Recovery of Productivity and Species Diversity in Tussock Tundra following Disturbance

Milan C. Vavrek, Ned Fetcher, James B. McGraw, G. R. Shaver, F. Stuart Chapin III, and Brian Bovard

Abstract

Tundra ecosystems appear to recover slowly from disturbance, but little long-term data concerning plant diversity has been available. We examined recovery of tundra vegetation in Alaska, U.S.A., 23 yr after fire and 24 yr after bulldozing. Primary productivity, depth of thaw, and vascular plant diversity were compared between disturbed and undisturbed tundra to determine whether recovery was complete. Productivity, species richness, and diversity did not differ between burned and unburned plots. Depth of thaw, however, remained greater in burned relative to unburned plots. In contrast, depth of thaw was the only characteristic that did not differ between bulldozed and control plots. Productivity and species richness were greater in bulldozed plots, but diversity was less than control plots. The differences between the two disturbances suggest that, ultimately, recovery depends more on the impact of disturbance on vegetation than changes in the abiotic environment. Vegetative propagules persisted in the soil after fire, but not bulldozing. Therefore, recolonization after fire included plants from the seed bank and vegetative propagules. Vegetation on bladed plots was dominated only by seed bank species. Thus, more than two decades after disturbance, recovery of tundra vegetation appeared to be a function of the nature of the disturbance.

Introduction

A common statement about tundra ecosystems is that they are "fragile" and slow to return to their original condition once disturbed (Billings and Mooney, 1968; Bliss, 1971). However, few studies have quantified long-term recovery to justify this statement. In some sites where secondary succession has been examined, plant cover returns to or exceeds predisturbance levels within only 6 to 10 yr (Chapin and Chapin, 1980; Fetcher et al., 1984; Racine et al., 1987; Walker et al., 1987; Walker and Walker, 1991; Landhauser and Wein, 1993). Primary production on disturbed sites frequently exceeds that on undisturbed sites as a result of changes in surface albedo, increases in soil temperature, and subsequent indirect effects of increased nutrient availability. Species richness and diversity appear to recover more slowly, although the evidence is more anecdotal than quantitative.

In this study, we examined two sites 23 yr after disturbance. Both sites occurred in cottongrass tundra communities, representative of much of northern circumpolar tundra (Britton, 1966; Wein and Bliss, 1974; Chapin and Chapin, 1980). In addition to cottongrass (Eriophorum vaginatum), dwarf shrubs (e.g., Ledum palustre, Vaccinium vitis-idaea, V. uliginosum, and Betula nana) represent a substantial portion of areal cover (25–45%; Wein and Bliss, 1973, 1974; McGraw and Shaver, 1982). We compared primary productivity, species diversity and depth of thaw within the disturbed sites relative to adjacent undisturbed tundra, and relative to data taken previously at both sites. Our objective was to determine whether recovery of the vascular plant community was complete after more than two decades. The first site, Mile 107 Elliott Highway, Alaska, was disturbed by fire in late June 1969 (Wein and Bliss, 1973). At the second site, Eagle Creek, Alaska, surface soil and vegetation (including roots and rhizomes) were removed with a bulldozer in mid-June of 1970 (20 × 50 m; Chapin and Chapin, 1980). After removal of the vegetation, organic material remained to a depth of 10 to 20 cm above the mineral soil (Chapin and Chapin, 1980). Short-term effects of these disturbances on primary productivity and vegetative cover at these two sites were reported by Wein and Bliss (1973) and Chapin and Chapin (1980). A second set of observations of the burned site, completed 13 yr after the fire, was reported by Fetcher et al. (1984). The Eagle Creek site was re-measured in 1981 by F. S. Chapin III and those results are also reported here.

Methods

Aboveground biomass of all vascular plant species was removed within 0.05-m² circular quadrats. Sampling occurred during the last 2 wk of July 1993. Sampled quadrats were located randomly along 30-m transects (n = 60: 3 transects × 10 quadrats/transect × 2 sites [burned/unburned]) at the Elliott Highway site (65°18'39"N, 151°55'0"W). At Eagle Creek (65°26'0"N, 145°30'0"W), 10 quadrats were selected along one 30-m transect in undisturbed tundra and 2 quadrats (also 0.05-m²) were placed...
within each of 5 randomly-chosen plots within the bulldozed area \((n = 20)\). Plots rather than a transect were used in the bulldozed area as the area had been subdivided previously in other research. Sampling procedure and sample size followed Fetcher et al. (1984), which allowed for comparisons of vegetation recovery through time. In addition, species area curves were used to confirm that the number of quadrats was sufficient to detect the majority of species present. Quadrats were considered random samples of the larger community as quadrat location along the transects was not the same across years. The original transects were also placed randomly. Species were separated and the current year’s growth was clipped from plants based on stem color and bud scars (“tussock plucking” described in Wein and Bliss [1974] and Shaver and Chapin [1980]). Biomass of all vascular plant species was included. Productivity values were underestimated as current year’s litter was not collected. Biomass was oven-dried \((65^\circ C)\) and weighed. Differences in productivity between disturbed and undisturbed vegetation across time were compared with a fixed-effects, 2-way analysis of variance (SAS JMP, Statistical Analysis Systems Institute, 1992). Each site was analyzed separately.

Vascular plant diversity was calculated using indices \(N_1\) and \(N_2\) from Hill’s family of diversity indices (Hill, 1973). These relatively simple indices are related to the Shannon-Weiner index and Simpson’s index and meet basic mathematical and ecological assumptions (Hill, 1973; Peet, 1974; Routledge, 1979). \(N_1\) represents the reciprocal of the geometric mean of proportional species abundance:

\[
N_1 = e^{-\sum_{i=1}^{n} p_i \ln p_i},
\]

where \(p_i\) is dry weight as a proportion of total dry weight for species \(i\). \(N_2\) is the reciprocal of the arithmetic mean proportional abundance:

\[
N_2 = \frac{1}{p_1^2 + p_2^2 + \ldots + p_n^2}
\]

where \(n\) is the number of species sampled. \(N_1\) is more sensitive to the presence of rare species while \(N_2\) is more sensitive to changes in abundance of common species. Means and standard errors for both species richness and diversity were calculated using Tukey’s jackknifed procedure to resample quadrat values (Sokal and Rohlf, 1995).

Depth of thaw was measured at the same time as cover (latter half of July 1993) by inserting a metal rod \((2\, \text{mm diameter})\) into the soil to the depth of permafrost (Fetcher et al., 1984) along the transects and plots used to measure primary productivity \((n = 102 \times 34\, \text{samples/transect})\) at Elliot highway; \(n = 10\) at Eagle Creek. The thawed portion of the soil contains actively growing roots and is the site for water and nutrient uptake. Thus, the thawed portion of the soil may influence rates of productivity. Analysis of variance was used to compare mean depth of thaw between disturbed and undisturbed vegetation (SAS, 1992).

**Results and Discussion**

The greater productivity of burned relative to unburned plots observed in 1982 (Fetcher et al., 1984) had disappeared by 1993, when no difference in productivity was found \((n = 30;\, \text{disturbance} \times \text{year interaction: } P = 0.003;\, \text{Fig. 1a})\). Productivity of the bulldozed site remained greater than that in control plots after 23 yr \((n = 10;\, P = 0.02;\, \text{Fig. 1b})\). Productivity of the bulldozed site did not change with time \((P = 0.36)\), nor did it change differentially over time as a function of the presence or absence of disturbance \((P = 0.87)\).

Recovery of species richness within disturbed sites also depended on the type of disturbance. Burned tundra had the same number of species as unburned tundra in 1993 (Tukey’s jackknifed means ± SE, pooled across transects: 14.9 ± 1.3 and 12.93 ± 1.3, respectively). Two shrubs, Alnus crispa and Arctostaphylos uva-ursi, however, did not become “re-established” within the burned plots. Shrubs in general may have greater difficulty becoming established after fire as a result of low numbers of buried viable seed and low germination rates (McGraw, 1980; McGraw and Vavrek, 1989). An additional shrub, Andromeda polifolia, and an herb, Petasites frigidus, were observed in control plots in 1982, but were absent from all plots in 1993. Petasites has been shown to resprout after fire (Landhausser and Wein, 1993) and was expected to re-appear. The absence of these two species may be the result of sparse or transitory distribution rather than disturbance (frequency of A. polifolia in control plots was 10% in 1982 and 0% in 1993; frequency of P. frigidus in control plots was 3.3% in 1982 and 0% in 1993). Similarly, the absence of Betula nana from control plots relative to bulldozed plots in 1993 may be attributed to sampling. Betula nana was present in only one plot in both the bulldozed and undisturbed tundra in 1981. On average, however, bulldozed plots contained more species than control plots in 1993 (jackknifed mean ± SE: 11.8 ± 1.2 vs. 7.0 ± 0.0). A grass species, Salix sp. (the grass and Salix species were sterile and could not be identified with certainty), and Eriophorum angustifolium were present in bull-
dozed plots in 1993 but absent from control plots. While these differences through time may have occurred because of sampling error (i.e., pseudoturnover), species richness (and diversity) is expected to be the same because identical sampling methods were employed, using quadrats re-located within meters of the original plots. Additionally, diversity indices sensitive to frequent and infrequent species were used. Thus, differences caused by infrequent species will not affect conclusions regarding recovery.

Diversity values of the burned vascular community were identical to those of unburned vegetation 24 yr after disturbance (Fig. 2a, b). Both indices showed that diversity decreased in unburned plots and increased in burned plots between 1982 and 1993. This may reflect gradual successional change in unburned plots and decreasing dominance of a few species in burned plots. In contrast, species diversity within bulldozed plots did not recover after 23 yr. Diversity did not increase in bulldozed plots and diversity of control plots decreased only slightly (due in part to loss of two infrequent species, Betula nana and Andromeda polifolia, from the sample). Thus, diversity of bulldozed vegetation remained significantly lower than control plots in 1993 (Fig. 2c, d).

Depth of thaw remained greater 24 yr after the fire in the burned area relative to unburned plots (mean ± SE: 45 ± 1 and 36 ± 1 cm; n = 102; P < 0.001). No data is available for depth of thaw before the fire. Therefore, it is not known if differences may have predated the fire. Transects, however, were originally paired across the fire boundary within 50 m of each other. Additionally, the difference in depth of thaw between burned and unburned tundra decreased since 1982 (P = 0.04, disturbance × year interaction). The depth of thaw was 35% greater in burned relative to unburned sites in 1982 and only 26% greater in 1993. There was no difference in depth to permafrost between the bulldozed and control tundra sites (mean ± SE: 40 ± 2 and 40 ± 2 cm; n = 10; P = 0.86) in 1993.

Although depth of thaw remained different for adjacent burned and unburned plots after 24 yr, this long-term environmental effect of fire appeared to have minimal effects on the vegetation since recovery of the plant community was nearly complete at the Elliott Highway site based on net annual productivity, species diversity, and species richness. Short-term studies have shown a relationship between high rates of vegetative cover or productivity with greater active layer depths after disturbance (Johnson and Viereck, 1983; Racine et al., 1983). Individual species may be responding differentially over the long-term to the differences in the active layer, however. For example, Eriophorum vaginatum roots forage in the entire active layer (Wein and Bliss, 1974; Chapin et al., 1979) and may be able to obtain additional resources at greater depths relative to shallow rooting species. Thus, a persistent increase in the active layer may prolong dominance by E. vaginatum. Tundra vegetation of burned plots, therefore, had recovered from fire within 24 yr of the original disturbance in terms of primary productivity, species richness, and species diversity. In contrast, differences in productivity, species richness and diversity in response to removal of aboveground vegetation with a bulldozer persisted after 23 yr.

The differences in recovery after the two types of disturbance may be attributed to vegetation persistence, recolonization and undisturbed community composition. Recovery from bulldozing depended primarily on recolonization from the deep seed bank (i.e., seeds present in the lowermost 10–20 cm layer of organic soil remaining after bulldozing) which encompassed few species, whereas plants sprouted from rhizomes and the shallow
seed bank in the burned tundra (fire in tundra removes less than 5 cm of wet organic matter; Racine, 1981). In bulldozed plots in 1981, Eriophorum vaginatum and Carex bigelowii, two species that have long-lived and deeply-buried viable seeds, accounted for 98% of the productivity and continued to dominate the community, representing 80% of the productivity in 1993. Eriophorum vaginatum and C. bigelowii together represented only ca. 38% of productivity in control plots, but undoubtedly served as an additional seed source for bulldozed plots. Other studies have also shown the successful and predominant colonization of these two species from seed banks (McGraw, 1980; Gartner et al., 1983). Calamagrostis canadensis also invaded these disturbed sites and is one of the two common invaders (with Epilobium angustifolium) of disturbed sites in mesic tundra (e.g., Cody, 1964, 1965; Hernandez, 1973; Chapin and Chapin, 1980; Landhauser and Wein, 1993). Seeds of Calamagrostis, and the sterile Salix and grass, were probably dispersed by wind into the disturbance. Colonization may also have occurred via vegetative growth from established plants located just beyond the disturbance boundary. Widespread colonization by vegetative growth is unlikely, however, considering the size of the disturbance (1000 m²) and slow growth rates in tundra.

A large number of seedlings, primarily E. vaginatum, were also initially recruited into the burned community. Most seedlings did not persist beyond 2 yr (Wein and Bliss, 1973), although flowering of E. vaginatum was stimulated by fire which resulted in a second wave of recruitment from seed (McGraw and Shaver, 1982). Immediately after the fire, rhizomatous species, E. vaginatum and Carex bigelowii, dominated the community. In addition to being rhizomatous, E. vaginatum forms tussocks which are resistant to fire (Ratliff, 1959; Racine et al., 1987). Previously dominant shrub species, Ledum palustre and Vaccinium uliginosum, were not able to regrow as readily and represented a reduced proportion of the biomass (Wein and Bliss, 1973). Thirteen years after the fire, E. vaginatum’s dominance had grown representing ca. 50% of dry weight biomass. The fire apparently released E. vaginatum from competition (e.g., Racine et al., 1987) and provided a short-term nutrient pulse (Wein and Bliss, 1973). By 1993, the proportion of E. vaginatum had returned to preburn levels (24%), but the proportion in control plots had also decreased dramatically to only 3% of total biomass (most of the decline occurring between 1970 and 1982). The decline in biomass of E. vaginatum tussocks may have been the result of continued invasion and thus increased interspecific competition within tussocks (Fetcher and Shaver, 1982; Fetcher, 1985). Ledum palustre had returned to prefire levels by 1993, but appeared to be increasing in the control plots as well. The decrease in biomass of E. vaginatum and increase in L. palustre biomass may also have been stimulated by climatic warming. Chapin et al. (1995) found similar changes in biomass in tussock tundra near Toolik Lake, Alaska, in response to an experimental increase in ambient temperature. Vaccinium uliginosum was also present as a greater proportion of the recovering community, but achieved only 60% of the control values by 1993. Thus 24 yr after the fire, the vascular plant community had virtually recovered in that species composition and abundance between burned and unburned plots were similar. Exceptions included greater proportions of E. vaginatum and Calamagrostis canadensis, and reduced V. uliginosum and Carex bigelowii within burned plots. These results are consistent with findings by Landhauser and Wein (1993) who found (in an arctic treeline site) increased proportion of biomass represented by E. vaginatum in burned plots, but found an increase in L. palustre as well.

Differences in recovery between disturbance types could be explained by site differences. Racine (1981) demonstrated that community type played an important role in recovery rates. Control plots in 1993 at Eagle Creek had lower species richness and productivity than the Elliott Highway site. Measurements of productivity have generally shown that the two sites were equivalent (Wein and Bliss, 1974). Slope (3–5°), elevation (700–730 m) and decomposition rates (1.59–2.17% weight loss of filter paper after one year [Wein and Bliss, 1974]) were also similar as well as depth of thaw (37–40 cm). Thus, while vascular plant community and environmental differences between the two sites may have influenced the rate of recovery after disturbance, general characteristics of both sites are similar.

Is the tundra a fragile ecosystem? The answer is equivocal. The completeness of the recovery of arctic tundra vegetation following disturbance clearly depends on the nature of the disturbance (Fig. 3). After one decade, the burned and bulldozed communities remained very different from controls and similar to each other, but a second decade revealed a contrast in successional patterns. Recovery of bulldozed plots was exceedingly slow and will probably take several more decades, whereas the burned site has nearly returned to its preburn condition. This contrast appears to have more to do with the effect of the disturbance on plants than on the physical environment. Removal of rhizomatous species apparently slowed recovery at the bulldozed site. Tundra species have mechanisms allowing them to persist through many kinds of naturally occurring disturbances (McGraw and Shaver, 1982). Tundra vegetation may correctly be viewed as fragile, when subjected to disturbances unlike those with which they have evolved (i.e., bulldozing).

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