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Vegetation Development over 25 Years without Grazing on Sagebrush-dominated Rangeland in Southeastern Idaho

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Abstract

Data from permanent vegetation transects, established on the Idaho National Engineering Laboratory Site in 1950, were analyzed to determine what changes had taken place in the vegetation complex over the past 25 years in the absence of grazing by domestic livestock. Cover of shrubs and perennial grasses has nearly doubled. Shrub cover in 1975 was 154% greater than in 1950; this change was almost entirely due to increases in cover of big sagebrush between 1957 and 1965. Cover of perennial grasses increased exponentially over the 25-year period, from 0.28% in 1950 to 5.8% in 1975. This was paralleled by significant increases in density and distribution of the four most important grasses on the study area. The 20-fold increase in perennial grass cover has not been at the expense of the shrub overstory. There was no obvious correlation between trends for perennial grass cover and precipitation patterns. Rather, the exponential growth is believed to reflect the availability of seeds as formerly depleted populations increase in size. No evidence of seral replacement, as predicted by classical succession, was found. The data seem more consistent with the "initial floristics/relative stability" concepts of vegetation development.

A widely held generalization about recovery of overgrazed rangelands following protection from grazing is that provided by classical successional theory: Vegetation development will be directional and predictable, leading to the re-establishment of a climax community (Stoddart et al. 1975; Heady 1975). If such a view is valid, then it becomes imperative that range scientists and managers know (a) the expected direction and how individual species will respond, (b) the expected time required for recovery, and (c) the nature of the climax community. If, on the other hand, the classical view is not valid, it is imperative that range scientists and managers seek appropriate alternative models and understand their implications for management and the interpretation of results of experiments as well as managerial decisions.

Past studies of vegetal dynamics on exclosures or other protected areas do not provide a clear choice regarding the validity of the classical model. McClean and Tisdale (1972) estimated that from 20 to 40 years were required for rough fescue and ponderosa pine ranges to recover to excellent condition under full rest. The developmental trends were generally similar across three sites in each range type, and the authors were able to generalize about the individual responses of a number of shrub, forb, and grass species. Thus, the trends appeared to be both directional and predictable. In contrast, Rice and Westoby (1978) found that vegetal changes on protected areas in semidesert shrub vegetation of northern Utah were neither consistent across sites nor predictable, and they concluded that the classical concept of range succession was not useful in interpreting the results of excluding grazers from those ranges. Similar results were reported for Texas ranges by Smeins et al. (1976), who found that vegetation change over 25 years had been primarily an adjustment in relative dominance of species rather than species replacement. They concluded that woody species, once established, tend to increase to a point of stabilization under complete protection, and they stated, "It seems probable that after each round of disturbance, natural or manmade, community development tends toward a relatively stable community, but fidel-

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ity of reestablishment of the same community composition on the same site after each disturbance is suggested to be relatively low." This is essentially a restatement of the initial floristics/relative stability hypothesis of vegetation development (Egler 1954; Niering and Goodwin 1974), which has found recent support among studies from a variety of ecosystems (Henry and Swan 1974; Niering and Goodwin 1974; Lyon and Stickney 1976).

In 1950 and 1957, 2,315 km² of semiarid, cold desert rangelands were purchased or withdrawn from the public domain to form the National Reactor Testing Station, which was later designated the Idaho National Engineering Laboratory (INEL) Site. In 1975, the site became a National Environmental Research Park and is presently administered by the U.S. Department of Energy. Vegetation studies were initiated on the Site in 1950 with the establishment of 99 permanent sample plots along two perpendicular transects. The original vegetation survey was established to determine what types of vegetation occurred on the Site and to provide baseline data for later assessment of the effects of nuclear reactor testing. Although there have been no detectable effects of radioactivity on the vegetation (Harniss and West 1973a), the transects have been maintained for ecological studies. Transect data were collected in 1950, 1957, and 1965, and trends in vegetation development through 1965 have been described by Harniss (1968) and Harniss and West (1973a, b). The present study was initiated in 1975, at which time the transect data were collected for a fourth time. The purposes of the study were to determine what changes had taken place in the vegetation complex over the past 25 years and to compare the trends for the 1965-1975 decade with those prior to 1965. Although the study does not provide a rigorous test of the validity of the classical successional model, the results raise further questions of its appliability and suggest that alternative models may be more useful for interpreting the results of such studies.

Study Area

The INEL Site lies along the western edge of the Upper Snake River Plain near the southeastern foothills of the Lost River and Lemhi mountain ranges. The climate is strongly influenced by the mountain ranges to the west. Average annual precipitation for the 1950-1978 period was 21 cm. Precipitation tends to be relatively uniform throughout the year except for a strong peak early in the growing season and a low during July (Fig. 1). On the average, 40% of the annual precipitation falls during April, May, and June. Mean annual temperature is about 5.5°C. Winters are cold with snowcover persisting from December through March; summers are hot, and temperatures may reach over 38°C. The frost free period averages 91 days; a minimum of 68 days and a maximum of 123 days have been recorded. Average elevation of the study area is about 1,490 m.

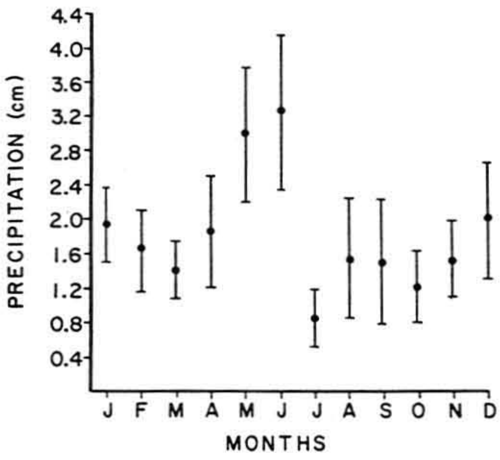

Fig. 1. *Annual precipitation pattern for the Idaho National Engineering Laboratory Site. Points represent averages for the period, 1950–1978. Vertical bars are 95% confidence intervals.*

The topography of the study area is flat to gently rolling, with occasional lava outcrops. Although the area is underlain by some 1,500 m of basalt, most INEL Site soil is derived from older silicic volcanics and paleozoic rocks from the surrounding mountains and buttes (McBride et al. 1978). Soils of the study area are primarily aeolian sandy loams and loess, but some alluvial deposits which are gravelly on the surface and underlain by a sandy loam occur along the Big Lost River (McBride et al. 1978). These soils would all be classified as *Aridisols* (USDA 1960).

The dominant and most conspicuous plant on the INEL Site is big sagebrush (*Artemisia tridentata* Nutt.). Most of the big sagebrush on the Site is *A. tridentata* subspecies *wyomingensis* (Winward and Tisdale 1977), but scattered populations which key (Winward and Tisdale 1977) to *A. tridentata* subspecies *tridentata* occur on deeper soils. Other conspicuous shrubs include green rabbitbrush *(Chrysothamnus viscidiflorus* (Hook.) Nutt.), prickly phlox *(Leptodactylon pungens* (Torr.) Nutt), and snakeweed *(Gutierrezia sarothrae* (Pursh) Britt. & Rusby.). The most important grasses are bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J.G. Smith), thick-spiked wheatgrass (*Agropyron dasytachyum* (Hook.) Scribn.), Indian ricegrass (*Oryzopsis hymenoides* (R. & S.) Ricker) and needle-and-thread grass (*Stipa comata* Trin. & Rupr.). Communities dominated by shadscale (*Atriplex confertifolia* (Torr. & Frem.) Wats.) or winterfat (*Ceratoides lanata* (Pursh) J.T. Howell) occur in depressions and open areas where soil is more alkaline. The most important grasses in these communities are bottlebrush squirreltail and Great Basin wildrye (*Elymus cinereus* Scribn. and Merrill.).

The early grazing history of the Site was not well documented, but some generalizations are possible. Much of the upper Snake River Plain has been grazed by sheep and cattle since the late 1800's (Harniss 1968). The area was used extensively for spring/fall sheep grazing. In addition, the Site was crossed by a trail used for large herds of cattle moving to eastern markets during the late 1870's (USAEC 1966). Harniss and West (1973a) concluded that competition for forage resulted in severe overgrazing prior to 1950. During World War II, 700 km² was closed to grazing for use as a Navy gunnery range. In 1950, grazing was excluded from 445 km² of the southcentral portion of the Site, and in 1957 an additional 240 km² were closed to livestock use (Harniss and West 1973a).

Methods

Collection of data followed the procedures established by D.L. Goodwin in 1950, as described by Harniss (1968), with minor modifications. Details of the overall sampling design and techniques can be found in Anderson et al. (1978). Permanently marked sample plots were established in 1950 at 1.6 km intervals along two perpendicular lines that transect the Site from north south and from east to west. Each plot consists of two 15.24-m transect lines and 20 density/frequency quadrats (0.3 × 1 m). Density and frequency of all perennial species were recorded in each of the 20 quadrats. Cover was determined by measuring the length of a tape intercepted by the crown of shrub species and the basal area of perennial grasses. No cover measurements were made for other species. In this study, cover is expressed as a percentage of the total transect length for a plot or sample of plots. Data were collected in 1950, 1957, 1965, and 1975. Because above-average precipitation was received during the 1975 growing season, data for the plots included in the present study were collected again in 1978 in an effort to determine the extent to which trends indicated by the 1975 data might be attributable to favorable growing conditions.

The original sampling design placed definite limits on the analyses that could be made. Density and frequency data were collected for all perennial species; however, these statistics alone are of limited value for assessing importance of the various species in the community, especially when different life forms are included in the analysis (Mueller-Dombois and Ellenberg 1974). Cover is thought to provide a more meaningful measure of the ecological significance of a species (Daubenmire 1968). Unfortunately, cover data were available only for shrubs and perennial grasses. We therefore chose to limit the analyses to these plants. They are by far the most abundant and important plants on the study area, and it seems unlikely that inclusion of perennial forbs would significantly alter the interpretation or conclusions.

For statistical analysis, it was necessary to assume that the original sampling design would provide random, representative samples of the vegetation. Because the original transect plots were established systematically, vegetation would have to be randomly distributed for such an assumption to be valid for the entire area. Clearly, this is not the case; distinct plant communities have been recognized by earlier investigators (Harniss 1968; Harniss and West 1973a; McBridge et al. 1978). However, it did seem reasonable to assume that the sample plots were established without bias and that data from plots within a vegetation type having a similar history were random samples of a relatively homogeneous plant community in which individuals were randomly distributed. Harniss and West (1973a) concluded that a large central portion of the Site was potentially a big sagebrush/bottlebrush squirreltail climax. We chose plots on the basis of overall floristic similarity from this and adjacent areas to form a sample of 36 plots, which provided a relatively large sample for the statistical analyses. Most of the plots fell within the areas designated as the *Artemisia tridentata/Chrysothamnus viscidiflorus/Sitanion hystrix* type or the *Artemisia tridentata/Oryzopsis hymenoides/Stipa comata* type by McBride et al. (1978). Seven of the 36 plots were within the area that remained open to grazing between 1950 and 1957. The other plots were all within the area which has not been grazed by domestic livestock since 1950.

The question that we asked statistically was: Has there been a significant change over the past 25 years (1950-1975) in the quantity (cover or density) of a particular species or group of species across the 36 plot sample? A randomized block analysis of variance was used to test for significance of overall trends. The Newman-Keuls multiple range test (Zar 1974) was used to compare mean values for a particular year with the corresponding values for each other sample date. We chose $\alpha = 0.05$ to indicate statistical significance. For individual species comparison, only those plots on which the species occurred were considered as samples. Thus, sample size was smaller than 36 in many cases.

The data revealed some apparent discrepancies in species identification by the various investigators over the years, especially among the wheatgrasses and bluegrasses. Therefore, species within each of these groups were lumped for the present analyses.

Results

In 1950, the 36 sample plots were dominated heavily by big sagebrush. Perennial grass cover amounted to only 0.28%; cover by shrub species was 17.2% with big sagebrush contributing 89% of that total (Fig. 2). Total cover of shrubs and perennial grasses was only 17.5%. These data indicate that the range was in fact in a deteriorated condition at the time grazing was excluded from the area. By 1975, total cover of shrubs and perennial grasses had nearly doubled; shrub cover was 154% of the 1950 value, and grass cover had increased to about 20 times its original value.

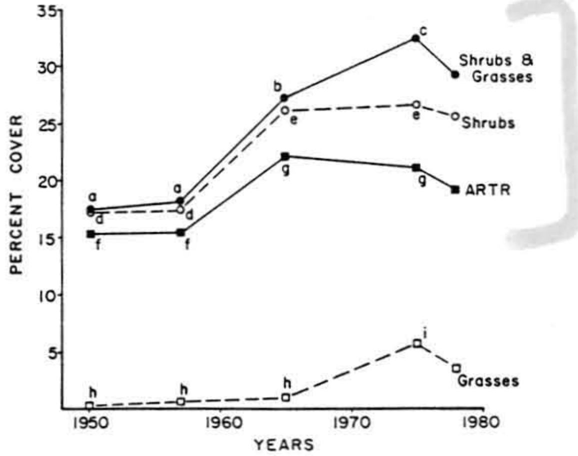

Fig. 2. *Cover of shrubs and perennial grasses for the 36-plot sample. On each line, different letters indicate that the corresponding means are significantly different at $\alpha = 0.05$. ARTR =* Artemisia tridentata.

Between 1950 and 1957, there was no significant change in shrub cover, but between 1957 and 1965, a 42% increase in the cover of big sagebrush was observed (Fig. 2). Cover of green rabbitbrush also appeared to increase during that period, but the difference was not statistically significant. The plot-to-plot and year-to-year variances in cover values for green rabbitbrush were much higher than for big sagebrush, and it is possible that actual trends for the former species were masked by the large error terms. For example, the coefficient of variation for big sagebrush across the 36 sample plots for 1965 was 39.9%; for green rabbitbrush it was 134%. The higher variability of the green rabbitbrush cover data suggests a higher turnover within the population for that species. There was no increase in shrub density between 1957 and 1965; therefore, the increase in cover of big sagebrush must have been due largely to an increase in the size of the canopy of individual plants. Precipitation during the 1957–1965 period was much more favorable than it was between 1950 and 1957 (Fig. 3). Thus, the increase in shrub cover may have resulted from more favorable moisture conditions (Harniss and West 1973b), or it may simply reflect increases in canopy size of maturing plants or release from grazing pressure. No significant changes in shrub cover were observed after 1965.

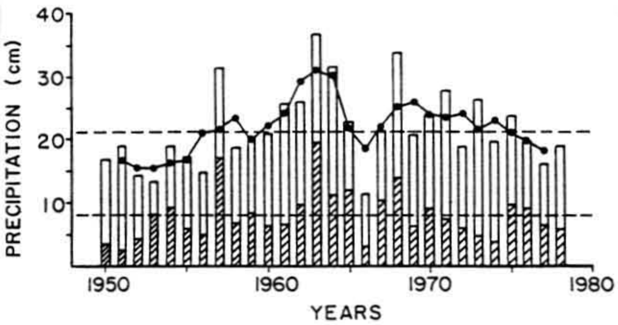

Fig. 3. *Yearly precipitation for the Idaho National Engineering Laboratory Site, 1950–1978. Vertical bars indicate annual totals; hatched portions represent precipitation falling during April, May, and June. Top dashed line is mean annual precipitation for the period; bottom dashed line is mean April–June precipitation. Solid line connects three-year sliding averages.*

Although the analysis of variance revealed no significant increase in total grass cover between 1950 and 1965 (Fig. 2), regression analysis indicated that total grass cover has increased exponentially since 1950 (Fig. 4). This suggests that the increases noted between 1950 and 1965 are real. A large increase in perennial grass cover was noted between 1965 and 1975 (Fig. 2), which resulted from a significant increase in the cover of all of the most important grasses on the area (Fig. 5).

The 1975 growing season was cool and above average in precipitation (Fig. 3), resulting in high productivity over the area. In contrast, the 1978 season was hot and quite dry. Thus comparison of the cover values for 1975 with those for 1978 should provide an indication of the effects of difference in precipitation on cover values. Figures 2 and 5 show that in all cases cover values for perennial grasses were lower in 1978. However, substitution of the 1978 data for the 1975 data does not affect the overall indication of trends. For each grass species (Fig. 5), the 1978 values were significantly higher than the 1965 (or earlier) values. Similarly, total grass cover in 1978 was significantly higher than the 1965 value, but there was no significant difference between total shrub cover in 1978 compared to that for 1965. In the case of bottlebrush squirreltail

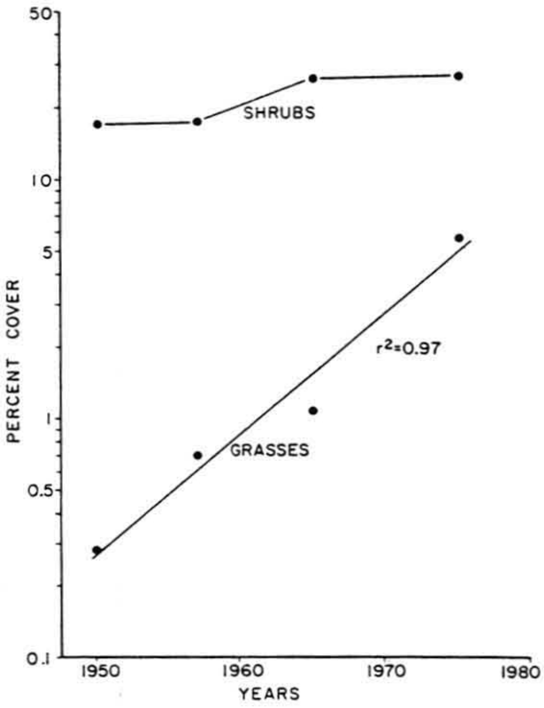

Fig. 4. *Semi-logarithmic plot of cover for shrubs and perennial grasses.*

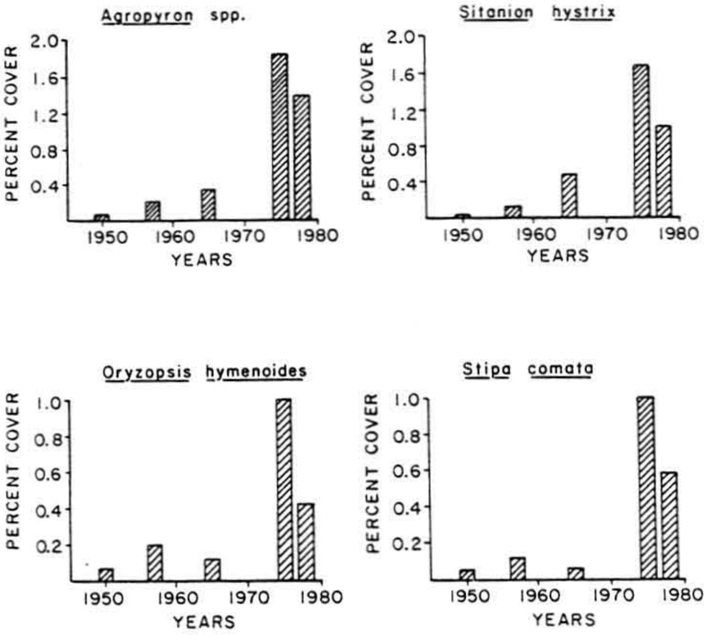

Fig. 5. *Trends in cover for the four dominant perennial grasses.* Agropyron spp. = *wheatgrasses;* Sitanion hystrix = *bottlebrush squirreltail;* Oryzopsis hymenoides = *Indian ricegrass;* Stipa comata = *needle-and-thread grass.*

(Fig. 5), substitution of the 1978 data for the 1975 data in the analysis of variance resulted in the 1965 value being significantly greater than those for 1950 and 1957; and, the 1978 mean was significantly greater than the 1965 value.

An important question is whether the increase in perennial grass cover between 1965 and 1975 resulted from an increase in the size of individual plants or an increase in the density and distribution of these species. With the exception of the wheatgrasses, which in this case include only rhizomatous species, significant increases in cover between 1965 and 1975 were accompanied by significant increases in density. In addition, the number of plots for which cover data were recorded for a species should be indicative of the general distribution and abundance of that species. The number of plots upon which grass cover was recorded over the 25-year period tended to increase (Table 1), and rather large increases were noted between 1965 and 1975 for the four dominant grasses, especially Indian ricegrass and needle-and-thread. These data clearly show that the overall increase in perennial grass cover was not due simply to an increase in the size of individual plants that intercepted the transect lines.

There were no apparent differences in trends for the 1950 to 1957 period or for the entire 25-year period between the seven plots which were open to livestock grazing until 1957 compared with the 29 that are within the area closed in 1950. Because of the similarity in trends and overall vegetal composition, and because we have no way of knowing whether those plots were actually grazed during that period, we included those plots in the overall analysis.

Discussion

Several recent studies suggest that forest and shrub communities may be exceptionally stable in the absence of external perturbations and that community composition may depend more upon the nature of previous disturbances and the flora that developed immediately thereafter than upon successional development (Henry and Swan 1974; Lyon and Stickney 1976; Niering and Goodwin 1974). Niering and Goodwin's (1974) data from the hardwoods forest region in Connecticut demonstrate the high stability of well-established shrub cover and its resistance to invasion by other species. In addition, they cite numerous studies that challenge the traditional views of succession and support their conclusion that "old field vegetation development . . . is not necessarily an orderly or predictable process. . . . " The results of a study in which the 300-year history of a New Hampshire forest was reconstructed indicated that "autogenic succession" did not contribute significantly to changes in vegetation composition over the period (Henry and Swan 1974). Rather, disturbance was an important factor, operating in concert with the behavior of individual species.

Table 1. Number of plots for which cover data were recorded for the major grass species.

	Sample Dates			
Species	1950	1957	1965	1975
Indian ricegrass	9	17	11	28
Needle-and-thread	6	11	8	19
Bottlebrush squirreltail	9	15	28	32
Wheatgrasses	10	13	15	20

Vegetation data from the INEL Site suggest that we are witnessing a similar situation on the sagebrush-dominated ecosystems of the Snake River Plain. Prior to 1950, stable communities dominated by long-lived shrub species had developed. The extent to which grazing practices may have influenced the development and structure of these communities is not known, but the data from 1950 certainly support the assumption that the area was heavily grazed. There have been no major disturbances such as fire, herbicide use, or mechanical treatment on the study area since 1950. After 25 years of protection from grazing by domestic livestock, the plant communities are still dominated by shrubs. In 1975, cover of big sagebrush was 54% greater than it was in 1950 (Fig. 2). This apparently was not accompanied by a significant increase in shrub density, suggesting that the population of dominant shrubs has been relatively stable over the 25-year period. Despite the high turnover within the rabbitbrush population, neither cover nor density changed significantly over the period. We found no evidence of seral replacement of this species. In the absence of a major perturbation, it seems unlikely that the composition of the shrub overstory will change much with time.

In contrast, the populations of perennial grasses have not remained stable over the study period. There are some important differences in the trends over the past decade compared to those reported by earlier investigators, and there are some important differences in our interpretations of the trends for the entire period. Harniss (1968) and Harniss and West (1973b) reported that Indian ricegrass and needle-and-thread decreased in importance between 1950 and 1965. Total perennial grass cover increased over the same period because of increases in bottlebrush squirreltail. Based on these apparent trends and the concomitant increase in the big sagebrush cover, Harniss and West (1973a, b) concluded that the area was probably an *Artemisia tridentata/Sitanion hystrix* climax. Clearly, the present data do not support such a conclusion. Cover for both Indian ricegrass and needle-and-thread, as well as that for the wheatgrasses and bottlebrush squirreltail, has increased dramatically over the past decade. Although our analysis also showed that the mean cover values for Indian ricegrass and needle-and-thread were lower in 1965 than in 1957, the differences were not statistically significant. We prefer the interpretation, based on the exponential increase in perennial grass cover over the 25-year period coupled with the fact that all of the major grasses showed large increases between 1965 and 1975, that all of these species have increased exponentially during the study period. Thus, it seems probable that the apparent decrease in cover of Indian ricegrass and needle-and-thread between 1957 and 1965 was simply a result of random error rather than an actual trend.

The increase in shrub cover between 1957 and 1965 may have been in response to generally more favorable precipitation during that period (Fig. 3). There is no apparent correlation, however, between precipitation patterns and the overall trend for perennial grass cover. On an annual basis, precipitation over the past decade has been somewhat above the average for the entire study period, but that has not been true for precipitation during the growing season. Although there is no doubt that year-to-year variations in precipitation will affect perennial grass cover on the study site, as shown clearly by comparing the 1975 and 1978 data (Fig. 2), we must look elsewhere for an explanation that would account for a 20-fold increase. It seems probable that there were few remnant perennial grasses present in 1950 and that the results through 1965 reflect the scarcity of seed sources. Increases in cover during this "lag phase" in the growth of perennial grass populations were hardly noticeable, but over the past decade we have witnessed the effect of exponential increase as propagules become more readily available.

These observations may provide some insights for the interpretation of previous exclosure studies. Numerous investigators have reported that "recovery" of depleted rangelands is slow, especially in arid environments (see e.g. Gardner 1950; Rice and Westoby 1978; Smeins et al. 1976). McLean and Tisdale (1972) reported that on rough fescue and ponderosa pine zone ranges protected for 20 to 40 years most improvements came about in the last ten years of protection, with relatively little improvement during the first ten. These results suggest that a general pattern may be slow change during the first decade or so of rest followed by more rapid revegetation as previously depleted populations build up their size and seed production. Aridity and poor initial condition would tend to lengthen the time before noticeable improvement would be detected.

The increase in grass cover on the INEL Site has not been at the expense of the shrub overstory. In the absence of a major disturbance, such as fire, we would predict that the grasses will reach some sort of stable equilibrium with the present shrub community. Although the trends for perennial grasses appear to be directional, we have no evidence of seral replacement among the grass species.

The results of most long-term vegetation studies on western rangeland have been interpreted in terms of classical successional theory, i.e., the recovery of depleted rangeland should follow a directional and predictable progression toward a climax community (Haskell 1945; McLean and Tisdale 1972; Harniss and West 1973a,b; Smith and Schmutz 1975; Tisdale et al. 1969). The relative stability/initial floristics model (Egler 1954) provides an alternative paradigm with which to interpret the results of such studies. Perhaps the most important consequence of the model is that one would expect that many different assemblages of the same species could form relatively stable communities on a given site. The relative abundances of the component species would depend largely on the disturbance history, the nature of past disturbances, and the vegetal composition at the time of disturbance. Any of the relatively stable community assemblages might be considered "climax." Such a model may prove to be more useful as an aid to managers who attempt to understand the vegetal patterns that they are confronted with than the classical model which predicts a single climax community.

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