionts, and thus are not disadvantaged by the lack of propagules (Reeves et al., 1979; Janos, 1980).

35

Disturbed Sites can be Ideal for Weeds

Fertilizing strongly favors weeds, which grow quickly only with available nutrients (Chapin, 1980). Some early successional species are so keyed to nutrient availability that even seed germination may be triggered by high soil nitrate levels (Bazzaz, 1979). In competition, weeds are favored in high nutrient conditions. The dominance of fast-growing species is exaggerated by nutrient additions, with weedy grasses especially favored (Harper, 1977). There is much more mortality of all groups of plants at high nutrient levels, but the toll may be especially heavy on mid- and late-successional species (Parrish and Bazzaz, 1982). It is only in the low-nutrient, relatively harsh conditions for which natives are so superbly adapted that they can hold their own in competition against early successional weedy plants. The key to management of weeds is to create the conditions in which the natives can out perform them.

SUGGESTED SOLUTION: ANTIFERTILIZATION

A partial solution to the problems pointed out above is reinoculation with mycorrhizal fungi. The methodology of inoculation is poorly developed. Success depends heavily on the nature of the inoculum, timing and manner of application, condition of the soil, and such cultural factors as biocide treatment and fertilization. Inoculation is probably necessary on most disturbed sites (Call and McKell, 1984; Hall, 1980; Mosse et al., 1981). However, mycorrhizal inoculation is not sufficient assurance of success. The ruderals that can out compete our natives are commonly nonmycorrhizal. Even without symbionts, they grow fast and in a nutrient-rich soil are probably better competitors than mycorrhizal stress tolerators. In Hall's competition experiment (1978) between the mycorrhiza-dependent white clover and the less mycorrhiza-dependent perennial ryegrass, the performance of white clover was improved by inoculation. However, the improvement was not sufficient to shift the outcome of the experiment, in which ryegrass dominated. In the field, it is clear that the presence of mycorrhizal plant species is not in itself sufficient to eliminate nonmycorrhizal species. Miller (1979) found that inoculum levels equaled those in an adjacent undisturbed community.

We would like to be able to fully exploit our knowledge of mineral nutrition strategies, and create an environment that favors stress-tolerators rather than ruderals. While growth rate of the intended species can be somewhat improved by fertilization, growth rate of the undesired volunteers will be sharply increased. I would like to submit the concept of antifertilization; actually removing nutrients from the soil. By doing so, we should be able to reduce the growth rate of the undesirable species so much that they are no longer competitive. In effect, we could recreate the conditions in which stress tolerant, mycorrhizal plants are the only ones that can grow and reproduce.

Among the possible ways to "antifertilize" are use of an intermediate crop to remove soil nutrients, addition of organic carbon to immobilize nutrients in the microbial biomass, and binding of soil nutrients with inorganic chemical reactions.

An intermediate crop, which can be removed along with the nutrients it has accumulated, may in some circumstances be an attractive way of decreasing fertility. However, the fraction of the nutrient stock that is removed may be small, and subsequent removal of the intermediate crop requires a renewal of the disturbance.

The effects on soil nutrients of such treatments as wheat straw or sawdust can be anticipated from what is known about microbial immobilization (Alexander, 1971; Fenchel and Blackburn, 1979). The effect is primarily on nitrogen: bacteria and fungi require additional nitrogen to process the newly available carbon, and draw it from surrounding soil.

When the added carbon has been respired by soil microbes, available nitrogen will again be released to the soil. Phosphorus can also be tied up in this way; a phosphorus-specific effect could probably be brought about by adding supplemental N to partially satisfy the needs of the decomposers. Microbial immobilization is thought to be more significant than plant uptake as a sink for available nutrients in some ecosystems. Vitousek and Matson (1984)

concluded that five times as much nitrogen went into microbial biomass as into new plant growth in a disturbed southern pine forest.

The availability of several nutrient elements, especially phosphorus, is strongly dependent on soil pH and the concentrations of certain compounds in the soil (Buckman and Brady, 1969). It may be possible, by adding agricultural lime, to make phosphorus unavailable to any but mycorrhizal stress-tolerators. There are upper limits to the pH that can be tolerated by both the desired plants and the fungi, so such treatment must be carried out with a foreknowledge of the acceptable range.

There are also inorganic additions that remove phosphorus from the available pool. Bolan et al., (1984) used iron hydroxides to irreversibly bind soil phosphorus; the greater the addition of the hydroxides, the greater was the superiority of mycorrhizal over nonmycorrhizal plants. The reaction depended on dry diffusion of the very insoluble iron hydroxides. There are pH-dependent reactions with iron that could probably be used in certain cases.

These potential means of antifertilization are supported by decades soil-science literature. These factors have always been considered serious problems in agriculture, where specially-selected ruderals are grown in monoculture. Before we can use them routinely, however, we need to know more about creating soil problems where none existed. Only by working out appropriate application techniques and correct rates of application can we realistically assess feasibility and costs of these various alternatives.

There is no doubt that the weed problem is one of the most serious in revegetation, that the disturbance creates a flush of nutrient availability, and that the natives are hopelessly outmatched in growth rate under those conditions. If we can find cost-effective ways to "anti-fertilize," we will be able to rob the weed population of its unfair advantage on disturbed sites.

LITERATURE CITED

Alexander, M. 1971. *Microbial Ecology*. John Wiley and Sons, New York.

Bazzaz, F.A. 1979. The physiological ecology of plant succession. *Ann. Rev. Ecol. Syst.*, 10:351-371.

Bolan, N.S., A.D. Robson, N.J. Barrow, and A.G. Aylmore. 1984. Specific activity of phosphorus in mycorrhizal and non-mycorrhizal plants in relation to the availability of phosphorus to plants. *Soil Biol. Biochem.*, 16:299-304

Bormann. F.H., and G.E. Likens. 1979. *Pattern and process in a forested ecosystem*. Springer-Verlag, New York.

Buckman, H.O., and N.C. Brady. 1969. *The nature and properties of soils*. Seventh edition. The Macmillan Company, New York.

Call, C.A., and C.M. McKell. 1984. Field estabishment of fourwing saltbush in processed oil shale and disturbed native soil as influenced by vesicular-arbuscular mycorrhizae. *Great Basin Naturalist*, 44:363-371.

Chapin. F.S. III. 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. System*, 11:233-260.

Chapin. F.S. 1983. Patterns of nutrient absorption and use by plants from natural and man-modified environments. In: H.A. Mooney and M. Godron (eds), *Disturbance and Ecosystems-systems*. Springer-Verlag, Berlin Heidelberg, pp. 175-187.

Coley, P.D., J.P. Bryant, and F.S. Chapin III. 1985. Resource availability and plant herbivore defense. *Science*, 280:895-899.

Fenchel T., and T.H. Blackburn. 1979. *Bacteria and Mineral Cycling*. Academic Press, London.

Grime, J.P. 1978. Interpretation of small-scale patterns in the distribution of plant species in space and time. In: A.J.H. Freysen and J.W. Woldendorp (eds), *Structure and Functioning of Plant Populations*. Elsevier, North-Holland, Amsterdam, New York, pp. 101-104.

Grime. J.P., and R. Hunt. 1975. Relative growth rate: its range and adaptive significance in a local flora. *J. Ecol.*, 63:393-422.

Hall, L R. 1978. Effects of endomycorrhizas on the competitive ability of white clover. *N. Z. J. Agr. Res.*, 21:509-515.

Harper, J.L. 1977. *Population biology of plants*. Academic Press, London.

Hayman, D.S. 1978. Endomycorrhizae. In: Y. JR. Dommergues and S.V. Krupa (eds), *Interactions between nonpathogenic soil microorganisms and plants*. Elsevier Scientific Publishing Company, Amsterdam, pp. 401-442.

Janos, D.P. 1980. Mycorrhizae influence tropical succession. *Biotropica*, 12 (supplement):56-64

Jones, H.G. 1983. *Plants and microclimate*. Cambridge University Press, Cambridge.

Miller, R.M. 1979. Some occurrences of vesicular-arbuscular mycorrhizae in natural and disturbed ecosystems of the Red Desert. *Can. J. Bot.*, 57:619-623

Monk, C.D. 1966. An ecological significance of evergreenness. *Ecology*, 47:504-505.

Mooney, H.A. 1973. The carbon balances of plants. *Annual Review of Ecology and Systematics*, XXX:316-346.

Mooney, H.A., and S.L. Gulmon. 1979. The determinants of plant productivity—natural versus man-modified communities. In: H.A. Mooney and M. Godron (eds.), *Disturbance and Ecosystems*. Springer-Verlan, Berlin, Heidelberg, pp. 146-158.

Mosse, B., D.P. Stribley, and F. Le Tacon. 1981. Ecology of mycorrhizae and mycorrhizal fungi. *Advances in Microbial Ecology*, 5:137-210.

Parrish, J.A.D., and F.A. Bazzaz. 1982. Responses of plants from three successional communities to a nutrient gradient. *Journal of Ecology*, 70:233-248.

Reeves. F.B., D. Wagner, T. Moorman, and J. Kiel. 1979. The role of endomycorrhizae in revegetation practices in the semiacid west. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. *Am. J. Bot.* 66:6-13.

Small, E. 1972. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. *Canadian Journal of Botany*, 50:2227-2233.

St.John, T.V., D.C. Coleman, and C.P.P. Reid. 1983. Growth and spatial distribution of nutrient absorbing organs: selective exploitation of soil heterogeneity. *Plant and Soil*, 71(1-3):487-493.

Vitousek, P.M., J.R. Gosz, C.C. Grier, J.M. Melillo, and W.A. Reiners. 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. *Eco. Monogr.*, 52:155-177.

Vitousek, P.M., and P.A. Matson. 1984. Mechanisms of nitrogen retention in forest ecosystems: a field experiment. *Science*, 225:51-62.

Walker, L.R., and F.S. Chapin. 1986. Physiological controls over seeding growth in primary succession on an Alaskan floodplain. *Ecology*, 67:1508-1523.

Walter, H. 1984. *Vegetation of the earth*. Third Edition. Springer-Verlag. Berlin, Heidelberg.