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Native species can be successfully used to revegetate tundra disturbances,
but procedures differ among sites and must be consistent with the natural
patterns of disturbance and colonization in these ecosystems. Tussock tundra
is effectively recolonized by buried seed contained in the surface organic mat
and requires no additional treatment. Gravelly sites must be sown or planted and
modified to provide an appropriate moisture and nutrient regime. Management
of disturbed tundra systems is discussed.

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REVEGETATION OF ALASKAN DISTURBED
SITES BY NATIVE TUNDRA
SPECIES

Final Report

F.S. Chapin, G.R. Shaver, and A.E. Linkins
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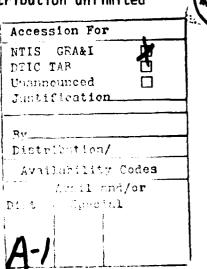Approved for public release; distribution unlimited

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INTRODUCTION

This report summarizes the results of nine years of research on the revegetation of arctic disturbed sites by native tundra plants. In the Arctic, large areas of native tundra vegetation are inevitably disturbed or eliminated by development. Proper management requires that those areas be revegetated and ultimately restored to a state as close to the original as is economically and logistically feasible. Current revegetation methods depend strongly on the use of plants that are not native to the disturbed regions, and often require expensive and labor intensive fertilization and planting procedures (Johnson 1981). The use of these non-native plants is usually effective in ameliorating problems such as rapid soil erosion, but it may actually reduce the restoration of native plant populations either directly through competition or secondarily through fertilization and other environmental modifications (Hernandez 1973, Chapin and Chapin 1980). Thus community restoration should incorporate native plants whenever possible, particularly if it can be done at a lower cost.

Two approaches were used in this research. The first involved a series of studies of native plant population dynamics, especially seed sources and seedling establishment on both natural and artificial disturbances. These studies established the basic patterns of seed production, seed germination, and growth in native tundra plants, and some of the major controlling factors. The second line of research dealt with controls on total primary production, nutrient cycling, and the regulation of species and growth form composition in whole tundra vegetation. Underlying this research was the assumption that natural revegetation and recovery from disturbance are largely mediated by changes in nutrient cycling. Detailed descriptions of the methods have been published in the open literature.

POPULATION DYNAMICS AND GROWTH

The establishment of native plants on disturbed sites depends on survival through all stages of the plant life cycle. For the purpose of this research these stages were divided into separate studies of seed production, seed storage, seed germination, seedling demography, and seedling growth. We have dealt with two major community types: tussock tundra, which is the most widespread community type on the northern foothills of the arctic coastal plain, and vegetation of gravelly substrates which are the most difficult to revegetate if disturbed.

An initial hypothesis was that revegetation by native plants might be promoted by fertilizing undisturbed areas adjacent to disturbances, to increase seed production and presumably also seed input to the disturbance. Primary production of tussock tundra is strongly nutrient limited (Shaver and Chapin 1980), and flowering of E. vaginatum (the dominant species) is highly responsive to fertilization.

Eriophorum vaginatum seed is easily wind dispersed and should readily be blown from fertilized areas to adjacent disturbances. However, flowering varies greatly from year to year; in control plots at Eagle Creek it ranged over 3 orders of magnitude, from 0.04 ± 0.02 to 19.0 ± 3.9 inflorescences m^{-2} between 1976 and 1982. Although fertilization increased flowering, the effect was greatest in high flowering years such as 1978. In years of low flowering fertilization had little or no significant effect. Because of this annual variation the effects of fertilization are unpredictable, and one cannot depend on fertilization of undisturbed tundra to supply seed to adjacent disturbances. Fertilization of adjacent areas may be useful as a supplementary technique.

A second potential seed source for use in revegetation is the pool of ungerminated seeds that may accumulate in the soil of undisturbed tundra ecosystems. Large buried seed pools have been found in many other ecosystems (Grubb 1977, Grime 1979), but their size and significance in tundra were unknown before this work began. At both Eagle Creek (McGraw 1980) and at Kuparuk Ridge, Alaska (Gartner 1982, Gartner et al. 1983), significant numbers of Carex spp. and Eriophorum spp. seed were found in the upper 10-15 cm of organic soil of undisturbed tussock tundra. These seed germinate readily when the soil is exposed and warmed by removal of vegetation.

In experimental disturbances at Eagle Creek and Kuparuk Ridge, most of the seedlings that appeared on the plots came from buried seed (Chester and Shaver 1982, Gartner et al. 1983). The seedlings could not have come from external seed rain because most of them appeared on the plots in June or early July, before any seed were produced or shed by plants in the surrounding undisturbed tundra. The seedlings appeared without manipulation other than vegetation removal, suggesting that buried seed in the upper layers of soil are potentially an important source of seed in the restoration of disturbed sites using native plants.

The germination characteristics of native tundra seeds are typical of many disturbance-adapted species (Bliss 1971). In studies of Eriophorum vaginatum germination, in particular (Wein and MacLean 1973, Gartner et al. 1986), the seeds generally have no strong constitutive dormancy mechanisms. Instead, Eriophorum seed germinates most readily under the conditions likely to occur only on disturbed sites, i.e., at soil temperatures of 20°C or higher. Germination is increased in the light, in accord with the higher light intensities at the soil surface that prevail on disturbances. These studies support the conclusion that periodic disturbance represents an important opportunity for seed reproduction in natural tundra, that native plants have been selected to respond to disturbance by maintenance of a large pool of seeds that germinate readily, and that this adaptation is of potential use in developing management schemes (Gartner 1982).

The native seedlings that appear in experimental disturbances are not evenly distributed. Sedge (Eriophorum and Carex seedlings are much

more abundant on organic substrates, whereas native grass species are more evenly divided between mineral and organic areas (Gartner 1982, Gartner et al. 1983). This pattern has two principal causes. Initially the more important is the distribution of seeds in the seed bank. Few or no seeds are stored in the deeper mineral layers of soil. Thus the deeper the removal of vegetation and soil, the fewer the remaining seedlings. Grasses are rare or absent from the buried seed pool (McGraw 1980, Gartner et al. 1986), and their low seedling densities and even distribution may result from a dependence on external seed input. A second reason for the greater total abundance of seedlings on organic substrates is that seedling germination rates are higher and mortality rates lower there. When seeds of E. vaginatum and Calamagrostis canadensis were sown artificially on organic and mineral soils, the germination percentages were 3-5 times higher on the organic areas (Gartner 1982). Mortality rates were higher on mineral soils in part due to much greater needle ice action, which heaves seedlings out of the soil. Gartner (1982) found over 80% of seedlings heaved in the mineral soil after 2 years, but less than 20% heaved in the organic soil. Actual seedling mortality rates were lower but followed the same pattern.

Growth rates of the native grass and sedge seedlings are not significantly different on organic vs. mineral soils in the field. Thus the major differences in native plant cover after 4 years' growth on organic vs. mineral soils were due to seedling density differences rather than differences in growth rates (Gartner 1982).

The general conclusion from this portion of the research is that maintenance or replacement of the original organic mat is vital to the recovery of native graminoid species following disturbance, both because the organic mat already contains a major potential source of native plant seed and because it is the most favorable substrate for germination of seeds derived from external sources. This is in contrast to the normal practice of removing the organic mat and preparing a mineral seed bed, which is more favorable for both germination and growth of introduced non-native grasses (Mitchell 1979).

The study suggests that revegetation of stable moist organic soils in arctic Alaska can be accomplished with native species, and the following procedure should be tested:

(i) Organic soils should be stockpiled and then returned to the site following disturbance. At Kuparuk Ridge these contained sufficient Eriophorum and Carex seed to effectively colonize the disturbance. Other tundra organic soils have similar buried seed pools (McGraw 1980). Moreover, most tundra vascular plants are effective at vegetative propagation (Bliss 1971), so that any tillers or stems remaining alive in the organic material may enhance recovery. The organic mat provides a large reservoir of nutrients and acts as a slow-release fertilizer at the relatively warm temperatures that prevail following vegetation removal (Chapin and Van Cleve 1978). The organic mat also minimizes frost heaving of seedlings and, if moist, provides a favorable site for germination of sedge seedlings. In addition, the organic mat may harbor mycorrhizal fungi that enhance seedling growth.

(ii) Fertilizers should only be applied if Carex or grass are the predominant species that germinate, or if stimulation of moss cover is desirable. Eriophorum seedlings did not respond to fertilization.

(iii) If necessary, seed should be added to supplement the buried seed pool. Eriophorum is particularly suitable because seeds mature synchronously, plants seed prolifically (100-1000 germinable seeds m^{-2}) for several years following fire or on fertilized undisturbed sites (Wein and Bliss 1973), and seed can be easily hand-collected. Eriophorum seed is easily cleaned with small-seed cleaners and retains viability under refrigeration for at least 5 years (Gartner 1982). Calamagrostis canadensis, which is commercially available, also grew effectively where present, particularly on mineral soil or after fertilizer application. Calamagrostis and other native grasses, such as Arctagrostis latifolia and Poa arctica, offer potential as seed sources for revegetation. They are not prominent members of the undisturbed tundra, but are quite abundant in fertilized undisturbed tundra.

Revegetation practices that capitalize upon the demographic patterns of native plant species are likely to be more effective and less expensive than the current practice of repeated fertilization and seeding with exotic grasses.

Our more recent work has focused upon gravelly disturbed sites where past revegetation efforts have been largely unsuccessful. Pot tests showed that grasses seeded on these gravelly soils had very poor establishment and growth, even with regular watering. However, nutrient addition greatly enhanced growth. This explains why previous revegetation efforts required large repeated nutrient addition to get even moderate grass growth on such sites.

Unlike the highly organic tussock tundra, the heath community that normally occupies gravelly sites has little organic soil accumulation (< 2 cm) and almost no buried seed. Thus natural revegetation of such sites depends almost entirely upon current seed rain. The native species that could potentially occupy such sites occur naturally on river gravel bars, and we have documented the natural pattern of establishment in such sites. The major colonizers fall into two groups: (1) heavy-seeded species whose spread into new areas is dependent upon flood waters or relatively short-distance dispersal over snow. These species spread slowly into new habitat and have complex dormancy mechanism. Most are nitrogen fixers and grow well in gravelly soils when innoculated with appropriate microorganisms. The second group consists of light-seeded species such as willow and dwarf fireweed. These species arrive at distant disturbed sites at a moderate (but unpredictable) frequency. Thus seed rain is an undependable source of propagules in gravelly disturbed sites unless they are very close to a riparian seed source.

Water may be the main limitation to initial establishment of native species in gravelly disturbed sites. Nutrient addition actually inhibits germination and initial establishment by lowering the water potential of the soil solution and increasing drought stress. Surface treatments that create microsites of higher water availability (e.g. scarification to produce small troughs) enhance initial establishment.

We also planted out seedlings of native species that we thought would establish well in gravelly sites: willow, alder, and two legumes. These show high over-winter survival, but did not respond strongly to water or nutrient addition.

Thus it seems that native species have potential to revegetate gravelly disturbed sites but that the approach used must differ drastically from that in tussock tundra. In gravel sites the natural

seed supply is generally small and undependable and must be supplemented by sowing or planting of appropriate species. Surface preparation that creates moist microsites is highly desirable but early fertilizer addition is undesirable. Once plants begin to establish, no additional fertilization or other treatments appear necessary for site restoration.

NUTRIENTS, GROWTH, AND COMMUNITY REGULATION

Productivity of tundra vegetation is in general nutrient-limited (Haag 1974, McKendrick et al. 1978, Shaver and Chapin 1980), and nutrient availability has major consequences for the distribution and abundance of native tundra plants. As in virtually all terrestrial ecosystems, physical disturbance to tundra disrupts the normal patterns of nutrient availability (Gersper and Challinor 1975). To study the effects of disturbance-related changes in nutrient availability in tundra, we combined descriptive comparisons of disturbed and undisturbed sites with controlled manipulation of nutrient availability in fertilization experiments. The research was organized around two basic questions: First, how might an increase in nutrient availability by fertilization improve the recovery of native plant populations following disturbance? Second, in the later stages of recovery how might manipulation of nutrient availability affect the composition of the native plant community?

Fertilization has various effects on native plant growth, depending on species, time since disturbance, and type of vegetation. On recently disturbed sites (less than 5 years old), fertilization increased growth of native Carex and grass seedlings but not of Eriophorum seedlings (Gartner et al. 1983). There was no difference in responsiveness between mineral and organic substrates. However, after 10 years' recovery on a bulldozed organic site at Eagle Creek, Chapin and Chapin (1980) found no long-term fertilization effect. Cover by native species, primarily E. vaginatum, was nearly 100% in both fertilized and unfertilized plots, whether or not seed of various non-native grass species had been sown following the disturbance.

The lack of a long-term fertilization effect on native plant recovery on disturbed sites is consistent with the long-term vegetation responses on unmanaged disturbances such as vehicle tracks. Production and biomass of native plants on 7-10 year old vehicle tracks is as much as 2-5 times that of undisturbed tundra (Chapin and Shaver 1981). The high productivity of old disturbed sites is accompanied by an even greater increase in annual uptake of N and P (Wein and Bliss 1974, Chapin and Shaver 1981). The native vegetation of these sites is dominated by rapidly growing graminoids and occasionally some deciduous shrubs, all characteristic indicators of high nutrient availability.

Both the fertilization experiments and the descriptive studies of older disturbances suggest that nutrient availability is relatively non-limiting after about 5 years on a disturbance if the site is relatively moist and covered with an organic soil. Fertilization thus may improve native plant recovery in the first year or two but there is no need to continue the application except perhaps on dry mineral soils.

In fact, fertilization may cause a shift away from normal patterns of plant nutrient uptake. In Eriophorum vaginatum, acid phosphatase activity at the root surface is positively correlated with soil organic matter, suggesting a well-developed ability to use organic phosphorus as

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a source of inorganic phosphates. In potted plants, $\underline{E.\ vaginatum}$ growth rates were twice as high on organic than on mineral soils, despite nonsignificant differences in the field (Gartner 1982). The acid phosphate enzyme system is suppressed by the presence of inorganic phosphate. Addition of inorganic fertilizers or removal of organic soil horizons may reduce success of native plants by suppressing an efficient nutrient uptake mechanism and altering competitive interactions in phosphorus uptake.

Once an adequate cover of native species is established, restoration of a natural community must involve manipulation of the relative abundances of species and growth forms. Nutrient availability is a key variable in this process, the major problem being that nutrient cycling rates are very rapid on old disturbances. Fertilization experiments have shown that when N and P are added to undisturbed tundra, the vegetation becomes more like that on old disturbances (Shaver and Chapin 1980 and unpublished). Thus management of older disturbances should be focused on slowing down nutrient movement and decreasing nutrient availability.

Nutrient cycling on disturbed sites differs from undisturbed tundra in several aspects. Possibly one of the most important of these is soil temperature, which averaged about 2°C higher at 10 cm depth in old vehicle tracks than in undisturbed tundra (Chapin and Shaver 1981). Chapin and Shaver (1981) estimated the effects of a 2°C temperature change on individual nutrient cycling processes and concluded that although the soil temperature difference was significant it could not alone explain the higher productivity in vehicle tracks. Other factors such as differences in the rate of soil water and nutrient movement are now under investigation as explanations for the differences between disturbed and undisturbed sites.

Evidence for greater nutrient movement in vehicle tracks comes from a litter bag experiment in which both N and P immobilization by $\underline{Eriophorum}$ litter was greater by a factor of 4-8 in wet vehicle tracks than in mesic undisturbed tundra. This greater immobilization is accompanied by much lower phosphatase and cellulase enzyme activity and higher soil respiration rates (Herbein 1981). Furthermore, there is a more complete decomposition of cellulose in the vehicle track, as indicated by the lower ratios of exocellulase:endocellulase activity and the higher proportion of cellulose-derived CO_2 evolved from track soils.

These results suggest that nutrient availability to plants might be reduced by management attempts to (1) lower soil temperature and depth of soil thaw, (2) increase nutrient immobilization in litter, (3) decrease soil oxygen, and (4) decrease both surface and subsurface soil water movement. All of these objectives might be achieved at least in part by increasing the thickness of the upper soil organic mat, and providing carbon-rich and nutrient-poor organic litter to the soil. This could be accomplished first by preserving as much as possible of the original organic soil and second by adding sawdust or some other heavy mulch to old disturbances. Experimental attempts to reduce nutrient availability by adding corn starch and sugar to undisturbed tundra have suggested but not confirmed that this approach should work (Shaver and Chapin 1980, Marion et al. 1982). The long term goal is the creation of conditions that are more favorable for native species and more typical of the normal nutrient-limited tundra vegetation.

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