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By ROBERT H. WEBB, JOHN W. STEIGER, and
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The Response of Vegetation to Disturbance in Death Valley National Monument, California

By Robert H. Webb, John W. Steiger, *and* Evelyn B. Newman

Abstract

The response of desert plant assemblages to disturbance was studied in Death Valley National Monument, California. Plant assemblages on debris flows, alluvial terraces, five abandoned townsites, and a pipeline corridor were measured to quantify recovery rates and to develop a model of change in desert vegetation. A review of the literature revealed that little was known about the nature and rate of recovery in disturbed desert ecosystems.

Plant succession models are commonly used to describe vegetation dynamics that occur after disturbances. Plant succession refers to sequential, directional changes in the species composition of a plant assemblage that are caused by forces internal and (or) external to the assemblage. The nature of these forces is controversial and dependent upon which model is used; most plant ecologists ascribe them to biological processes. As a result, a common mistaken belief is that plant succession does not occur in deserts because sequential, directional changes have not been consistently observed and measured and the influence of biological processes is assumed to be negligible.

Vegetation assemblages occurring on debris flows of different age illustrate sequential, directional changes in the species composition of areas in the Panamint Range dominated by Coleogyne ramosissima. Debris flows were differentiated in age on the basis of the degree of soil development. The species composition changed on debris flows of increasing age, as indicated by increasing soil development, from species with short lifespans oriented to rapid recruitment (for example, Lupinus excubitus) to a mixture of species (for example, Ephedra nevadensis, Lycium andersonii, and Grayia spinosa) to long-lived, maintenance-oriented species (for example, Coleogyne). This primary succession sequence, so named because it occurs on a newly created surface, requires thousands of years for the change in dominants from short-lived, reproduction-oriented to long-lived, maintenance-oriented species.

The recovery of vegetation assemblages at the Skidoo townsite and in the Skidoo pipeline corridor indicates a pattern of vegetation change similar to that measured on the debris flows. These disturbed sites, with recovery periods after abandonment of between 42 and 74 years, were generally colonized by short-lived, reproduction-oriented species (for example, Chrysothamnus viscidiflorus, and perennial grasses) with variable colonization by other species (for example, Grayia, Ephedra, and Coleogyne). The time required for complete recovery of disturbed sites appears to depend on the stage of the predisturbance primary succession. Soil compaction, a possible inhibitor of vegetation establishment, was estimated to require a century for complete amelioration but did not appear to substantively affect the course of recovery.

Vegetation assemblages occurring on alluvial terraces of different age illustrate sequential, directional changes in the species composition of areas dominated by Larrea tridentata in the Black Mountains. Alluvial terraces of increasing age indicated a primary succession sequence of initial colonization by short-lived, reproduction-oriented species (for example, Hymenoclea salsola) and subsequent changes to dominance by long-lived, maintenance-oriented species (for example, Larrea, Ambrosia dumosa). Larrea became established in the early stages of this sequence. The soils developed on the alluvial terraces indicate that thousands of years are required for these changes. Buried soils exhumed by erosion complicated the successional sequence, which suggests a strong influence of soil properties on vegetative composition.

The townsites of Greenwater, Furnace, Kunze, and Gold Valley, all abandoned for 73 years, had vegetation assemblages generally dominated by short-lived, reproduction-oriented species (for example, Hymenoclea, Stipa speciosa). Other longer lived species (for example, Ephedra, Grayia) also became established in varying quantities, but Larrea, the predisturbance dominant/codominant, had conspicuously low cover and density on these disturbed sites. Soil compaction was estimated to require a century for amelioration but did not substantively affect vegetation establishment. Ordinations using Wisconsin polar ordination and principal-components analysis indicated a clear differentiation of species composition between disturbed and undisturbed sites.

A climatic fluctuation to cooler and (or) wetter conditions could explain the low density and cover of Larrea in townsites. An analysis of eight fossil and five modern packrat (Neotoma sp.) middens collected at Larrea's upper elevation limit indicated that Coleogyne's lower elevation limit, now coincident with Larrea's upper elevation limit, has decreased a minimum of 50 m within the last 500 years. This change is in accord with upper treeline declines and other evidence of a change to cooler and (or) wetter conditions in the Western United States. All four townsites where

Larrea is of conspicuously lower density and cover in the colonizing assemblage were built at the upper elevation limit for this species. Because of the climatic change, Larrea may now only be able to rarely reproduce at its upper elevation limit, hence complicating the course of recovery of the townsites.

The changes in species composition on naturally disturbed or human-disturbed sites in Death Valley indicate that succession occurs in desert plant assemblages. Evidence from nearly every study site indicated that species compositions change with time after disturbances and that the types of species involved in all stages of change have similar life-history strategies. Plant succession is best defined as sequential, directional changes in species composition of a vegetation assemblage. This definition obviates the need for explicitly linked driving forces behind the succession. The successional sequences found in Death Valley apparently require thousands of years from colonization to stages dominated by long-lived, maintenance-oriented species, and they are affected by climatic fluctuations and geomorphic processes. Secondary succession occurs in abandoned townsites because the species composition of colonizing assemblages mirrors that of the primary succession sequences.

The forces responsible for vegetation dynamics change from internally derived (autogenic) to externally derived (allogenic) as the succession progresses. Colonizing species alter microclimates and soil chemistry, indicating autogenic forces. The allogenic force of pedogenesis appears to be responsible for species composition changes over long time periods. Allogenesis ultimately is the most important force because pedogenesis and erosion are responsible for alteration and destruction of surfaces and climatic changes can alter the viability of species. The life-history strategies of the species that form assemblages determine how an assemblage will respond to autogenic and allogenic forces. Therefore, definitions of recovery of disturbed desert plant assemblages are arbitrary and must be linked with ongoing successional processes in ambient, undisturbed plant assemblages.

INTRODUCTION

Humans have had a substantial effect on desert soils and vegetation in Death Valley since explorers and prospectors first arrived more than a century ago. As a result, the northern Mojave Desert has a legacy of abandoned trails, roads, townsites, and utility corridors, which usually can be easily identified in the landscape. Human-induced disturbances will be perpetuated as the population of the Southwest increases, and many of these new disturbance sites, like those in Death Valley, will be abandoned and natural processes will return the landscape to some semblance of its predisturbance condition. The course of this recovery from disturbance is the topic of this study. How desert soils and vegetation recover following the abandonment of disturbed areas is little known, partially because of the paucity of data on natural soil and vegetation processes.

This study presents a model of the response of vegetation to disturbance in Death Valley National Monument. The model was developed by applying generally recognized, but often conflicting, concepts of vegetation and soil processes to data from sites with a variety of vegetation types and disturbance histories. In the first section of this paper, extensive literature reviews are provided to discuss the development of these concepts and clarify the confusion often associated with their use. In the second section, site-specific studies within two floristically distinct areas are treated separately to magnify the variability inherent in the response of vegetation to disturbance.

The response of vegetation to disturbance in the Panamint Range on the west side of Death Valley (fig. 1) is discussed in the first three studies. In Wood Canyon, recent debris flows were studied to determine the initial recovery from extremely severe natural disturbance and were compared to sequentially older debris flows nearby to evaluate the effect of soil development on the recovery process. Fourteen kilometers to the north, the abandoned townsite of Skidoo was used to determine the recovery from a less severe disturbance, but one that had varying levels of soil compaction. The study of the Skidoo pipeline corridor, which traverses the Panamints, evaluated the effect of geomorphic surface on the recovery process.

The next two case studies discuss the response of vegetation to disturbance at lower elevations in the Black Mountains on the east side of Death Valley (fig. 1). Alluvial terraces of different age in Gold Valley contribute additional information about the effect of soil development and geomorphic surface on the recovery process. The nearby townsites of Gold Valley, Greenwater, Furnace, and Kunze provide further information about recovery from human-induced disturbance. The final study examines the history of vegetation change during the late Holocene through analyses of fossil packrat middens, and suggestions are made as to how climatic changes might affect the revegetation patterns observed in Death Valley.

A discussion of the general revegetation patterns indicated by the suite of studies is presented in the final section. The relation between all disturbed and control sites within each geographic area are analyzed using statistical and graphical analyses. Based on these analyses, a conceptual model is developed in which to view patterns of revegetation, or "succession." Finally, the forces behind the response of vegetation to disturbance are discussed in the context of the proposed model.

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Human Use of the Death Valley Area

Humans have inhabited the Death Valley region for many thousands of years. Their influence on the arid ecosystem accelerated with the arrival of immigrants from Europe and the Eastern United States, who usually were more concerned with exploitation of mineral resources than permanent settlement. As a consequence, some areas were settled and abandoned

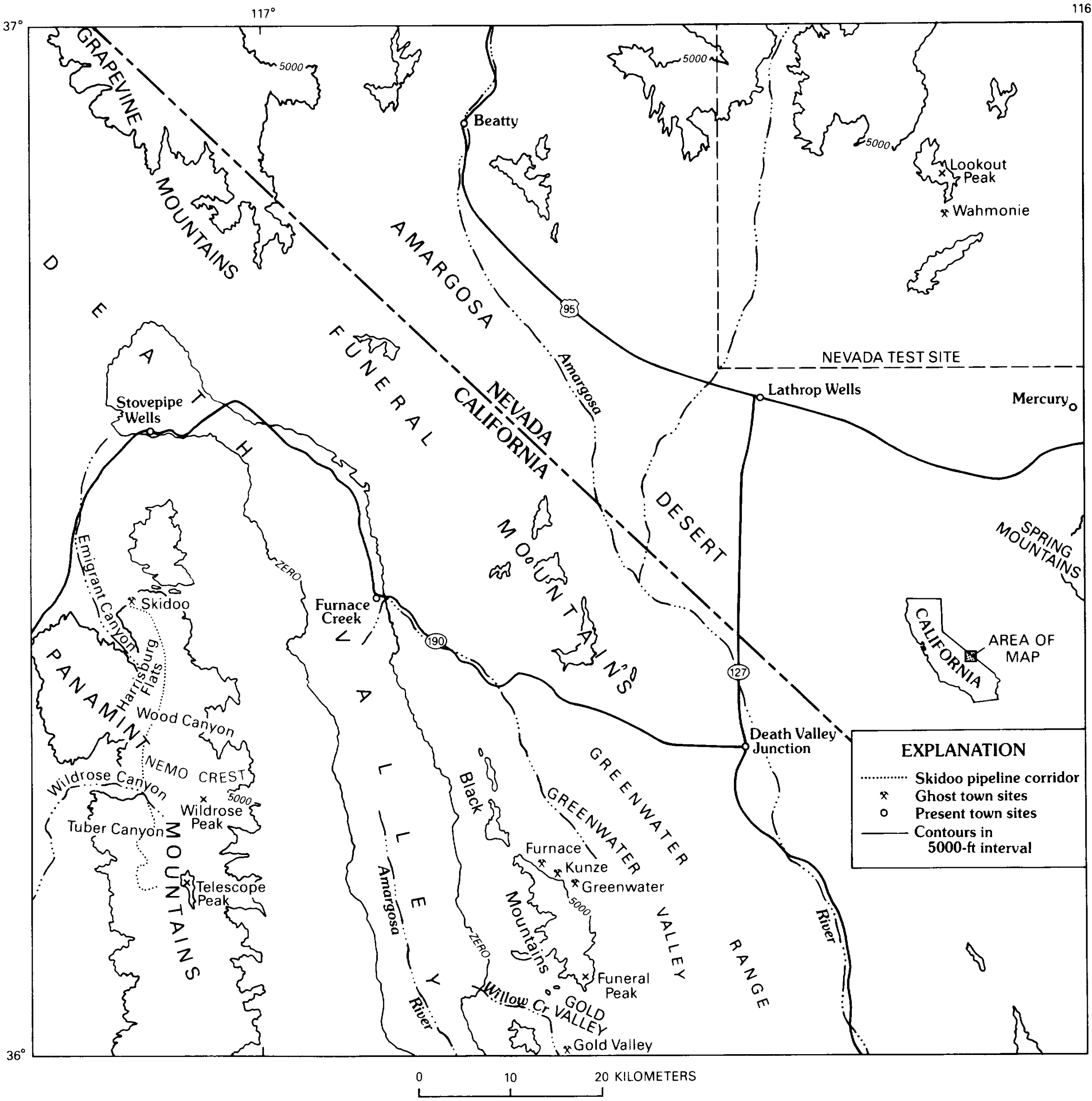


Figure 1. Location of study sites in and near Death Valley National Monument, California.

within a short time period and have remained unused since abandonment. These disturbed-then-abandoned areas are analogous to current disturbances in the Mojave Desert, including offroad-vehicle use, mining, and road and subdivision construction (Webb and Wilshire, 1979).

Prehistoric people occupied sites in the Death Valley area throughout the Holocene (Hunt, 1975, p. 157-162). Apparently no prehistoric occupation caused widespread disturbances to soils and vegetation, although some large farm sites are still discernible (Greene, 1981, p. 362-398). The first historical accounts of the Death Valley area were made in 1849, and mining began in the early 1860's in eastern Inyo County (Greene, 1981, p. 1-2). Prospecting became more extensive in the early 1900's with the publication of maps and the discovery of gold at Goldfield in southern Nevada. The towns of Skidoo, Greenwater, Furnace, Kunze, and Gold Valley were founded during this period near promising mine sites. Most mining operations (with the exception of Skidoo) were unprofitable and the townsites were abandoned within a short time. Sporadic rushes occurred in the northern Mojave Desert until the Great Depression of 1929. Several mines still operate within Death Valley National Monument, which was established in 1933 (Greene, 1981; Latschar, 1981).

Death Valley National Monument, with its extensive mining history, is exceptionally well endowed with potential sites for the study of recovery from disturbance. Mining operations created localized areas of disturbance to vegetation and soils that ceased when the mines closed, and further disturbance to these sites has been minimized by U.S. National Park Service policy and the isolation of the sites. These attributes make Death Valley National Monument an ideal location for the study of recovery of desert soils and vegetation.

SOIL AND VEGETATION PROCESSES IMPORTANT TO REVEGETATION

Soil Processes

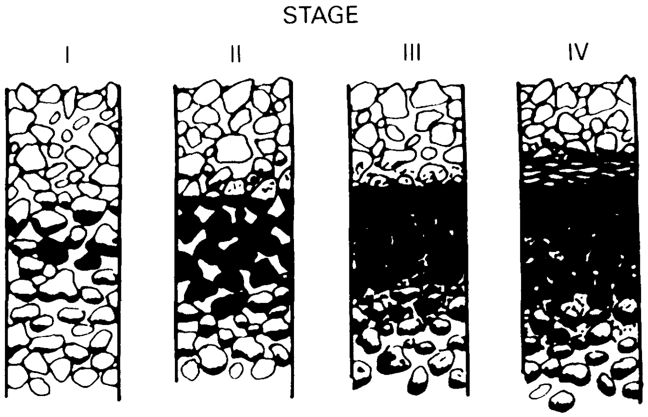
Rates of Soil Formation in Deserts

Soil types and rates of soil formation are important to the understanding of the response of vegetation to disturbance in arid regions. Most soils in deserts are primarily mineral bodies that form in response to weathering and plant and animal colonization of geologic deposits. The parameters most important to soil formation are climate, parent material, vegetation, topography, and time (Jenny, 1941; Birkeland, 1974). The features of desert soils that are indicative of age include desert pavements and varnish, argillic (clay enriched) horizons, and calcic (carbonate enriched) horizons (Birkeland, 1974).

Pavements form at the surface of desert soils in response to deflation and wetting and drying of the surface soil (Elvidge and Iverson, 1983). The parent material is an important factor, because easily weathered rocks will disintegrate before pavements can form. Pavements typically are varnished with iron-manganese compounds and are underlain by A horizons (see below) with vesicular pores. Pavements can form within several hundred years on gravelly, cobbly deposits, but varnish is believed to require 3,000 to 5,000 yr for a visible coat and greater than 10,000 yr for a thick coat (Elvidge and Iverson, 1983).

Soil horizons generally form parallel to the ground surface in response to the establishment of vegetation and leaching by rain water. The A horizon is a zone of leaching and accumulation of organic material (Soil Survey Staff, 1975, p. 160). The B horizon is a zone of accumulation of clay minerals translocated from the A horizon, and of alteration of in situ minerals by chemical weathering. B horizons that show a significant alteration in color are called cambic B horizons, whereas B horizons with significant clay accumulations are called argillic horizons (Soil Survey Staff, 1975). Carbonate dissolved in soil water is precipitated in or below the B horizon, forming carbonate-enriched C horizons (nomenclature for carbonate horizons appears in fig. 2). Carbonate in the parent material slows the translocation of clays (Goss and others, 1973), and some soils have an argillic horizon overlying the carbonate-enriched horizon. Gile and others (1981, table 65, p. 163), for example, show that the development of B horizons is slower in calcareous than in noncalcareous parent materials.

Argillic and carbonate-enriched horizons are the most commonly used morphological indicators of the age of soils in deserts. Most pedogenic clay and carbonate in desert soils is derived primarily from dustfall and subsequent translocation despite the presence of carbonate and weatherable minerals in the parent material (Gile, 1975; Bachman and Machette, 1977, p. 36-38). Carbonate accumulation is a more reliable indicator of soil age than clay accumulation because the rate of clay accumulation is dependent upon the amount of carbonate in



EXPLANATION

Stage	Description of carbonate content for high-gravel soils
I	Thin, discontinuous pebble coatings
II	Continuous pebble coatings with some interpebble fillings
III	Interpebble space filled but not plugged
IV	Plugged horizon capped by a laminar horizon

Figure 2. Carbonate morphology classification of Gile and others (1981, p. 66-67)

the soil. The rate of carbonate accumulation in soils is dependent on the timing and amount of rainfall, the annual fluctuations in temperature and evapotranspiration, soil pH, the rate of carbonate influx in dustfall, and stability of the soil surface (Arkley, 1963; Bachman and Machette, 1977).

Considerable data are available for the rate of soil formation in the Desert Soil Project area near Las Cruces, New Mexico (Gile and Grossman, 1979; Gile and others, 1981). Precipitation in the Las Cruces area is 210-250 mm/yr with more than half of this amount occurring as summer thunderstorms (Gile and others, 1981, p. 19); this seasonal rainfall pattern differs from the winter-dominated pattern in the Death Valley area (see fig. 3). The mean annual temperature in Las Cruces is 16 °C. Soils in the Las Cruces area have formed on low- to high-carbonate alluvium with low to high gravel and cobble contents. The parent material for the alluvium is rhyolite and monzonite for low-carbonate deposits and mixtures of limestone, sandstone, and (or) igneous rocks for high-carbonate materials. The vegetation is Chihuahuan Desert Larrea tridentata (creosote bush) assemblages on the younger deposits.

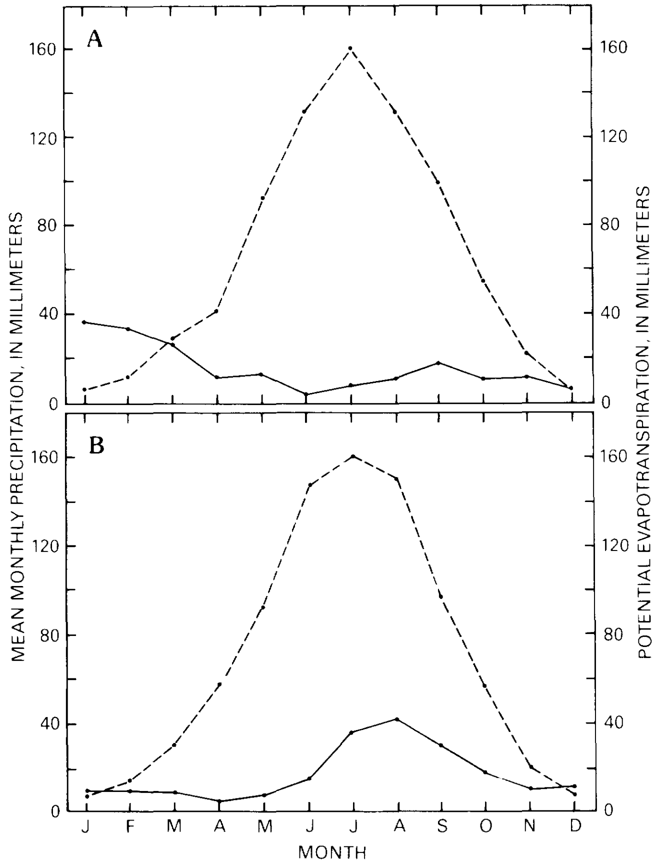


Figure 3. Mean monthly precipitation (dashed lines) and potential evapotranspiration (solid lines) for two desert areas. Potential evapotranspiration was calculated graphically using the Thornwaite method (Palmer and Havens, 1958) and data from Kurzius (1981) and Gile and others (1981). A, Wildrose Canyon, Death Valley National Monument. B, Las Cruces, New Mexico.

The influence of a Chihuahuan Desert Larrea assemblage versus the influence of Mojave Desert assemblages on soil formation rates is unknown. Both vegetation types are currently dominated by woody perennials, although the vegetation around Las Cruces prior to the introduction of domestic livestock was possibly dominated by perennial grasses (Buffington and Herbel, 1965). Vegetation type affects both the A-horizon thickness (Birkeland, 1974, p. 198) and the soil chemical properties (Charley and West, 1975; Garcia-Moya and McKell, 1970). Different species transpire at different rates, suggesting a possible influence on carbonate accumulation and chemical weathering. However, Evans and others (1982, p. 217) measured no appreciable differences in transpiration among plant species, including Larrea and perennial grasses, and in total evapotranspiration between plots with and without plants. Hence, climate as manifested by evaporation potential is more important than vegetation in influencing soil morphology.

Gile (1975) and Gile and others (1981, p. 164) state that stage I carbonate horizons are a major feature of pedogenesis in the Holocene in southern New Mexico with the oldest Holocene soils having stage II accumulations of carbonate (see fig. 2 for definitions). The influence of parent materials on carbonate accumulation is difficult to assess, although Gile and others (1981, p. 163) did not consider parent material differences, other than the presence of limestone in the alluvium, which is important to carbonate accumulation during the Holocene. In high-gravel, high-carbonate parent materials near Las Cruces, discontinuous pebble coatings appear in 100 to 1,100(?) yr old deposits; thin continuous pebble coatings are present in 1,100 to 2,100(?) yr old deposits; and pebble coatings increase in thickness in 2,200 to 4,600(?) yr old deposits (table 65 of Gile and others, 1981, p. 163). In high-gravel, low-carbonate material, this chronology for the development of carbonate morphology is the same as for high-carbonate materials, but cambic B horizons also appear. Very thin argillic horizons appear in 2,200 to 4,600(?) yr old deposits if the horizon is underlain by a stage I carbonate horizon. Stage III carbonate horizons indicate a soil age in excess of 25,000(?) yr.

The rate of soil development is poorly understood for Mojave Desert soils. In one of the few studies of soil geomorphology in the Mojave Desert, Bull (1975) presented a chronology of the development of calcic horizons in the lower Colorado River region of California and Arizona. The age control for this chronology is based on correlation with soils near Las Cruces and is speculative. This chronology has since been used for assigning ages to the Quaternary deposits of the area (Carr and Dickey, 1980; Carr and others, 1980; Dickey and others, 1980). The rainfall in the lower Colorado River region varies from 65 to 97 mm annually, and the mean annual temperature is 21 to 22 °C. Therefore, soils on the lower Colorado River would be expected to form more slowly than soils in Las Cruces, given the same type of parent material, slope, exposure, vegetation, and carbonate dust influx, because leaching and vegetation influences would be less.

For the lower Colorado River area, Bull (1975) reports that pebble coatings and varnish are absent in deposits younger than about 2,000(?) yr old; thin, discontinuous pebble coatings and lightly varnished pavements characterize 2,000 to 5,000(?) yr old deposits; discontinuous (stage I) to continuous (stage II) pebble coatings and darkly varnished pavements characterize 5,000 to 13,000(?) yr old deposits; and stage II to stage III carbonate appears in 25,000 to 125,000(?) yr old deposits.

Processes of Soil Recovery from Compaction

Soil compaction, an important factor in the recovery of vegetation, is caused by forces generated by humans, livestock, and vehicles traveling over the soil. Compaction is manifested by an increase in soil density and strength and a decrease in infiltration rate. Loosening of highly compacted soils is generally ascribed to the physical processes of clay-mineral expansion during wetting-and-drying cycles and freeze-thaw heaving, and to biological activity. The rate at which a compacted soil loosens depends on the amount of smectitic clays in the soil, the depth of water penetration, the frequency of wetting-and-drying cycles, and the depth of compaction in the soil. In arid areas with winter-dominated rainfall, wetting-and-drying cycles are infrequent because the soil tends to remain damp during the winter and early spring and dry during the rest of the year. The effectiveness of freeze-thaw loosening is dependent upon the amount of soil water, the soil texture (Akram and Kemper, 1979), the depth and rate of frost penetration, and the amount and depth of compaction. Freeze-thaw loosening would probably be most effective in deserts with prolonged, cold winters (for example, the Great Basin Desert), which allow frost to penetrate the subsurface.

Biological activity is very important in loosening compacted soils. Plants loosen the soil around their roots, and small channels are left after the roots die. Animals burrow in soils, loosening compacted zones. The effectiveness of biological activity in loosening compacted soil is partially dependent on the rate at which vegetation and animals reoccupy disturbed sites.

Many recent studies have discussed the rate of recovery from compaction. Webb (1982) showed that subsurface compaction remained and lightly compacted soils did not significantly loosen after one year in a Mojave Desert loamy sand. This pattern also has been observed in more humid regions (Orr, 1975; Thorud and Frissell, 1976; Vorhees and others, 1978). In addition, poorly drained soils require twice as much recovery time than do well-drained soils in the USSR (Ivanov, 1976), which illustrates the effectiveness of wetting-and-drying cycles. Estimates of the recovery time for compacted soils range from about a decade (Thorud and Frissell, 1976; Blake and others, 1976; Dickerson, 1976) to a half century (Greacen and Sands, 1980). One study (Webb and Wilshire, 1979) concluded that compacted soils in a Mojave Desert ghost town required about a century for total amelioration.

The Effects of Soil Compaction on Plant Growth

Many agricultural studies have noted equivocal effects of compaction on plant growth. Soil strength appears to be the most important property that limits plant growth (Taylor and Burnett, 1964). Taylor and Gardner (1963, p. 156) report a high negative correlation between penetration of cotton seedling taproots and soil penetration resistance in sandy soils. Similar results have been measured for other crops (Zimmerman and Kardos, 1961).

Highly compacted soil layers restrict roots to shallow depths (Phillips and Kirkham, 1962; Grimes and others, 1972) and decrease plant heights and yields (Lowry and others, 1970). Although Raghaven and others (1979b) report that plant root densities decrease with increasing soil densities, plant yields are optimum in soil with a slightly increased bulk density (Raghaven and others, 1979a, p. 72-73). This finding suggests that the above-ground portion of the plant may be positively affected by low levels of compaction despite the shorter and deformed roots caused by this compaction (Warnaars and Eavis, 1972). Desert plants are adapted to an environment of continual stresses, and therefore the addition of soil compaction may not be as important as other environmental factors in affecting establishment and growth of vegetation.

Vegetation Processes

Models of Plant Succession

The revegetation of disturbed areas is often modeled using the controversial concept of plant succession. "Succession" refers to sequential and directional changes in, or observed sequences of, the species composition of an assemblage of vegetation at a particular site through time (Mueller-Dombois and Ellenberg, 1974, p. 374; Miles, 1979, p. 13). "Primary succession" refers to the colonization and subsequent sequential changes in vegetation on newly formed substrates or previously bare surfaces, whereas "secondary succession" refers to the reestablishment of vegetation on a disturbed site (Horn, 1974, p. 25; Miles, 1979, p. 47, 54). The distinction between primary and secondary succession is ambiguous if the substrate was previously occupied by vegetation (Miles, 1979; MacMahon, 1980).

Succession begins with the establishment of colonizing species on denuded or newly created surfaces. The relative contribution of these species to the total plant assemblage (species composition) changes with time as the colonizing species are replaced by other invading species. The rate of change in species composition decreases with time from an initially rapid turnover to an assemblage that changes little in composition with time. The end point in succession is commonly termed the "climax community" (Clements, 1916).

The forces controlling succession in a plant assemblage are either externally derived (allogenic) or internally derived (autogenic). Tansley (1935, p. 267) suggests that there is usually a clear dominance of one type of force over the other even though both are present in all successions, whereas White (1979, p. 261) suggests that a continuum exists between allogenic and autogenic forces. Allogenic succession is controlled by factors such as geomorphic processes and climatic shifts. Autogenic succession, on the other hand, is controlled by the species themselves through direct interaction with other species and by their alteration of the microenvironment.

Identification of the relative importance of autogenesis or allogenesis in causing succession is extremely difficult (Drury and Nisbet, 1973; White, 1979), in part because succession is a composite of the interaction of these forces (Whittaker, 1975, p. 171; Ricklefs, 1973, p. 760). Also, the distinction between autogenesis and allogenesis is vague if individual species have time to alter their life-history strategies in response to the successional forces. However, the terms are useful in classifying the forces behind succession according to the control of geomorphic and climatic processes or the control of plant interactions and plant-induced modifications of soils.

Clements (1916) presented an autogenic model of succession that has been widely applied. His model is based on the force of reaction by which early successional species modify the substrate in a way that relinquishes competitive superiority to later successional species. Clementsian succession terminates in the establishment of the climax community, an assemblage that varies little in composition with time. This model has been abandoned by some modern ecologists (Pickett, 1976, p. 107), because of Clements' overgeneralizations (particularly the holistic and supraorganismic community concept) and the deterministic nature of the theory (McIntosh, 1980, p. 18-23). Reaction is now considered one of an array of forces responsible for successions (MacMahon, 1980, 1981).

Climax-community models are inseparable from succession models (Drury and Nisbet, 1973, p. 332; Miles, 1979, p. 48), and there is considerable controversy over the definition of the climax community. According to Mueller-Dombois and Ellenberg (1974, p. 404) there are two major conceptual difficulties with climax models. The concept of stability of composition in time has been applied to spatial relationships without careful consideration of spatial controls such as lithology and microclimate variability. Also, the concept of climax implies indefinite geomorphic, pedogenic, and climatic stability, which generally cannot be expected. White (1979, p. 372) considered the problem of reconciling climax with the dynamic nature of all vegetation assemblages and suggested that either the climax community be defined explicitly for each case or the term be abandoned in favor of less ambiguous concepts.

Many models of succession have been proposed that are either based on or are in response to Clements' ideas. A model of community-controlled succession, described in editions of popular ecology texts (Odum, 1975; Whittaker, 1975), dominated successional thought in the 1960's and 1970's. After this model was severely criticized (Drury and Nisbet, 1973), partly for its emphasis on Clementsian reaction as the primary force, other models were proposed that discounted the holistic nature of an evolving community that permeated the community-controlled model (McIntosh, 1980, 1981). A life-history or adaptive strategy approach to succession is taken in papers by Horn (1974), Pickett (1976), and Van Hulst (1978). This approach views succession as an individualistic, plant-by-plant replacement process in which adaptations to stress, including disturbance, and competition are the most important controlling factors. In a similar manner, Grime (1979) presented a model of succession based on the adaptations of individual species to differing intensities of stress and disturbance.

Using a more mechanistic approach to the modeling of succession, Connell and Slayter (1977) presented three models that could account for most autogenic successions. The "facilitation model" occurs on sites in which soil modification by colonizing species is beneficial and necessary to the establishment of later species (the "reaction" of Clements (1916)); the "tolerance model" occurs when soil modification by colonizing species is not necessary to the establishment of later species; and the "inhibition model" occurs when soil modification by colonizing species is deleterious to later species.

Perhaps the most comprehensive approach to succession is the model described by MacMahon (1980, 1981), which uses Clements' original terminology with minor but important redefinitions and clarifications. This model incorporates both the disturbance and environmental forces behind vegetation change and places an important emphasis on the effect of "residuals" (the surviving seedbank or soil alterations by the predisturbance vegetation). The relative importance of allogenic and autogenic mechanisms vary according to these factors and the life-history strategies of the species involved. For a more complete review of general succession models, see Miles (1979), MacMahon (1980), and McIntosh (1980, 1981).

Succession in Deserts

"Study nature, not books." —Louis Agassiz

The occurrence or nonoccurrence of succession in deserts has been debated since researchers first studied desert plant ecology. Shreve (1925) was one of the first to describe the physiography and plants of the California deserts. He referred to the vegetation as being in a "very static condition" and stated (p. 102):

> In a consideration of the dynamic aspects of the vegetation of a region in which the initial, sequential and final stages of a succession are characterized by the same species, and often by the same individuals, it is doubtful whether these conceptions (i.e. succession), formed in regions with a very dissimilar vegetation, are of much real utility.

The harsh environment, adaptations to high-stress conditions, and the simplicity of the flora precluded any succession of the type proposed by Clements (1916).

Muller (1940) studied the changes in a Chihuahuan Desert vegetation assemblage on clay beds exhibiting various states of erosion or deposition. He concluded that Clementsian succession did not apply because all invading species were members of the original vegetation assemblage, not species alien to the assemblage. However, Muller was viewing vegetation growing on texturally different substrates (Muller, 1940, p. 208-209); moreover, he inferred a sequence of erosion and deposition without temporal control.

Shreve (1942, p. 203-204), in a widely quoted passage, stated:

> Destruction of the original vegetation results in the appearance of seedlings, which not only constitute the first stage of succession but include in their number the individuals which will ultimately restore directly the original vegetation. It may be said that successions do not take place in desert vegetation and they cannot, therefore, be telescoped. It is at least certain that the succession concept would never have been developed in a study of the vegetation of arid regions. One of the principal reasons for the abeyance of successional phenomena is the almost total lack of reaction by the plant on its habitat. The existence of a plant in a given spot for many years does nothing to make that spot a better habitat for some other plant or some other species. Fallen leaves and twigs are blown away, or small accumulations of organic matter are washed away, to be carried ultimately to the nearest flood plain or playa. Also little happens to change the character of the soil or its water-holding capacity. Only in the rich stands of desert vegetation is there a local amelioration of conditions due to the presence of large and long established perennials.

Shreve based this conclusion on observations but did not provide quantitative evidence to support it.

Several other researchers have agreed with Muller's and Shreve's conclusions. Hunt (1966, p. 54) believed that reaction could not be important in the assemblages of widely spaced individuals on the floor of Death Valley. Pianka (1974, p. 249) denied the existence of autogenic succession due to the purported non-existence of soils in deserts. Beatley (1976) recognized that autogenesis might become more important as the amount of precipitation increases along an environmental gradient. Her discussion of the substrate control (p.72) is similar to that of Shreve (1942):

> At the lower and middle elevations in this region [Mojave and Transition Desert], soils are scarcely modified by the soil-forming processes; hence the substrates are usually not fundamentally different after disturbance than before. In the absence of climate change, the only species able to occupy the soil after disturbance are still the original species, i.e., most native species are the colonizing species in the region.

Rowlands and Adams (1980, p. 174) summarized their support of the Shreve-Muller conclusions with respect to the Mojave Desert by stating:

> Desert vegetation upon destruction replaces itself directly by new seedlings of the same species. Characteristically, in deserts, species of the original vegetation continue to occupy disturbed sites with population increases in some species (i.e. colonizing species) and declines in others. But, floristically distinct assemblages, or seral stages, between initial and climax communities, which in humid regions occur in orderly and predictable sequences, are not present.

Wells (1961) presented an argument supporting the occurrence of succession in deserts based on the study of revegetation in streets of a Mojave Desert ghost town in Nevada. Wells found that the initial colonizers were species that are normally found in washes or naturally disturbed habitats, and he argued that these species were analogous to colonizers in more humid regions (p. 671). Shields and Wells (1962) argued for secondary succession in a study of revegetation of areas in the Nevada Test Site devastated by nuclear explosions. Egler (1962) challenged Wells' (1961) conclusions based on the presence of colonizing species in the undisturbed assemblage. Egler's argument apparently was based on the definition of a Clementsian climax, an issue that was peripheral to Wells' data. Webb and Wilshire (1979) revisited Wells' (1961) site and concluded that secondary succession had occurred; however, the role of individual species in the succession was ambiguous.

Karpiscak (1980) studied the invasion of annuals and perennials into abandoned agricultural fields in the Sonoran Desert of southern Arizona. He found that the initial colonizers were nonnative annuals such as <u>Salsola</u> <u>iberica</u>, and that these annuals were sequentially replaced by other annual and perennial species with time. Karpiscak (1980, p. 156) argued that Shreve could not have viewed succession because the time required for succession to occur is far greater than human lifespans, and that few disturbances occurred during the time Shreve studied the Sonoran Desert. Furthermore, the alien annual species that now dominate the early stages of secondary succession were not as abundant at the time of Shreve's observations.

Vasek and others (1975a, p. 12) studied revegetation along a pipeline corridor in the southern Mojave Desert and invoked an argument for secondary succession similar to Wells' (1961):

> We conclude, then, that the species of the mature creosote bush scrub community have some capability as colonizers, and that the primary colonizing species form a small but significant fraction of the mature creosote bush scrub community. Thus, a characteristic of the creosote bush scrub community is that its species are probably adapted in varying degree to continual, but relatively slight disturbance. Within this relatively sparse vegetation there is always some open ground subject to soil shifting, wind and water erosion, and other slight disturbances, and stands of creosote scrub occur in a variety of successional stages.

Vasek and others (1975a) combined observations and data to formulate this conclusion. Lathrop and Archbold (1980b, p.

225) agreed with Vasek and others but noted that in some cases the colonizers of disturbed sites had the same species composition as the undisturbed assemblage. Vasek (1980a, p. 147), studying secondary succession in an excavation in the Mojave Desert, stated that succession in deserts is comparable to succession in other climatic regimes. However, the pioneer species Vasek found were also members of the undisturbed assemblage (p. 139); hence, the succession Vasek reported is similar to the revegetation patterns observed by Muller and Shreve.

Vasek and Lund (1980) presented an autogenic model of primary plant succession on the margin of a playa in the southern Mojave Desert. In their model, halophytes become established in mud cracks in the playa and accumulate mounds of eolian sediments. Eventually, Atriplex torreyi (saltbush) is able to colonize these mounds, which are less saline than the playa clays. The individual Atriplex grows large and in turn traps more sediments on its mound. The mounds eventually are colonized by the saltbush scrub assemblage surrounding the lake. Although the composition of vegetation at a site changes predictably with time, the substrate also changes from salt-bearing clay to relatively salt-free sand through the addition of eolian sediments.

Vasek (1983, p. 22) combined his ideas with those of Whittaker (1975) and Pickett (1976) and described five stages of succession especially important in deserts:

(1) Early stages of succession are characterized by communities with colonizing individuals with relatively uniform, low stature, and rather short life spans.

(2) The commmunity increases in height, structural complexity, stratification, and biomass as the early successional species are replaced by later successional species and by elements of the mature community.

(3) Productivity and species diversity increase, as does niche complementarity, as the community increasingly affects the microclimate and soil development.

(4) A shift from producing to maintaining, i.e., a decrease in productivity, occurs as late successional species are replaced by longer-lived climax species.

(5) As very long-lived species accumulate biomass, productivity stabilizes at maintenance levels, intermediate long-lived species gradually decrease in population size and extreme stability prevails as selection for competitive ability results in dominance by one or a very few long-lived species.

This model states that autogenic processes are important in the early stages and that a climax community will be attained. Vasek's model is very similar to that proposed by Clements and does not account for successions involving little or no compositional change.

MacMahon (1980, p. 30, 32; 1981, p. 27) suggested that the conspicuousness of succession among assemblages in different climatic regimes may be related to the amount and variability of rainfall. Rowlands (1980, p. 105) stated that plant succession does occur in arid and semiarid regions, but he apparently considered succession as dependent on the species composition of the assemblage. Rowlands' model, termed "parasuccession" (p. 104), lies conceptually between the models of Shreve and Vasek. Zedler (1981, p. 426-429) suggested that successional concepts and terminology developed for forest ecosystems are inadequate for application to desert successions. Single events that would qualify as a disturbance in deciduous forests would produce little or no compositional change in arid ecosystems; and when there is a compositional change in arid ecosystems, it does not seem to be part of a predictable, unidirectional successional sequence.

Much of the preceding controversy stems from which definition or model of succession each researcher used. Conclusions from many of these studies are based on deductions from incomplete observations. In addition, some researchers have formulated widely applied succession models that are based only on studies of limited geographic areas. Some of the controversy involves the importance or lack thereof of soils and soil-formation rates. Soils do form in arid climates, albeit slowly (see Gile, 1975; Gile and others, 1981). Most models of primary succession (Muller, 1940; Shreve, 1942; Pianka, 1974; Beatley, 1976) have not considered soil-formation rates or the local effects of individual shrubs on soil chemistry.

Individual plants alter the chemistry of desert soils (Roberts, 1950; Paulsen, 1953; Charley and West, 1975; Romney and others, 1980). Wallace and others (1980, p. 217) asserted that the division of the desert surface into highly productive areas directly under shrub mounds and poorly productive areas elsewhere is of the "utmost importance to the maintenance of the Mojave Desert type of ecosystem." Garcia-Moya and McKell (1970, p. 86-87) concluded a study of soil nitrogen in a Mojave Desert wash assemblage with the statement:

> Accumulation of plant debris and fine soil adds significantly to the soil organic matter in the vicinity of a shrub ....Thus, the potential contribution of nitrogen from the shrub when it dies, the accumulated litter and organic matter under the shrub, and the nitrogen in the surface layer of soil under the shrub canopy all create "islands of fertility" in association with desert shrubs.

This study and studies in other arid regions (Batanouny and Batanouny, 1968; Sharma, 1973; Sharma and Tongway, 1973; Tiedemann and Klemnedson, 1973) demonstrate that desert shrubs do significantly affect soils. The greater abundance and different species composition of desert annuals under shrubs than in intershrub areas (Muller, 1953; Halvorson and Patten, 1975) further illustrates this effect. Under shrubs, more nutrients are available, evaporation is decreased, and temperature extremes are reduced (Rickard, 1965; Charley, 1972; Wallace and others, 1980; West, 1983b). Blackburn (1975) found that infiltration rates on Artemisia-dominated mounds were three to four times greater than on intershrub surfaces in Utah. The importance of shrubs in the establishment of saguaros (Cereus giganteus) and other desert succulents is well established for the Sonoran Desert (Turner and others, 1966; Steenbergh and Lowe, 1976, 1977). Mycorrhizae (root fungus) in plant litter is known to help in survival of Larrea seedlings in Death Valley (Sheps, 1973). Although the importance of this autogenic process has not been established in a successional framework, the existence of an autogenic component in the dynamics of desert assemblages cannot be ignored.

How much compositional change is required for the observed vegetation dynamics to be declared a succession is another controversial issue. Are colonizing species always members of the undisturbed assemblage (hence no succession; Muller, 1940; Shreve, 1942; Beatley, 1976), or are they members of different assemblages that invade disturbed sites (hence succession; Wells, 1961; Vasek and others, 1975a; Vasek, 1980a, 1983)? This argument depends upon which model of succession is used and whether the size of the plant assemblage is important. Wells (1961) argued for succession based on the occurrence of species in upland sites that normally inhabit washes. On the other hand, Egler (1962) argued against succession because small washes pervade Wells' site, leading to integration of wash and upland assemblages. The extreme case of whether succession occurs in an assemblage composed of two species, as occurs at low elevations in the Mojave Desert, depends on whether one defines succession according to the Clementsian view (for example, Hunt, 1966) or some related model, or whether one defines succession merely as changes following disturbances (for example, F.C. Vasek, written commun., 1981).

This review indicates that the concept of desert succession is controversial, involves many semantic arguments, and has been inadequately documented. Vasek and Lund (1980) firmly established an autogenic primary plant succession on the margins of a dry lake in the southern Mojave Desert. Dry lakes, however, constitute only 1.1 percent of the land surface area in the deserts of the Southwestern United States (see Cooke and Warren, 1973, p. 53). Since alluvial fans occupy a much larger percentage of desert surface area (31 percent), studies of vegetation dynamics in assemblages on alluvial-fan surfaces might be more useful in developing succession models for arid environments.

Recovery of Desert Vegetation

Utility corridors in the Mojave Desert have provided information on recovery of vegetation following disturbance. Although utility corridors are the most often used sites for artificial revegetation attempts (Kay, 1979), most of the disturbed land nearby is abandoned to recover naturally once the pipeline or transmission line is in place. Vasek and others (1975a) studied a 12-yr-old pipeline corridor in the southern Mojave Desert. They found that revegetation was highly variable; in general, the most productive sites showed the most recovery, as indicated by the reestablishment of "long-lived" perennials. Vasek and others (1975a, p. 10) used a linear extrapolation to estimate 30 to 40 yr for restoration at the most productive sites, but they further stated that the linear model is unrealistic and that "many centuries" is probably a more realistic estimate (p. 12).

Vasek and others (1975b) studied 33-yr-old transmission-line corridors in the same regions that showed varying degrees of disturbance ranging from "slight" under transmission wires to "drastic" under pylons. They found that the contribution by Larrea to the total plant cover under the pylons was 12 to 73 percent lower than its contribution in the undisturbed area (p. 122-123). The total ground cover, however, was higher under the pylons than in the undisturbed area in four of five study areas, with a large contribution in cover coming from short-lived species, including Hymenoclea salsola (cheesebush). The variability of recovery under the pylons was high compared with the less-disturbed areas. Vasek and others (1975b, p. 129) concluded that after 33 yr revegetation has occurred to the extent that the quality of vegetation, as measured with an index of cover contribution by long-lived perennials, approaches that of the undisturbed areas. Vasek and others also found that vegetation levels under the wires and along road edges were slightly enhanced, apparently because of water harvesting (Johnson and others, 1975).

Lathrop and Archbold (1980a) studied revegetation along two Mojave Desert aqueducts constructed in 1913 and 1970. Using a linear estimate of aboveground biomass calculated from total-percentage cover data, they estimated a recovery time of about 60 yr for the aqueduct right-of-way. The shrubs Chrysothamnus nauseosus and C. paniculatus (rabbitbrush) contributed the greatest biomass of shrubs (34-38 percent) in the 1913 right-of-way but were insignificant (1.5 percent) in the control area; similarly, the biomass contribution of Chrysothamnus was 19.5-21.7 percent along the 1970 aqueduct compared with 0.9 percent in the control area), although Hymenoclea contributed the greatest biomass (25.1-30.6 percent; table 2 of Lathrop and Archbold, 1980a., p. 142). They concluded that the vegetation along the 1913 aqueduct, while virtually recovered with respect to total cover, biomass, and cover contributed by "long-lived" species, is "subclimax vegetation" (p. 146-147).

Lathrop and Archbold (1980b) studied numerous utility corridors throughout the southern Mojave Desert. They concluded that the predictability of recovery times is difficult and dependent on the degree of disturbance; the site productivity characteristics, including soil quality, climate, and species composition of the undisturbed vegetation; the proximity and relative lifespan for colonizing species; and the variability of vegetation, soil, and intensity of disturbance within the area (p. 224). Using a linear model to estimate biomass (p. 224), Lathrop and Archbold (1980b, p. 225) predicted a recovery time of a century. Lathrop and Archbold (1980a, b) stated that an estimate of recovery based on vegetative composition could be "at least three times greater" than the estimate based on biomass, assuming that recovery follows a linear trend.

Webb and Wilshire (1979) studied the recovery of desert vegetation in the Mojave Desert ghost town of Wahmonie, Nevada (fig. 1). The species composition of vegetation in the townsite (abandoned 51 yr), dominated by Hymenoclea and

Stipa speciosa (needlegrass), was different from that of the surrounding vegetation, which was dominated by Larrea. The recovery time of soil compaction was estimated to be a century (p. 296), and a comparison of compacted versus noncompacted sites indicated a strong influence of compaction on revegetation (p. 298). The recovery time for total plant cover was estimated to be 40 yr (p. 300). The data from this study are compared with those from ghost towns in Death Valley National Monument in a later section.

Life-History Strategies

Estimates of recovery depend, in part, on the analyses used to describe an assemblage. Most recovery studies indicate that nonspecific population parameters, such as total plant cover, are reestablished much sooner than specific parameters, such as species composition. Vasek and others (1975a, b) developed an index based on the longevity of individual species to take into account both the quantitative and qualitative parameters of a given assemblage. To calculate this index, however, it is necessary to categorize perennials into longevity classes on the basis of "size or long-term observation" (Vasek and others, 1975a, p. 3). Data on the longevity of Mojave Desert species are very scarce, and recent studies (West and others, 1979) have questioned the importance of longevity in assemblage stability. Longevity is an important aspect of stability, but it should be considered together with other species attributes that affect plant assemblages.

In order to compare the rate and mechanics of recovery among different assemblages, it is necessary to compare the attributes of each species that affect the revegetation pattern. Life-history strategies are categories into which species can be classified according to these attributes. In reality, life-history strategies are as numerous as the species themselves, wherein each strategy is a set of attributes that has evolved in response to a fluctuating environment and interaction with other species. However, a basis of comparison is needed in order to contrast revegetation across different assemblages, and the use of strategy classification appears to be the most appropriate.

Grime (1979, p.7) presented three primary strategy classifications for all plants: (1) competitors, which exploit conditions of low environmental stress and low external disturbance; (2) stress tolerators, which are adapted to conditions of high environmental stress and low disturbance; and (3) ruderals, which are adapted to conditions of low stress yet high disturbance. These strategies have been reconciled with the more familiar r- and K-selection strategies of MacArthur and Wilson (1967; Grime, 1979, p. 52).

The three strategies are end points in a continuum of possible strategies. Grime (1979, p. 56) also described secondary strategy classifications within this continuum. Two are important for this discussion: (1) stress-tolerant ruderals—annual and perennial species found in unproductive environments with short lifespans, high reproductive capacity, and an ability to colonize disturbed sites quickly; and (2) stress-tolerant competitors—perennial species found in unproductive environments with relatively short to long lifespans, low to medium reproductive capacity, and an ability to survive without abundant resources. For desert perennials, the strategies available appear to be the extremes of stress tolerators, stress-tolerant ruderals, and stress-tolerant competitors (Grime, 1979, p. 150). Grime (1979, p. 24, 67, 149) considered most desert perennials as stress-tolerant competitors, with some categorized as stress tolerators. His framework for grouping plants according to life-history strategy appears in table 1.

The use of Grime's classification scheme as a tool in understanding revegetation is limited by its degree of generalization. The criteria for classifying a species into a particular life-history strategy are numerous and, in many instances, either poorly defined or speculative. Rarely will a species have all the characteristics of one strategy as defined by Grime; in some cases, a species may have characteristics that fit a number of strategies. Consequently, the researcher must determine which life-history characteristics are important to the dynamics under study. This subjectivity can lead to circular arguments. For example, classifying a species as long lived based on its occurrence in a successional sequence will probably lead to the conclusion that long-lived species dominate the later stages of succession (for example, Vasek and others, 1975a, b; Vasek, 1980a, 1983).

Furthermore, Grime (1979, p. 76) notes that there is a large quantity of published evidence for genetic variation within a species, and that this variation is sufficient to "enlarge substantially the strategic and ecologic range of the species." He cites several papers describing a common European grass with populations that "differ considerably in life-history." Populations of the same species adapted to local conditions along an environmental gradient, such as elevation, are often termed "ecotypes," and several researchers have emphasized the importance of ecotypes in understanding vegetation dynamics in the Mojave and Great Basin Deserts (terms apply to plant ecology, not physiography; Wallace and others, 1980). A population at one end of a species' environmental gradient may exhibit a different life-history strategy than a population at the other end.

However, Grime's approach allows a finer resolution for classification than does the r and K approach of MacArthur and Wilson (1967), and it includes important aspects of adaptive strategies not taken into account by the longevity approach of Vasek. Thus, Grime's approach provides a more powerful analytical tool in characterizing revegetation across sites with different species composition. However, it is important to realize the limitations and weaknesses of Grime's approach before application.

Two aspects of life history not explicitly considered by Grime but possibly of importance are the species' carbon-reduction pathway and mycorrhizal (root fungus) status. Three types of photosynthetic strategy occur in plants: C3 or Calvin cycle, C4 or Krantz cycle, and CAM or Crassulacean acid metabolism (McNaughton and Wolf, 1979, p. 106-107). The C3 pathway is the most common, while CAM species tend to be succulents that are adapted to water conservation. C4 species are intermediate between C3 and CAM species in water-use efficiency.

The ecological significance of these differences is unclear (McNaughton and Wolf, 1979). However, because C4 species have a better water-use efficiency, higher temperature optima for photosynthesis, and tend to be "weeds" in deserts (Syvertsen and others, 1976, p. 312), they could possibly compete better than C3 species in the more stressful conditions inherent in the early stages of succession. Therefore, the C4 pathway may be an attribute of ruderal species. Johnson (1976, p. 146) reported that 85 percent of the flowering plants in the California deserts are C3 species, while 11 percent are C4 species and 4 percent are CAM species. Although this figure is preliminary, it does suggest that the C4 species are relatively unimportant in the Mojave Desert (Johnson, 1976, p. 152).

Reeves and others (1979) suggested that the lack of endomycorrhizae in roots may characterize species that behave as ruderals. Reeves and others found that 99 percent of individuals in an undisturbed Artemisia tridentata assemblage in Colorado were endomycorrhizal, whereas only 1 percent of the individuals colonizing a disturbed road were endomycorrhizal. Endomycorrhizae benefit the host plant by increasing its ability to absorb phosphorus, nitrogen, and other elements (Clay, 1981), by increasing its growth rate (Moorman and Reeves, 1979), and possibly by increasing its water-absorption ability. Sheps (1973) found that addition of "fungal-infected desert litter" improved survival and growth of Larrea seedlings in Death Valley. Endomycorrhizal infections increased the ability of Chrysothamnus nauseosus to colonize mine spoils in New Mexico (Lindsey and others, 1977). The percentage of mycorrhizal species was greater in disturbed than undisturbed semiarid areas in southern Arizona (Clay, 1981). Wallace and Romney (1972, p. 277-278) found abundant mycorrhizal fungi associated with the roots of most common Mojave Desert species; this finding suggests that mycorrhizal status is not a distinguishing characteristic of life-history strategies in the Mojave Desert.

The paucity of data on Mojave Desert perennials prevents a quantitative assessment of life-history strategy, as presented by Grime (1979, fig. 18, p. 73). However, some species can be tentatively classified under Grime's framework based on the characteristics of the life-history strategies (Grime, 1979, p. 48-49; table 1). Larrea is an archetypal stress tolerator on the basis of its longevity (Vasek, 1980b), evergreen leaves, low palatability, and ability to flower under any favorable conditions (Kay and others, 1977b). Hymenoclea salsola and Stipa speciosa are probably stress-tolerant ruderals because they are perennials with short lifespans and small stature, have the ability to quickly colonize disturbed sites, and can produce large quantities of seeds (Kay and others, 1977a). Salsola iberica is an archetypal ruderal because of its weedy nature, high seed production, and ability to colonize disturbed sites quickly (Shields and Wells, 1962; Rickard and Sauer, 1982; Karpiscak and Grosz, 1979; Karpiscak, 1980). Similarly, other Mojave Desert species can be tentatively classified according to Grime's framework based on published accounts (table 1). The rationale for the assignment of life-history strategy is based largely on observations of morphology, reproductive capacity, and behavior in disturbed sites; data are sparse for seed production, demography, or physiology for each species. Hence, this classification is tentative and should be tested against experimental data.

The Succession Model of Grime

Grime (1979) also presented a conceptual model of succession to accompany his life-history strategy framework. Although his model is based on his classification scheme, its verification does not necessarily follow acceptance of his life-history framework. However, one of the major criteria for Grime's classification scheme is the behavior of a species in a disturbed site; consequently, attempts to separate his classification framework from his successional model are difficult. Based on the premise that life-history strategies determine the course of succession, Grime (1979, fig. 42, p. 151) depicted succession in an unproductive (desert) habitat as progressing from ruderals, the initial colonizers of a disturbed site, through successive stages of stress-tolerant ruderals, stress-tolerant competitors, and stress tolerators. This model is simplistic because often species of all four life-history strategies are present at any one time, and the effects of allogenic processes are ignored.

Grime's classification framework and his successional model are used in this paper for two purposes. The first is to characterize succession across different but related assemblages. The second is to gain an insight into the use of Grime's classification framework and the value of his model in depicting succession. Species will be classified for two study areas, a primary succession sequence in Wood Canyon and a secondary succession sequence in the Greenwater district.

Paleoecology of the Death Valley Region

Climatic changes are an important allogenic force behind plant succession. Part of the difficulty in interpreting spatially distributed vegetation assemblages using the temporal framework of succession is the lack of knowledge of late Holocene climatic history. Despite many years of paleoclimatic study of the Southwest, relatively little is known about Holocene climatic fluctuations. It is generally agreed that a major climate change occurred at the beginning of the Holocene, although the timing and magnitude of the change are much debated.

An informal definition of epochs within the late Quaternary is needed for discussion of paleoclimates, paleoecology, and the ages of deposits. For the purposes of this paper, the Pleistocene-Holocene boundary, normally defined as 10,000 yr B.P. (Sohl and Wright, 1980; Palmer, 1983), is considered to be 11,000 yr B.P. for consistency with the paleoecological record (Van Devender, 1977). The late Pleistocene refers to 11,000 to 70,000 yr B.P. and the latest

Pleistocene refers to 11,000 to 22,000 yr B.P. The Holocene is divided into early, middle and late intervals in accordance with the paleoecological record (Van Devender, 1977) with ages of 8,000 to 11,000 yr B.P., 4,000 to 8,000 yr B.P., and 0 to 4,000 yr B.P., respectively.

Paleoecological records show that some plant assemblages of the latest Pleistocene were similar to those now found 500 to 1,000 m higher in elevation, or at more northerly latitudes. Convincing evidence for these changes is derived from the analysis of fossil packrat middens. Each midden, a debris pile left by Neotoma sp., contains plant parts collected from the local area, and therefore its age can be determined using radiocarbon analysis. The most complete fossil records from the vicinity of Death Valley come from the studies of Wells and Berger (1967) and Spaulding (1983) at the Nevada Test Site in southern Nevada (fig. 1). Their records document vegetational changes from 18,000 yr B.P. into the early Holocene.

Most plant species occurred at lower elevations during the late Pleistocene than today. At present, limber pine (Pinus flexilis) grows above 2,300 m in elevation (Beatley, 1976, p. 68), piñon (P. monophylla)-juniper (Juniperus osteosperma) assemblages occur above 1,900 m (Beatley, 1976, p. 67), and desert shrub assemblages occur below 1,900 m on the Nevada Test Site. A packrat midden dated at 41,300 yr B.P. containing fossils of a piñon-juniper assemblage was collected from a site now dominated by Larrea near Greenwater townsite (fig. 1; Cole and Webb, 1985). The piñon-juniper type of assemblage has not been recorded in the latest Pleistocene. Packrat middens dating from 18,000 yr B.P. on the Nevada Test Site record a P. flexilis and shadscale (Atriplex confertifolia) assemblage occurring as low as 1,800 m in elevation; a juniper-desert shrub assemblage was present at lower elevations (Spaulding, 1981, 1985). At the end of the Pleistocene (11,000 yr B.P.) the juniper-desert shrub assemblage moved upward and became limited to elevations above 900 m, although this assemblage remained below its modern elevational limit well into the Holocene (Van Devender, 1977, p. 190).

The now-widespread piñon-juniper assemblage reappeared in the early Holocene at elevations down to 1,500 m. P. monophylla, not recorded in 15,000 to 11,000 yr old middens on the Nevada Test Site (Spaulding, 1981), appears in the early Holocene while the evidence of P. flexilis in the fossil record decreases. Extremely xerophytic species such as Larrea and Ambrosia dumosa (burrobush) have not been found in early Holocene fossil sites as low as 800 m. Although assemblages similar to modern Larrea assemblages have been recorded as early as 10,000 yr B.P. in the Colorado Desert (K.L. Cole, unpub. data), Larrea probably arrived in the Death Valley area during the middle Holocene. Spaulding (1980) found fossils of Larrea in Eureka Valley, 150 km northwest of Death Valley, in middens as old as 3,930 yr, while Larrea was absent in several older middens.

Vegetation assemblages have continued to change throughout the Holocene. In the Sheep Range of southern Nevada, desert shrub assemblages replaced piñon-juniper woodlands by the middle Holocene (Spaulding, 1981, p. 191). Small elevational shifts occurred in the distribution of some species during the middle and late Holocene. Piñon-juniper assemblages occurred as much as 200 m below their modern limits at about 3,500 yr B.P. At higher elevations, the distributions of P. flexilis and bristlecone pine (P. longaeva) also may have been slightly lower in elevation at about 1,600 yr B.P. Fossils suggesting modern vegetation assemblages were found in middens dated at about 800 yr B.P. (Spaulding, 1981, p. 194).

In the Grand Canyon, most modern dominant species replaced Pleistocene species by 8,400 yr B.P. (Cole, 1982, p. 1143; Phillips, 1977). The lower limits of piñon-juniper assemblages may have been higher than their present distributions in the middle Holocene. These records are consistent with the first half of the warm-dry Altithermal proposed by Antevs (1955) for the Great Basin Desert. Five packrat middens younger than 2,300 yr old contain evidence of plant assemblages that are very similar to modern assemblages (Cole, 1981).

Other indicators of paleoclimates are consistent with the distribution of vegetation assemblages as indicated by packrat middens. Pollen analyses (for example, Mehringer, 1977) are generally consistent with the midden record. Changes in hydrologic conditions suggest Pleistocene-Holocene changes in water balances. Mehringer (1977, p. 113) reports that lakes began to dry in the early Holocene, and that the present water balance was attained by the middle Holocene. Smith (1968) reports that Searles Lake, southeast of Death Valley, had dried up by 9,000 yr B.P. However, Hunt and Mabey (1966, p. 2) report that a 10-m-deep lake was present in Death Valley during the middle Holocene, in contrast to the proposed warm-dry climate for that time (Antevs, 1955). This lake may have formed in the climatic conditions that were conducive to the lowering of woodland limits at about 3,500 yr B.P. in the Sheep Range (Spaulding, 1981). Based on an analysis of tree-ring widths and upper and lower elevational limits for P. longaeva, LaMarche (1973, p. 653-658) concluded that conditions at high elevations (2,700 to 3,500 m) were warm and dry during the middle Holocene.

Paleoclimatic interpretations are often complicated because vegetation assemblages rarely behave as units during climatic fluctuations, but rather as individual species that change their distribution. For example, shadscale (Atriplex confertifolia), a xeric dominant of Great Basin Desert assemblages, occurred 500 m above its present highest elevation around 15,000 yr B.P., whereas most other species normally associated with shadscale grew at lower elevations than at present (Van Devender and Spaulding, 1979, p. 708; Spaulding, 1981). Factors such as migration following a climatic change (Davis, 1969), vegetational inertia (Smith, 1965; Gorham, 1957), and the retention of Pleistocene soils (Cole, 1981) also determine the arrival times of species at their modern distributional limits. Faunal interaction with vegetation is another effect that is poorly understood. These factors create a lag time between a climatic change and changes in vegetation assemblages. The study of modern ecosystems usually requires the assumption that modern vegetation is in equilibrium with fauna and climate and that no changes will occur without a climatic change. The presence of Holocene packrat middens several hundred meters from Greenwater and Gold Valley townsites (fig. 1) provides some information on the variability of vegetation assemblages during the late Holocene.

METHODS

Soil and vegetation measurements were made on debris flows in Wood Canyon; on alluvial terraces in Gold Valley; in and adjacent to the abandoned townsites of Greenwater, Furnace, Kunze, Gold Valley, and Skidoo; and along the corridor of the dismantled Skidoo pipeline (fig. 1). Numerous methods were used to quantitatively describe desert soils and vegetation. Once a townsite or geomorphic feature of interest was located, study sites were selected based on the variability of soils and vegetation and the history of the site. During the fieldwork of this project (May-June 1981; October and December 1981; March 1982; April and May 1983), several methods were tested to determine their accuracy, precision, and sampling properties.

Study-Site Selection

Study sites were selected after an initial reconnaissance. Criteria for the selection were (1) spatially uniform vegetation, (2) spatially uniform soil texture and surficial rock cover, (3) large enough area to be representative of surrounding vegetation and soil, (4) temporal and spatial uniformity of disturbances, and (5) the availability of nearby controls representing undisturbed conditions.

Uniformity in geomorphic surface and vegetation usually was determined visually. All townsite study areas were on alluvial fans with surfaces of approximately the same age and texture as the parent material. Aerial photography was used to determine the extent of geomorphic surfaces and disturbances and to locate possible representative control sites. Large-scale, black-and-white aerial photographs were available for different years at each study area. All Death Valley National Monument sites were photographed in 1948 (U.S. Geological Survey, 1:48,000), 1969 (Death Valley National Monument, 1:36,000), and 1976 (Death Valley National Monument, 1:26,000). The 1948 aerial photographs for Greenwater Valley townsites and Skidoo were enlarged to 1:24,000 scale for field mapping of disturbances.

Soils

Soils were described according to the taxonomy of the Soil Survey Staff (1975, p. 459-477). Soil pits were located in the approximate center of the geomorphic surface or disturbed site under consideration. Soil textures were determined analytically using sieves and the hydrometer method (Day, 1965). Calcium-carbonate content was measured using the gravimetric (Allison and Moody, 1965, p. 1386-1387) and the Chittick methods (M.N. Machette, written commun., 1982) on the <2-mm soil fraction.

The degree of residual compaction in townsite soils was measured and compared with undisturbed soil and soil in active roads. This analysis is based on the assumptions that the soil in a townsite was compacted to the same degree when the townsite was occupied as the soil in the active road was at the time of measurement, and that the soil in the control did not receive significant use during occupation. We justified the latter assumption by choice of control sites away from the center of the townsite, and the former assumption by the mechanics of compaction. Within the magnitudes of the ground pressure applied by feet, hooves, or wheels, soil density should increase logarithmically with increasing application of surface pressure to a maximum density (Webb, 1983). Soil compacts more easily when wet than when dry (Webb, 1983), and all townsites were occupied during winter months. Given the duration of occupation (9 months to 11 years), trampling most likely would have been ubiquitous and the soil compacted to a uniformly high level.

Sites for soil measurement were selected nonrandomly to obtain a representative sample of the soil properties. Sample points were always located in intershrub areas; this introduces the bias of probable higher compaction. The sample points were also distributed around the study site to average the soil properties measured. All measurements were considered indices of compaction, not absolute measures of the soil properties.

The soil properties measured were penetration depth, penetration resistance, shear strength, bulk density, and moisture content. Penetration depth was regarded as the depth to which a cone, 920 mm^2 in area with a 30° nose angle, could be pushed into the soil; at least 70 measurements were made at each site. Penetration resistance was measured using a penetrometer equipped with a cone, 130 mm^2 in area with a 30° nose angle, that recorded penetration resistance to depths of 30 cm (Carter, 1967); at least 20 measurements were made at each site. Soil shear strength was measured using the Cohron[1] sheargraph (Karafiath and Nowatzki, 1978, p. 480-481) at Gold Valley townsite. Bulk density was measured using a 54-mm-diameter, thin-walled soil core sampler (Blake, 1965); at least ten 137-cm^3 samples were taken for each site and oven dried to calculate density and moisture content.

Reproducibility of the penetration-depth test was excellent; a remeasurement of a site in Greenwater townsite five months after the initial measurement yielded an identical mean (9.88 cm) with slightly lower standard deviation (1.21

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[1] Any use of trade names and trademarks is for descriptive purposes only and does not constitute endorsement by the U.S. Geological Survey.

cm vs. 1.67 cm) for 70 measurements. The penetrometer measurements were correlated with other, more fundamental indices of soil compaction, including bulk density and infiltration rate (Hillel, 1980, p. 344; Webb and Wilshire, 1979, table 1, p. 295), and can be used to estimate recovery from compaction.

The soil properties measured in the active roads, historically disturbed sites, and undisturbed sites were compared to determine recovery. A linear model of recovery was used at all sites because only three disturbance times could be identified, yielding only two degrees of freedom in the model.

Vegetation

Vegetation Measurements

Vegetation measurements included density, percent cover, and dimensions of individual shrubs. Species identification and nomenclature follow Munz (1974; see table 43). Plant densities were measured using 50-m-long, 2-m-wide belt transects, and percent cover was measured using 50-m-long line intercepts on the margins of the belt transects. Belt transects and line intercepts have been found to be the best methods for sampling density and cover of desert vegetation (Braun, 1974, p. 80). Transects were placed nonrandomly to obtain the best representative sample of each study site. Shrub dimensions were measured on individuals of abundant woody perennials. At least 30 individuals were selected randomly using a point-quarter technique (Cottam and Curtis, 1956, p. 456) with 5-pace spacings within the local transect areas.

Errors in measurement were estimated to permit comparisons and provide an index of reliability for the data. Standard errors of the mean values were calculated for the density and cover transects in each area. The base reliability of the density measurements, assuming an accuracy in count of ±1 individual per transect, was ±50 individuals/ha for each transect; hence, the results for density were rounded to 100 individuals/ha. The major source of error in the density measurements was the problem of definition of an "individual"; some species, particularly Ephedra, can develop into clumps with significant overlap in foliage. For this study, an individual was considered a separate plant from surrounding individuals of the same species if it had less than 50 percent of an overlap. Percent cover was assumed to be accurate to one decimal place because intercepted foliage was measured to the nearest 5 cm in each 50 m of line intercept. Density and cover data were not analyzed using statistics because these variables were not randomly sampled and assumptions concerning the normality of the distributions could not be tested.

Dry-weight biomass was estimated for all species for which volume data could be collected. Volumes were calculated to estimate biomass, but these volumes contained significant errors due to the sampling technique. R. B. Hunter (oral commun., 1981) suggested an operator variability of ±20 percent on volumes of shrubs. This error is small compared with errors due to the definition of individual shrubs and to the variability in shrub shapes. The biomass was calculated as the product of the mean shrub volume (modeled as a right elliptical tube), the mean density, and a regression coefficient relating volume to biomass. The regression coefficients used were derived from species on the Nevada Test Site (R.B. Hunter, written commun., 1981; table 2), a close and comparable geographic area. Biomass regression coefficients vary with geographical area (see table 2), number of samples, operator error, season of measurement, and definition of an individual shrub; consequently, the reliability of the dry-weight biomass figures is questionable, and they cannot be presented without some estimation of error.

A standard error for each biomass calculation was calculated as

$$SE^2 = (V*D*SER)^2 + (D*R*SEV)^2 + (V*R*SED)^2 \qquad (1)$$

where V and D are the mean volume and density, respectively; SEV and SED are the standard errors of the mean volume and density, respectively; and R and SER are the biomass regression coefficient and standard deviation, respectively. Considering the other variables involved in the biomass estimation, the values of SE are probably less than the actual error.

For comparison among sites, biomass values were needed for species without measured shrub volumes. In these cases the mean shrub volume and standard error were either estimated from a sample of less than 30 individuals or assumed to be similar to another population measured nearby. This method introduced an additional error in the biomass estimation that could not be readily quantified, but it was usually small because of the low density of the species.

The cover of cryptogamic crusts was measured at Skidoo townsite (fig. 1), the only site studied with significant presence of crusts. Cryptogamic crusts are composed of nonvascular plants such as lichens, mosses, and algae. Forty 0.5 x 0.2 m (0.10 m^2) quadrats were distributed randomly in disturbed and control sites. Percent cover was estimated visually using the six cover classes as described by Daubenmire (1959). No attempt was made to differentiate taxonomic classes. Standard deviations were calculated for each site and a recovery time was estimated using a linear model.

Ordination

Ordination is a method of graphically arranging sites according to the composition of the vegetation. Ordination generates compositional axes, or directions of change of assemblage composition, which may reflect the more important environmental gradients (Whittaker, 1975) such as elevation, exposure, and disturbance. This technique summarizes assemblage data by producing a two-dimensional graph in which similar sites are clustered together and dissimilar sites are spread apart (Gauch, 1982, p. 118).

Two of the most well known and widely accepted ordination techniques—Wisconsin polar ordination and principal-components analysis—were used. Other techniques exist that may be considered superior (see Gauch, 1982, p. 166-167), but they are not as familiar to most researchers. The Wisconsin polar ordination method (Bray and Curtis, 1957) was selected based on (1) the familiarity of the technique to most plant ecologists, (2) its relative conceptual simplicity, (3) its large yield of information with least computational effort, and (4) the success of the method in identifying otherwise unrecognizable patterns (Whittaker and Gauch, in Whittaker, 1973). However, this method requires a degree of subjectivity in choosing sites as end points of the axes defining the ordination graph.

The similarity index used in the Wisconsin polar ordination method is percentage similarity (PS; Gauch, 1982, p. 112). Percentage dissimilarity (PD) was calculated using 100 percent as the similarity of replicated samples. PS values for replicate samples usually are less than 100 percent; Bray and Curtis (1957) and Beals (1960) obtained average PD values between replications of 82 and 85 percent, respectively. However, the ordination itself is not significantly affected by using 100 percent to calculate PD, because the dissimilarities between sites (as illustrated by geometric distances between the points on the ordination) are relative (Mueller-Dombois and Ellenberg, 1974, p. 279).

Criteria for end-point selection in the Wisconsin polar ordination method included several arbitrary rules developed by Bray and Curtis (1957), Swan and Dix (1966), and Newsome and Dix (1968) in order to reduce the degree of subjectivity. End points were selected based on the greatest difference in the PD values of the data set. In addition, each end point had to have at least three PS values greater than 50 percent; this criterion helps avoid the choice of a site that may be too unrelated to the majority of sites and thus may dampen the spread. In addition, end points for the Y-axis had to lie within the mid-50 percent range of the X-axis; this criterion also serves to eliminate tight clustering. Several end points failed to meet all the criteria but were selected as the best end points available. Readers are referred to Mueller-Dombois and Ellenberg (1974, p. 277-286) and Gauch (1982, p. 126-135) for a discussion of Wisconsin polar ordination.

Principal-components analysis generates axes objectively by deriving successive orthogonal axes according to the maximum variance possible in the data set. This method often gives distorted or ecologically meaningless axes, a problem that is not as significant with the Wisconsin polar ordination method. Consequently, the two methods are complementary (see Gauch, 1982, p. 167). Principal-components analysis uses correlation coefficients as the similarity index. This ordination begins with the same matrix as used in the Wisconsin polar ordination method, except that correlation coefficients are calculated between all sites instead of the percentage similarity. The ordination is developed from the eigenvalues of the resultant square matrix of correlation coefficients. The analysis was performed on the U.S. Geological Survey Multics Computer System using available programs (Miesch, 1982). Readers are referred to Gauch (1982, p. 135-144) or Sneath and Sokal (1973, p. 245-247) for a discussion of the mathematics underlying principal-components analysis.

Reproducibility and Spatial Variability

Reproducibility of the vegetation data was field tested in Gold Valley (fig. 1). Experiments were designed to show (1) the variability introduced by different operators viewing the same transects, and (2) the variability introduced by different operators viewing transects with slightly different placements. In the latter case, transects were roughly marked, and each operator fixed the transect lines before their respective measurements. In the former case, transect lines were fixed, and each operator measured exactly the same transect.

The reproducibility of data for transects in which the operators placed the lines before measurement appears in table 3. Most measurements agree within the presented standard error of the mean values given. Percentage-similarity values calculated for cover were 89, 93, and 89 percent for operators A vs. B, A vs. C, and B vs. C, respectively. PS values for density were 88, 89, and 93 percent for A vs. B, A vs. C, and B vs. C, respectively. These values indicate a high degree of reproducibility.

The reproducibility of data for transects in which different operators measured the same fixed transect appears in table 4. Agreement among the operators is better, with PS values for cover of 94, 92, and 96 percent and for density of 95, 93, and 93 percent for A vs. B, A vs. C, and B vs. C, respectively. Again, a high degree of reproducibility is indicated, which suggests that PS values lower than 80 percent indicate different plant assemblages, as commonly suggested (Gauch, 1982).

Line-intercept data from Greenwater townsite (fig. 1) were analyzed to determine spatial variability problems in sampling specific patches of vegetation. Twelve and fourteen 50-m line intercepts were measured in undisturbed and disturbed sites, respectively. The mean ±1 standard error for 66 PS values for the undisturbed site and 91 PS values for the disturbed site were 68.7±1.2 percent and 69.4±0.9 percent, respectively. The PS values ranged from 35 to 88 percent in the undisturbed site and 48 to 86 percent in the disturbed site. However, the percentage similarity calculated between the undisturbed and disturbed sites, based on the mean values of cover for each, was 52.5 percent. This suggests that two patches of vegetation may be similar if their PS value is greater than 70 percent.

Correlation coefficients were also calculated for the data from Greenwater townsite. The mean ±1 standard error for 66 correlation coefficients for the undisturbed site and 91 correlation coefficients for the disturbed site were 0.60 ±0.033 and 0.69±0.017, respectively. However, the mean correlation coefficient between 168 paired undisturbed- and disturbed-site transects was -0.05±0.15, indicating no correlation. An ordination based on the principal-components analysis (not shown) depicted the undisturbed- and disturbed-site transects as distinctly separate clusters of points.

The importance of variability due to short-term climatic fluctuations with respect to differences in vegetation measured between recovering and undisturbed sites is illustrated by comparison of two studies (Beatley, 1979, 1980; Webb and Wilshire, 1979). The townsite of Wahmonie, Nevada (fig. 1), was built in response to a mining boom and was abandoned in 1928 (Webb and Wilshire, 1979). Beatley (1979, 1980) collected line-intercept data from a small section of the townsite and a nearby control in 1963 and 1975 to measure the fluctuation in cover with fluctuation in climate. In 1979, Webb and Wilshire (1979) collected line intercept data from several areas (including Beatley's sites) to examine the revegetation of the townsite. Beatley included dead vegetation in her total-cover measurement, which Webb and Wilshire did not, and her data suggested that about 12 to 13 percent of the total cover for all her sites was contributed by dead vegetation. Also, Beatley did not measure perennial grasses, which contributed significant cover (up to 7.7 percent) in Webb and Wilshire's measurements. Despite these differences, the percentage similarity and correlation coefficient for Beatley's 1963 measurement and Webb and Wilshire's 1979 measurement in the same undisturbed site (table 5) are 80 percent and 0.94, respectively, which indicates a high degree of reproducibility in measurement of desert vegetation by independent researchers at different times. Also, the climatically induced cover changes over 16 yr (Beatley, 1980) are much less than those observed after 51 yr of recovery in Wahmonie townsite. These results suggest that comparisons between disturbed and undisturbed vegetation assemblages may be obtained reliably regardless of the climatically induced status of the vegetation (that is, whether it is a good or a bad year for plant growth).

PRIMARY PLANT SUCCESSION ON DEBRIS FLOWS IN WOOD CANYON

Wood Canyon, located in the Panamint Range near the western rim of Death Valley (fig. 1), is infrequently subjected to intense storms that result in debris flows. The Wood Canyon case study describes the response of vegetation to this natural type of disturbance. The creation of a surface by a debris flow eliminates the influence of residual biotic effects (MacMahon, 1980, 1981), and primary plant succession occurs. In Wood Canyon, debris flows that occurred at different times are mantled with vegetation assemblages of different species composition, which suggests that soil development may influence revegetation of disturbed sites. The results from Wood Canyon are compared in a later section with results from Skidoo townsite (fig. 1), where revegetation occurred on a different type of disturbance—the abandoned mining-town streets.

Climatic data are sparse in the Panamint Range. The weather station nearest to Wood Canyon is at an elevation of 1,250 m in Wildrose Canyon, 10 km south. This station reports a mean annual precipitation and temperature of 191 mm and 14 °C, respectively, based on a 10-yr record (Kurzius, 1981, p. 14-17; fig. 3). Hunt and others (1966, p. B7) estimate a mean annual precipitation of 250 to 350 mm for the crest of the Panamints. Hence, we estimate the mean annual precipitation at Wood Canyon to be between 200 and 250 mm. Wood Canyon ranges in elevation from 1,585 m at its mouth to 2,350 m on the south rim; hence, its mean annual temperature may be several degrees cooler than the 600-m-lower Wildrose Canyon weather station.

Bedrock on the north and south slopes of the canyon consists of quartzites and metaconglomerates of the Proterozoic Kingston Peak(?) Formation. Bedrock of the eastern reaches of Wood Canyon consists of the Tertiary granite north of the main wash, and Late Proterozoic Noonday(?) Dolomite, and Kingston Peak(?) Formation (after Hunt and Mabey, 1966, plate I) to the east and south of the main wash. Alluvium in the eastern section of the canyon also contains clasts of limestones, schists, and calcareous sandstones. In addition, the granite is capped with a limestone unit.

The vegetation in Wood Canyon can be characterized as Transition Desert Coleogyne assemblages and Great Basin desert Artemisia and Artemisia-Pinus-Juniper assemblages (Beatley, 1976, p. 41-68). The Coleogyne assemblage occupies the entire valley below 1,830 m elevation, and it can be found even higher on most of the south-facing slopes. The Artemisia-Pinus-Juniper assemblage begins at 1,800 to 2,000 m on steep north-facing slopes and at 2,320 m on south-facing slopes to the south of Wood Canyon. It is separated from the Coleogyne assemblage on north-facing slopes by an Artemisia assemblage.

The Coleogyne assemblage in Wood Canyon is a mosaic of vegetation patches with different dominant species. Coleogyne ramosissima (blackbrush) dominates most patches, sometimes to the exclusion of other perennials. However, there are discrete patches where Lycium andersonii (Anderson's thornbush), Grayia spinosa (spiny hopsage), and Ephedra nevadensis (Mormon tea) assume dominance. Lycium, Grayia, and Ephedra also occur in the Coleogyne-dominated patches but vary in proportion to each other and to Coleogyne on different surfaces of the alluvial fans. The boundaries between these patches are sharp rather than gradational and appear to be related to differences in the ages of surfaces on the fan. The plant species found in the study sites at Wood Canyon are listed in table 47.

The Debris Flows

The 1976 Debris Flow

In early February 1976, heavy rainstorms caused flooding and debris flows in the Panamint Range. Total daily rainfall amounts on February 6th to 10th at Wildrose Canyon Ranger Station were 5, 10, 9, 28, and 2 mm, respectively. Roads in Wildrose Canyon were closed because of flooding, and the road from Wildrose Canyon to Furnace Creek was washed out at Emigrant Canyon (Pete Sanchez, oral commun., 1981). The National Park Service took aerial photographs of the entire Death Valley National Monument area during March 1976 and preserved an invaluable record of this event. Intense rainfall apparently fell on the crest of the Panamints between Telescope Peak and Harrisburg Flats, because all the canyons to the west of the crest in this area contain debris-flow deposits and scoured channels. The greatest flood damage and largest debris flows occurred in Wood Canyon and two canyons directly to the north.

Wood Canyon contains a vivid record of the 1976 debris flows (fig. 4) superimposed on older debris flows. Large flows extend from the eastern margins of the canyon, with no new flows originating from the north or south sides of the canyon. Two very large flows originated in the Kingston Peak(?) Formation and Noonday(?) Dolomite on the southeast side of the canyon, while two fairly large and several small flows originated in granite to the east (fig. 5). Flooding concurrent with the debris flows scoured the vegetation from the main drainage (fig. 4), which appeared to have significant vegetation cover in both 1948 and 1969 aerial photographs. Neither the 1948 nor 1969 aerial photographs showed evidence of fresh debris flows, which indicates that debris flows occur infrequently in this canyon.

The northernmost large flow originating in granite, debris flow 1 on figure 5, was examined in detail for surficial and internal morphology. This flow (fig. 6) has features typical of other debris flows (Johnson, 1970, fig. 12.2, p. 435; Bull, 1977, p. 236-239; Costa and Jarrett, 1981, p. 321), including prominent lateral deposits on levees near the fan apex, a poorly sorted matrix ranging from cobbles to fine sand, and snouts composed almost entirely of boulders, cobbles, and gravel (figs. 4-6). At least three waves of deposition are apparent in the aerial photograph, and additional small lobate deposits can be observed in the flows.

A study site was selected on the terminal deposit where debris flow 1 bifurcated into arms on an 8° to 10° slope. The texture of the deposit is poorly sorted, cobbly, gravelly, loamy sand to sandy loam with no apparent bedding (table 6). The terminal deposit appeared to be 1 to 1.5 m thick, and the surface was very rough with large cobbles protruding through a sandy matrix. Cobbles on the surface and in the profile showed little weathering. During deposition, all vegetation in the path of the flow was destroyed, and plants at the margins of the flow were partially buried in debris. A sheet of sand, 1 to 5 cm thick and coincident with the debris flow, extended from the margins of the arms 1 to 10 m onto adjacent deposits.

Vegetation had appeared on the 1976 debris flow by the time of our measurements in June 1981. The most ubiquitous

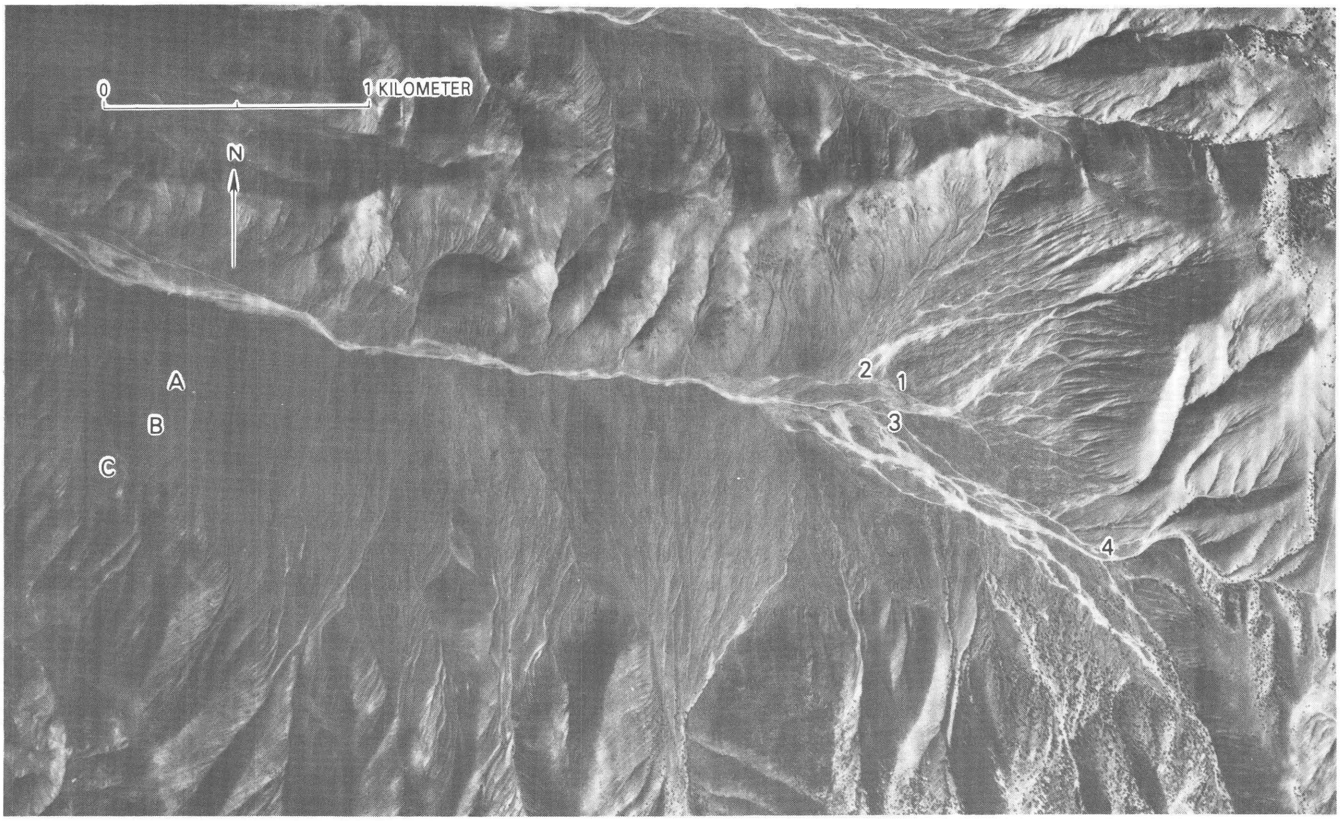


Figure 4. Aerial photograph of Wood Canyon showing recent debris flows. Flows A, B, and C originated in the Proterozoic Kingston Peak(?) Formation and flows 1, 2, 3, and 4 originated in the Tertiary granite. Photographed March 1976 (National Park Service, photograph number DEVA 19-30).

colonizer was Erodium cicutarium, an annual that formed dense stands on some parts of the flow surface. Erodium appeared to be generally responsible for the presence of an organic-enriched A horizon in the soil. Another annual, Bromus rubens, was present on the flow but not to the extent of the Erodium. Few other annuals were observed. Annuals were not measured because of extreme spatial and temporal variability.

The perennial species present on the 5-yr-old deposit were generally not found in the adjacent vegetation (tables 7, 47). The obvious clumping (figs. 5, 7) of colonizing perennials made vegetation measurements difficult to interpret; however, Lupinus excubitus was the dominant species on the arms of debris flow 1. Above these arms, Chrysothamnus nauseosus formed a large clump (visible in the middle distance in fig. 6), and on flows to the south, very large Atriplex canescens individuals dominated the colonizing assemblage. In general, individuals growing on the 1976 debris flows were very large and much more vigorous than the individuals of the surrounding vegetation. In addition, growth of plants on the margins of the flows was also enhanced, probably as a result of increased supply of water from the barren surfaces. Thirty-one species of perennials were found on the 1976 debris flows, thirteen of which were not found in the vegetation on adjacent deposits (see table 47).

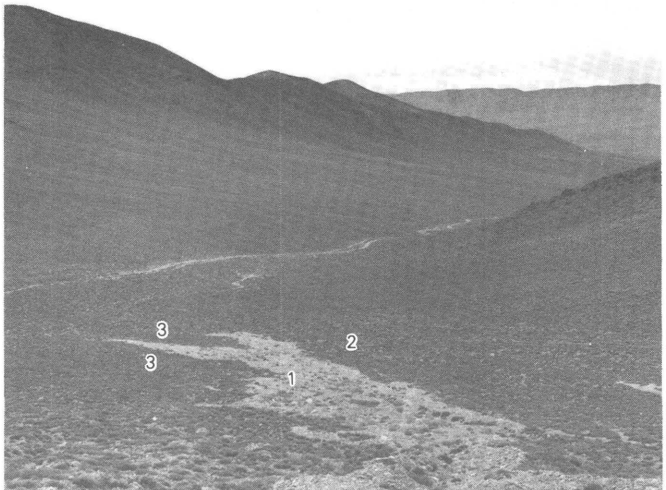


Figure 5. Debris flow 1 and adjacent, older flows 2 and 3 originating in the Tertiary granite in eastern Wood Canyon. View is toward the west. Photographed December 1981.

Debris flow 1 is representative of older debris flows in Wood Canyon. Adjacent, older deposits have surface morphologies and subsurface structures similar to those in the 1976 flows (fig. 7), and thus debris flow 1 can be used to represent the initial state of these adjacent and older deposits.

Older Debris Flows Originating in Granitic Rocks

Examination of deposits near the 1976 debris flows indicated that debris-flow deposits are the most common valley fill exposed in Wood Canyon. A stratigraphic profile in the main drainage shows a series of depositional events from the same source area (fig. 4; table 6). Textural variations suggest that at least four debris-flow deposits are represented in the upper 143 cm of this section. These deposits, each 27 to 45 cm thick, have the pedogenic features of stage I to stage II carbonate horizons (table 6; see fig. 2 for nomenclature on carbonate stages). Cambic or argillic B horizons are not present, probably because the soils are young (Gile and others, 1981). A buried soil below 143 cm is characterized by an argillic horizon and a stage IV carbonate horizon, suggesting a long hiatus in deposition that probably occurred during the late Pleistocene.

Three debris flows were representative of all the flows originating in granite, and an examination of 1948 and 1969 aerial photographs indicated that none had occurred within the last 40 years. Debris flow 2 (figs. 4, 5), 50 m north of debris flow 1, consisted of a heterogeneous mass of fragments of the granite, sandstone, and metaconglomerate of the Kingston Peak(?) Formation, and schist. The snout and the surface of this flow were smoother than those of flow 1, and more fine-grained material was exposed. Some cobbles at the surface and within the soil profile were weathered and easily broken to grus. Debris flow 2, visible on 1969 aerial photographs, was partially covered during the 1976 flows and had the least surface area of all flows measured.

Debris flow 2 is a thin (25 cm thick) deposit overlying coarsely bedded fluvial deposits (table 6). A nearby channel exposure shows a soil developed in the fluvial deposits with a stage II carbonate horizon. Debris flow 2 subsequently buried this soil, and the stage I carbonate horizon in the top, or A horizon, of the fluvial deposit (table 6) is associated with pedogenesis on debris flow 2.

Annuals growing on flow 2 included Erodium and Bromus, with Erodium less abundant on flow 2 than on flow 1. The perennial vegetation on flow 2 is dominated by Ephedra, with Lycium and Grayia contributing significant cover (table 7). Coleogyne contributes 2.9 percent cover on this flow.

Debris flow 3, another older flow that is exposed around the arms of flow 1 (figs. 4, 5), also originated in the granite. It has some strongly weathered cobbles, is fairly smooth, and has a distinct terminus (fig. 7). The soil on the deposit (table 6) has a stage I carbonate horizon, no variations in soil texture with depth, and no B-horizon development. Pebbles in this horizon have continuous carbonate coatings on their bottoms and sides, with weak, discontinuous carbonate coatings on top. Debris flows similar in soil development and surficial morphology to debris flow 3 were the dominant surficial deposit originating from the granite.

Perennial vegetation on debris flow 3 is dominated by Coleogyne with 17.6 percent cover (table 7). Ephedra and Lycium contribute significant cover, but they have lower cover values than on flow 2. Adjacent debris flows, probably correlative with flow 3, had Lycium and Salazaria mexicana growing out of their cobbly snouts. Annuals on flow 3 included Erodium and Bromus, with Erodium less abundant than on the adjacent flow 1.

Debris flow 4, 100 m higher and 1 km southeast of debris flow 1 (fig. 4), has been bisected by a wash, thus exposing the profile of a soil (table 6). Only small remnants of flows of this age, all bisected, occur at the mouths of debris-flow chutes. The presence of a cambic B horizon and accumulation of stage III carbonate in the soil indicate that this flow is much older than flow 3. In addition, the depth to the stage III IIC_{ca} horizon is much greater than the depth to carbonate-enriched horizons in flows 2 and 3, and stage I carbonate appears in all overlying horizons. The respective depths to the stage III carbonate horizon and the superjacent stage I carbonate horizons indicate a polygenetic history; the stage III horizon was probably formed under a wetter climate than the stage I horizons. The presence of stage I carbonate in the A horizon suggests that upper horizons have been eroded; this is not unexpected given the deposit's age and the evidence of channel cutting.

Coleogyne dominates the perennial vegetation on debris flow 4 with 20.6 percent cover, and Ephedra nevadensis contributes an additional 5.5 percent cover (table 7), less than the cover of E. nevadensis on debris flow 3. The presence of Chrysothamnus teretifolius (1.0 percent cover) and occasional Ephedra viridis individuals on debris flow 4 probably reflects the 100-m elevation difference between this flow and the others. However, no other difference in floristic composition was apparent that could be attributed to a factor other than the degree of soil development.

Debris Flows Originating in Metasedimentary Rocks of the Kingston Peak(?) Formation

Three debris flows originating in the Kingston Peak(?) Formation on the south side of Wood Canyon provide additional information on primary plant succession (figs. 4, 8).

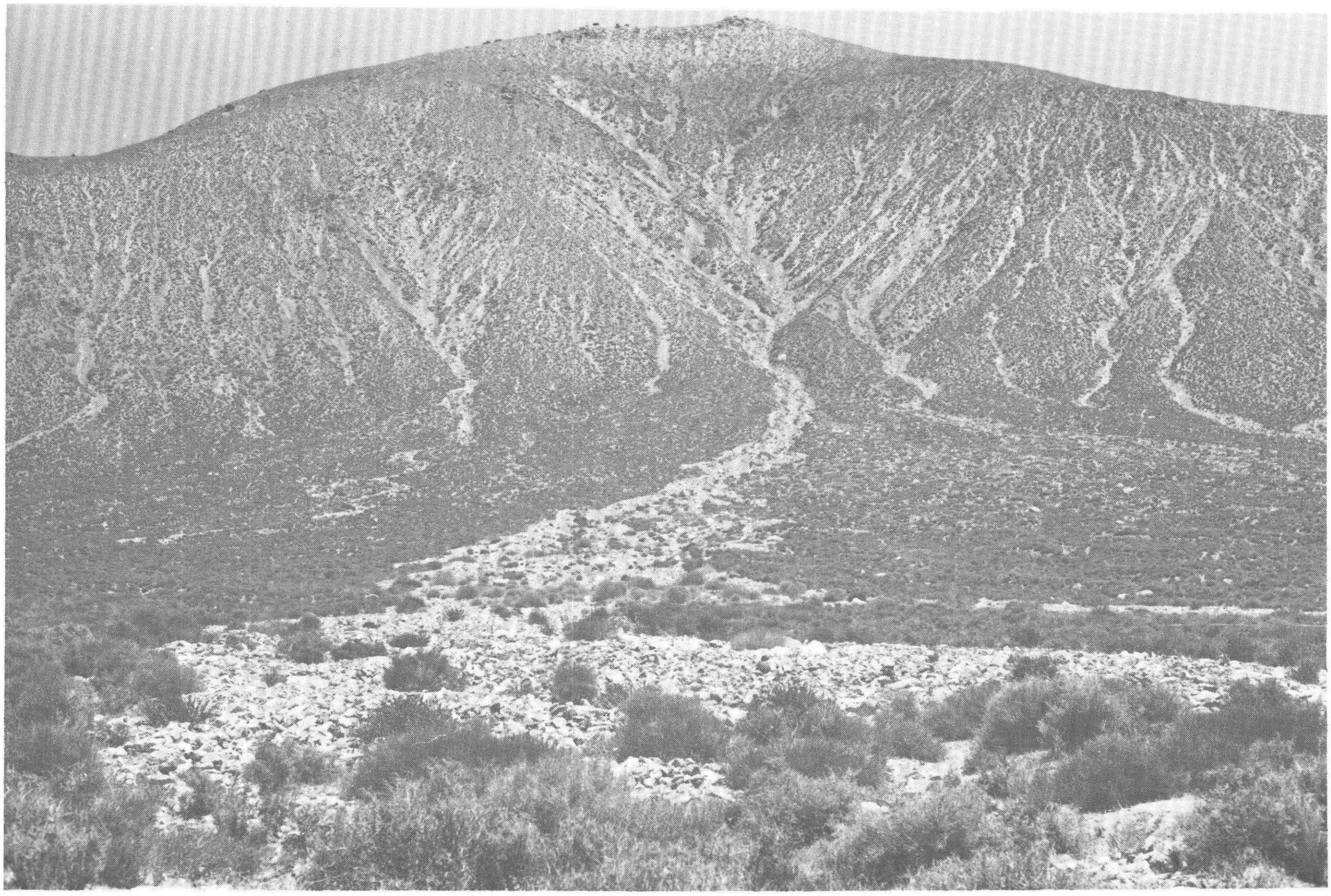


Figure 6. Snout of debris flow 1, viewed toward the east with the source area in the background. Photographed December 1981.

The route of a pipeline from Telescope Peak to Skidoo crosses these deposits (fig. 1) along a distance of 0.5 km, with an elevation difference of about 60 m. These three flows (A, B, and C in fig. 8) are all thickly mantled with vegetation but usually have well-defined snouts, poorly sorted matrices, and prominent lateral levees. They are representative of all debris flows originating from Kingston Peak(?) metasedimentary rocks.

Debris flow A is the lowest in elevation of the flows that the pipeline intersects. Stage II carbonate accumulation, a desert pavement with dark varnish, a vesicular A_{12} horizon, and an argillic horizon characterize the soil on this flow (table 6). Coleogyne dominates the perennial vegetation with 8.2 percent cover, with Lycium contributing an additional 7.3 percent cover (table 8). Debris flow C is the highest flow intersected by the pipeline corridor, and a stage II carbonate horizon, a desert pavement with dark varnish, a vesicular A_{12} horizon, and an argillic horizon characterize the soil developed on this flow (table 6). Vegetation on flow C is dominated by Coleogyne with 13.6 percent cover, and Ephedra nevadensis with 6.6 percent cover (table 8). Intermediate-elevation debris flow B, 40 cm thick and overlying a fluvial deposit, has a soil characterized by a stage I carbonate horizon, a desert pavement with weak varnish, and a weakly developed vesicular A_{12} horizon (table 6). Vegetation on flow B is dominated by Acamptopappus shockleyi, Grayia, and Lycium with 7.8, 7.6, and 6.1 percent cover, respectively; Coleogyne has 2.2 percent cover on this flow.

Estimation of the Ages of the Debris Flows

The ages of the debris flows can be estimated from the degree of soil development. Pedogenesis is a complex function of parent material, topography, climate, biota, and time (Birkeland, 1974). In Wood Canyon, this complex function is simplified because several of the parameters are constant. Parent material and topography are similar for the debris flows originating in the granite and Kingston Peak(?) Formation. Climatic fluctuations during the Holocene have been inferred for the northern Mojave Desert (see section on "Paleoecology of the Death Valley Region"); however, these fluctuations are relatively minor in comparison with current climatic variability (Mehringer, 1977) and can be assumed to

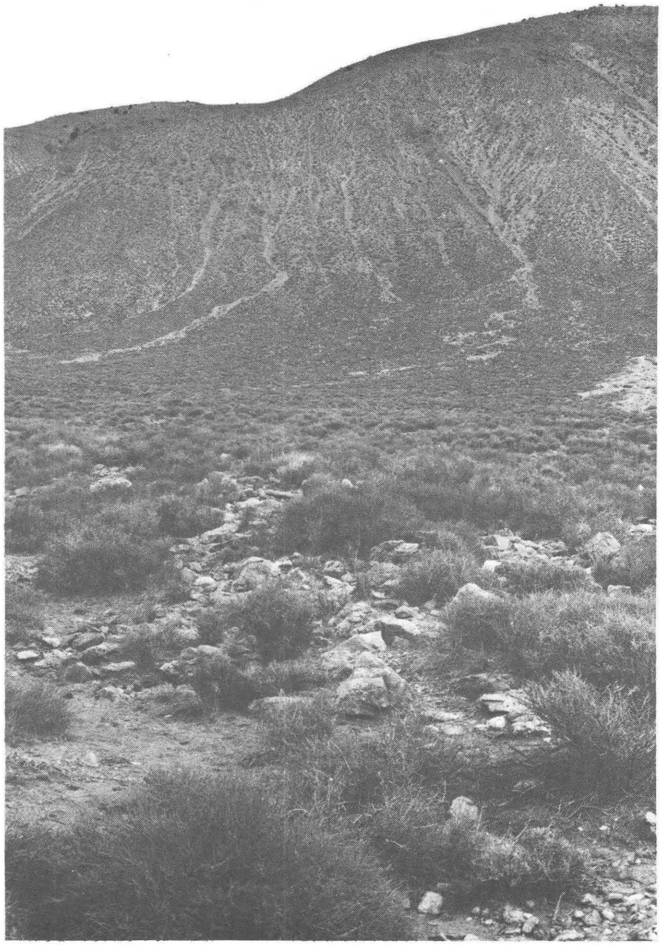


Figure 7. Snout of debris flow 3. Note the similarity with the snout of debris flow 1 in figure 6. Photographed June 1981.

Figure 8. Western Wood Canyon showing the Skidoo pipeline corridor and debris flows A, B, and C. The Skidoo pipeline corridor appears as a vertical line in the center of the photograph.

have had a negligible effect on soil development. Differences in the type of vegetation among the debris flows are slight, and the influence of these slight differences on soil morphology is probably negligible. Thus, differences in soil development on the debris flows mainly reflect differences in age.

The main distinction among the soils on debris flows 1, 2, and 3 is the degree to which carbonate has accumulated in the C horizons (table 9). The origin of carbonate in the soils of Wood Canyon is pedogenic, as distinguished from carbonate deposited along drainages (Lattman, 1973). The distinction between debris flows 2 and 3 involves a subdivision of the stage I carbonate nomenclature of Gile and others (1981, p. 67; see fig. 2 and table 9). The soil on debris flow 2 has continuous carbonate coating on the bottoms of pebbles and cobbles, whereas the soil on debris flow 3 has continuous carbonate coating on the bottoms and sides of pebbles and cobbles. Desert varnish cannot be used to distinguish between flows 2, 3, and 4 because weathering of granite to grus apparently occurs faster than varnish can form.

The soils on the debris flows originating in the Kingston Peak(?) Formation are differentiated by soil development and desert pavement and varnish. The soil on flow B, the youngest, has a lightly varnished desert pavement, no B horizon, and a stage I carbonate horizon. The soil on flow A has a well-varnished desert pavement, an argillic B horizon, and a stage II carbonate horizon. The soil on flow C is similar to that on flow A, although the B horizon on flow C is 10 cm thicker. The difference between the soils on flows A and C is not great enough to estimate a difference in age.

Ages can be assigned to the debris flows based on similarity of soil morphology with soils of other comparable areas that have been dated radiometrically. Correlations of carbonate horizons in different geographic areas are difficult because soil carbonate accumulates at different rates in response to local climate and dustfall (Bachman and Machette, 1977, p. 129-130). Consequently, correlations of soils based on carbonate morphologies are speculative, and the ages assigned are approximations.

The soil chronosequence developed at Las Cruces, New Mexico, is the most detailed and best dated sequence available in an environment similar to Wood Canyon. The mean annual temperature, seasonal rainfall, and influx rate of carbonate in dust are the most important criteria for assessing possible differences in carbonate-accumulation rates between the two sites. Differences in type of vegetation, type of parent material, and Holocene climatic fluctuations are relatively unimportant (see sections on "Soil Processes" and "Vegetation Processes"). The mean annual precipitation is similar between the two areas, although the precipitation in Wood Canyon is winter dominated, whereas that in Las Cruces is summer dominated (fig. 3B). However, the leaching index (Arkley, 1963, p. 239) is higher for Wood Canyon (52 mm) than for Las Cruces (6 mm), which suggests that carbonate in Wood Canyon should accumulate faster than in Las Cruces. The mean annual temperature in Wood Canyon (14 °C) is lower than in Las Cruces (16 °C), a difference that also suggests that Wood Canyon should be conducive to a faster carbonate-accumulation rate.

The Las Cruces area receives a high influx of carbonate in eolian dust (Gile and Grossman, 1979), and the influx rate is believed to be one of the highest in the Southwest (Bachman and Machette, 1977; M.N. Machette, oral commun., 1981). The influx rate of carbonate in eolian dust is unknown for the Panamint Range, but it is assumed to be less than for the Las Cruces area. The prevailing winds in the Wood Canyon area, inferred from Huning (1978, p. 106-107, 119) and personal observations, are from the west and southwest. The mountains west of Wood Canyon are composed of Pleistocene volcanic rocks and Pliocene and Pleistocene fanglomerates and conglomerates derived from Precambrian and Paleozoic rocks (Jennings, 1958; Hall and Stephens, 1962); the Precambrian and Paleozoic strata are primarily metasedimentary rocks, with minor dolomite and limestone. The Argus Range, 30 km west of Wood Canyon, is composed of Paleozoic limestone and metamorphic rocks and Mesozoic granitic rocks (Jennings, 1958). In contrast, the prevailing winds in Las Cruces supply carbonate-bearing dust from limestone and dolomitic limestone in the Robledo Mountains, 20 km to the west. Spring dust storms are common in the Las Cruces area (Gile and others, 1981, p. 19), whereas blowing dust is rare in the Panamint Range. Therefore, contingent on the hypothesis that eolian dustfall is the principal control of carbonate-accumulation rates in desert soils (Bachman and Machette, 1977, p. 126), the soils of the Wood Canyon debris flows are most likely older than those of similar carbonate morphology near Las Cruces.

A comparison of carbonate morphology among soils in Las Cruces and Wood Canyon establishes a chronosequence for the debris flows. Given that increasing development of carbonate horizons indicates increasing age, flow B is younger than flows A and C, flow 2 is younger than flow 4, and flows 3 and B are probably close in age. Debris flows 2, 3, and B are Holocene in age, based on their stage I carbonate horizons (table 6); flows 4, A, and C are late(?) Pleistocene in age.

Absolute ages can be estimated for the debris flows from additional evidence. The climate during the Pleistocene was conducive to a greater effective soil-moisture content than has been the climate during the Holocene (see section "Paleoecology of the Death Valley Region"). This greater effective soil moisture (and greater leaching index) presumably caused precipitation of pedogenic carbonate at greater depths in the soil (Arkley, 1963; Birkeland, 1974). Hence, superposition of carbonate in B horizons suggests that the soil age is greater than the Pleistocene-Holocene climatic change (about 11,000 yr B.P.). The superposition of carbonate in the IIB_{2tca} horizon of flow 4 (table 6) suggests that stage I to weak stage II carbonate horizons characterize the morphology of early Holocene soils.

We assume that well-developed stage I carbonate horizons are characteristic of early Holocene debris flows, and that stage II horizons are characteristic of latest Pleistocene debris flows. Hence, debris flow 2 is late Holocene in age based on a weakly developed stage I horizon. Flows 3 and B, assumed of similar age, are middle(?) Holocene in age on the basis of stage I carbonate horizons and the weakly developed desert pavement on flow B. Flows A and C are latest(?) Pleistocene or early Holocene in age on the basis of stage II carbonate horizons, well-developed desert pavements with varnish, and argillic horizons. Flow 4 is late Pleistocene in age, probably older than 25,000 yr, on the basis of its stage III carbonate horizon.

Discussion

Debris flows are the most common surficial deposits in the alluvial fans of Wood Canyon. This dominance is similar to that reported for the White Mountains of California (Beaty, 1974) and at Mt. Thames, New Zealand (Pierson, 1980). The proportion of fluvial to debris-flow deposits varies from fan to fan (Bull, 1977), but reports of debris-flow deposits as the most common surficial deposit appear to be rare, especially for the Mojave Desert. However, debris flows appear to be fairly common in the Death Valley area (Johnson, 1970; Hunt and Mabey, 1966).

The estimated ages of the debris flows suggests a recurrence interval for such events in Wood Canyon. Given the order of magnitude of the ages of flows 1, 2, and 3, a recurrence interval on the order of millenia is implied. This contrasts with Johnson's (1970, p. 438) estimate of a 30- to 100-yr recurrence interval for flows in the lower canyons on the west side of the Panamint Range, and with Beaty's (1974, p. 50) assertion that debris flows are a common event in the mountainous regions of the Western United States with a recurrence of 2-3 per 1,000 yr.

The vegetation on the Wood Canyon debris flows displays a directional change in species composition with time, and thus it represents a succession (Mueller-Dombois and Ellenberg, 1974, p. 374; Pickett, 1976, p. 109). A sequence of perhaps six stages occurs that apparently requires longer than 10,000 yr for completion. We stress that these stages are completely gradational, because each stage represents an arbitrary slice of time. The stages are as follows: (1) Annuals such as Erodium and Bromus are the initial colonizers of debris flows. Erodium was found on 6-mo-old spoil from soil pits. (2) Species generally not found in the vegetation immediately adjacent to the flows, such as Lupinus, Atriplex, Penstemon sp., Eriogonum sp., and Chrysothamnus sp. are the first shrub colonizers and are established within several years. (3) Additions of Lycium, Grayia, Ephedra nevadensis, and a few Coleogyne probably increase the cover to that of the surrounding vegetation within a matter of decades. Changes occurring after the reestablishment of cover probably occur on the order of centuries, but we do not have a deposit of this age at this site to support the hypothesis. (4) Ephedra dominates with Lycium and Grayia while colonizing species decrease in importance. This stage probably requires several thousand years for maximum expression. (5) Coleogyne increases at the expense of Ephedra, Lycium, and Grayia; this stage probably requires up to 5,000 yr. (6) Coleogyne forms a nearly pure stand to the exclusion of almost all other species except Ephedra. This stage is inferred from vegetation on deposits of greater than 10,000 yr in age (flow 4), which were deposited in a different climate with different ambient vegetation than that of today.

Although allogenic forces appear to predominate, autogenic forces contributed to alterations in the soil on the 1976 debris flows. Many of the individual plants trap organic debris and eolian dust. On fluvial surfaces, diverse organic material became trapped around the basal areas of most shrubs. On the interfluves, the vegetation mainly trapped litterfall, which under some plants such as Chrysothamnus nauseosus was up to 2 cm thick. On flow 1, several of the larger shrubs had collected enough debris to create small mounds. On flows 2 and 3, most of the vegetation, especially Coleogyne, is established on mounds. On flow 4, virtually none of the subdominants present, such as grasses, grew on intermound surfaces. Although grasses were growing more randomly on flow 1, greater numbers were found in the collected debris under shrubs such as Lupinus and Eriogonum fasciculatum. These observations are in agreement with the "fertile island" concept developed for the northern Mojave and Great Basin Deserts (Charley, 1972; Charley and West, 1975; Wallace and Romney, 1980) in which the mounds serve as vegetation-maintained reservoirs of minerals and organic matter that were initiated by the first colonizers (Wallace and Romney, 1980).

The autecology of Coleogyne is an important part of the succession. Coleogyne is known for its extremely slow growth rate (Bowns and West, 1976) and long lifespan of individuals; one individual in Utah has been reported in excess of 400 yr old (Christensen and Brown, 1963). Coleogyne is most often associated with extremely stable landforms that have undergone the maximum soil development found in desert environments (West, 1983a, p. 403). In southern Nevada, Coleogyne is associated with coarse-textured, calcareous soils (Wallace and Romney, 1972, p. 203; Beatley, 1976, p. 247). In Utah, Coleogyne is found on soils with stage IV carbonate horizons in nearly pure stands (Bowns and West, 1976, p. 8). Coleogyne assemblages were not found on young (2-3 m.y. old) basalt flows in southern Utah, although it dominates on adjacent soils and older basalt flows (Bowns and West, 1976, p. 8). The association of Coleogyne with old soils and the lack of Coleogyne on young basalt flows imply either an allogenically controlled succession with Coleogyne eventually dominating or an affinity of Coleogyne for calcium carbonate irrespective of the age of the surface.

Coleogyne individuals alter soil chemistry. Bowns and West (1976) reported an increase in total nitrogen and available phosphorus in soil beneath Coleogyne compared with intershrub soils. Coleogyne is often clustered on small mounds, evidently created by entrapment of eolian materials (West, 1983a, p. 403). Charley and West (1975, p. 959), in a study of the chemistry of soil beneath typical Great Basin Desert shrubs including Coleogyne, presented an idealized model showing soil organic matter increasing with time beneath a shrub. Their data indicate that Coleogyne and other species significantly alter soil chemistry.

Coleogyne's germination requirements could also explain why it does not initially colonize the debris flows. Individual plants produce few seeds (Burgess Kay, written commun., 1982), which are relatively large and less mobile than those of other species (West, 1983a, p. 408). Bowns and West (1976, p. 15, 18) reported that while some Coleogyne germinate on the surface, seedlings often emerge from rodent caches. Seedling survival was poor, with most seedlings not surviving beyond the cotyledonary stage. Seedling establishment and survival for most desert perennials occur in pulses in years of greater than average rainfall and reduced herbivore pressure following years with good seed production (Holmgren and Hutchings, 1972; Noy-Meir, 1973; Beatley, 1975, 1980; Wallace and Romney, 1972). Coleogyne assemblages are noticeably depauperate in seedlings and young plants (Bowns and West, 1976), an observation suggesting that pulse establishment is rare. Hence, Coleogyne appears to fit Grime's (1979, p. 48-49) definition of a stress tolerator.

This succession is complicated by several factors. Erodium and Bromus are generally believed to be exotics introduced from Europe (Munz, 1974, p. 490, 956). However, Wester (1981, p. 236-237) reports observations of abundant Erodium in California dating from the earliest Spanish occupation and believes that Erodium is native. Beatley (1966) notes that Bromus was introduced into southern Nevada before 1925, although Jepson (1925, p. 592) reported Bromus to be well established in parts of California by 1925. Therefore, the belief that Erodium and Bromus are "exotics" is questionable. However, despite the possibility that these species are native to central California, their introduction to the Mojave Desert appears to have occurred over the last several hundred years (see section "Paleoecological Studies in the Black Mountains"). Hence, Erodium and Bromus were probably not the initial colonizers of fresh debris flows in the past. The colonizing species of debris flows older than several hundred years are unknown.

Several incongruities exist between the succession observed on debris flows originating in granite and those originating in the Kingston Peak(?) metasedimentary rocks. Debris flows 3 and B are of similar age based on soil carbonate morphology, but flow 3 is dominated by Coleogyne whereas flow B is dominated by Acamptopappus. Consequently, the sequence of succession appears to depend on the type of parent material, the elevation and exposure, and the local microclimatic variability, and thus it cannot be quantitatively modeled without calibration to local conditions.

RECOVERY OF SKIDOO TOWNSITE AND THE SKIDOO PIPELINE

Human-induced disturbances are common features in the Panamint Range, and study of these features allows a comparison of primary succession with revegetation over relatively short time periods. This comparison is necessary to determine if secondary succession is a viable model for revegetation of disturbed sites, and consequently whether recovery times can be extrapolated from the succession model. The townsite of Skidoo was established in 1906 and abandoned in 1917. Historical accounts indicate a variety of disturbances, including different amounts of compaction and soil disruption with known recovery periods. The associated Skidoo pipeline corridor crosses many different geomorphic surfaces en route to a spring 35 km away, and it provides information about the control of geomorphic surfaces on the recovery process. These sites are typical of disturbances in the Panamints, and they can be used to obtain data for the model of succession.

Skidoo was built at an elevation of 1,730 m in a small valley near the northern extent of the Panamint Range. The mountains to the south and west of Skidoo are composed of Tertiary granite, while the mountains to the east and north are underlain by the Late Proterozoic Noonday(?) Dolomite (Hunt and Mabey, 1966, pl. 1). The soil developed on the valley alluvial deposits (table 10) suggests a Holocene age. The vegetation is a Grayia-Lycium assemblage as described by Beatley (1976, p. 47-48) that is a transition between Mojave and Great Basin Deserts. An Artemisia tridentata assemblage occurs on north-facing valley margins as the slope increases, and Coleogyne assemblages dominate on other hillslopes.

History of Skidoo and the Skidoo Pipeline

In January 1906, two prospectors located a rich ledge of gold in the northern Panamint Range (Greene, 1981, p. 608-609). By July, 40 claims were established, and the townsite of Skidoo was platted in a broad valley 1 km from the workings (fig. 9). In September 1906, streets 19 m wide were cleared in a grid pattern and a townsite map was registered. By May 1907, the population had grown to 400-500 persons with about 130 buildings constructed of framed canvas, wood, and iron (Greene, 1981, p. 635-636); most of the wood structures lined Skidoo Street between 1st and 5th Streets (fig. 10). A nationwide financial panic in mid-1907 caused many businesses to move or become bankrupt, reducing the population to 150 by early 1908 (Greene, 1981, p. 664). For the next nine years the mine continued to produce bullion, but the population steadily dwindled. Only 35 miners were employed in 1914 (Greene, 1981, p. 673), and only a "small population" remained by 1915 (p. 674; fig. 11). The Skidoo Mines Company closed permanently in September 1917 (Greene, 1981, p. 674-675), and the town was essentially abandoned.

Skidoo townsite has remained mostly undisturbed since 1917, although small areas have been disturbed during occasional mining operations. In 1922, only one person remained and a few buildings were reported still standing (Edna Perkins, 1922, quoted in Greene, 1981, p. 675). The Skidoo mine was reactivated and worked by 16 men in 1936 (p.

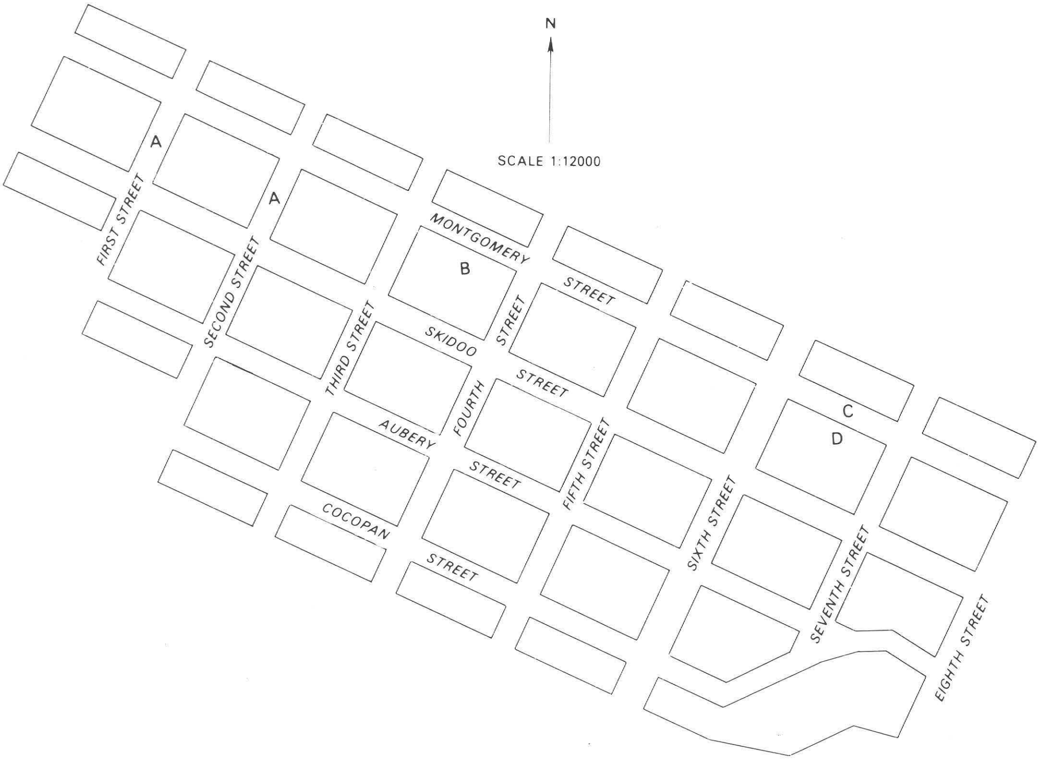


Figure 9. Map and aerial photograph of Skidoo townsite showing the locations of study sites. A, 1st and 2d Streets; B, 1st and 2d Streets control; C, Montgomery Street; D, Montgomery Street control; E, Old East Road; F, Old East Road control. Map is redrawn from a map registered with the Inyo County Recorders Office in 1906. Aerial photograph was taken in June 1959 and enlarged four times (Eros Data Center photograph number H&N-F, 8-89).

676). Within several months, some 30 other men were working mines in the area, with the main activity occurring at minesites 1-2 km west of the abandoned townsite. From 1942 to 1970 mineral activity was limited, although a tungsten boom in the early 1950's caused several hundred claims to be filed. During 1970, an extensive sampling program in the area resulted in about 30 new shafts and 7 open cuts over a 2-ha area northwest of the abandoned townsite (Greene, 1981, p. 680). However, the only additional disturbance in the townsite apparently occurred in the vicinity of Aubery and 3d Streets (fig. 9). In the early 1970's, the National Park Service built an interpretive sign along Skidoo Street between 4th and 5th Streets; visitors since have caused some soil disturbance, which decreases with distance from the sign (fig. 9).

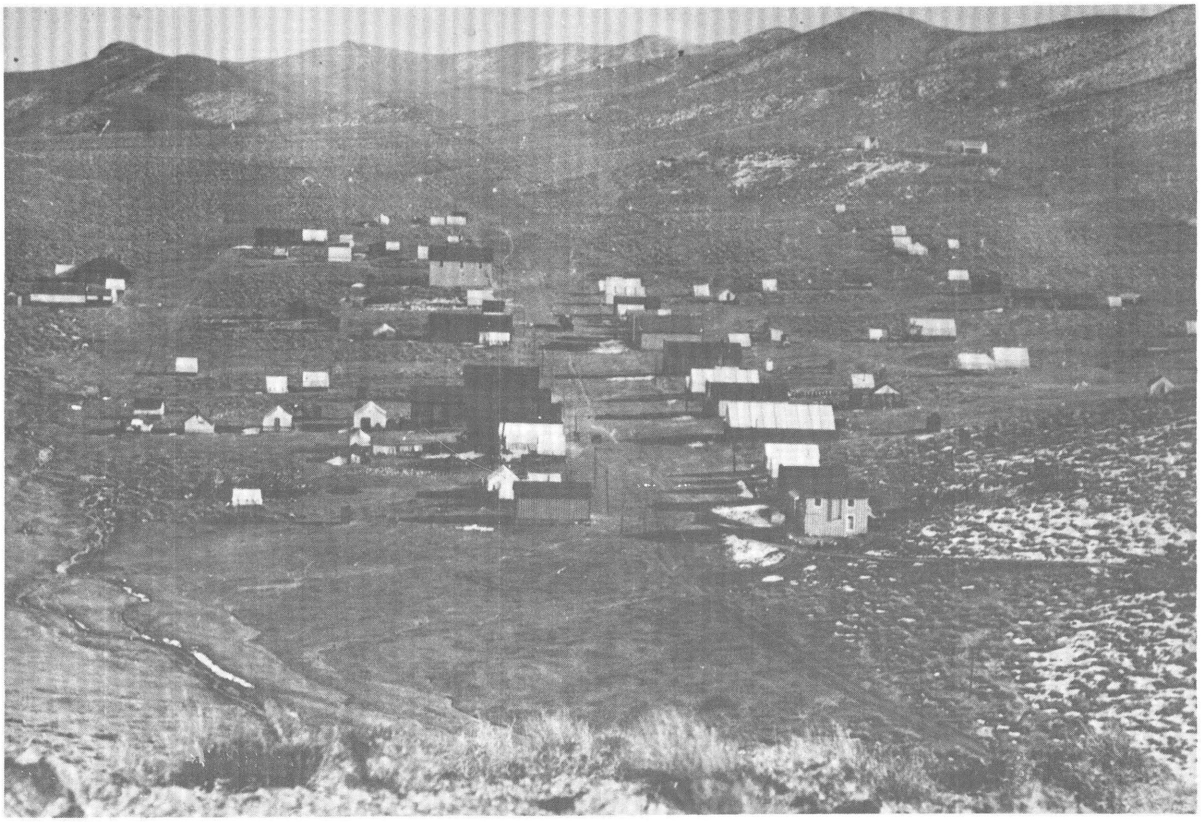
The Skidoo pipeline was built to transport water the 35 km between Birch Spring near Telescope Peak (fig. 1) and Skidoo. Construction began in 1906 with 8 km of pipe laid at the southern end (Greene, 1981, p. 659). Delays in obtaining supplies and rugged terrain limited construction to an additional 8 km by the mid-summer of 1907, and the pipeline was not completed until December 1907 (Greene, 1981, p. 652-659). The pipeline corridor ranges in elevation from 1,730 to 2,330 m and crosses all exposures on slopes ranging from 0° to 32° (fig. 12).

Only the southern end of the pipeline, from Birch Spring to a point north of the crest between Wildrose and Tuber Canyons (fig. 1), remains intact today. Easily accessible sections were salvaged for scrap in 1917 (p. 675), and the few remaining sections were salvaged by the Civilian Conservation Corps in 1938 (fig. 13). An access road exists along most of the pipeline corridor from Wildrose Canyon to Skidoo. Sections of the road are still in use, although most of the road has been closed off recently by the National Park Service or has been unused since the salvage operations.

Methods

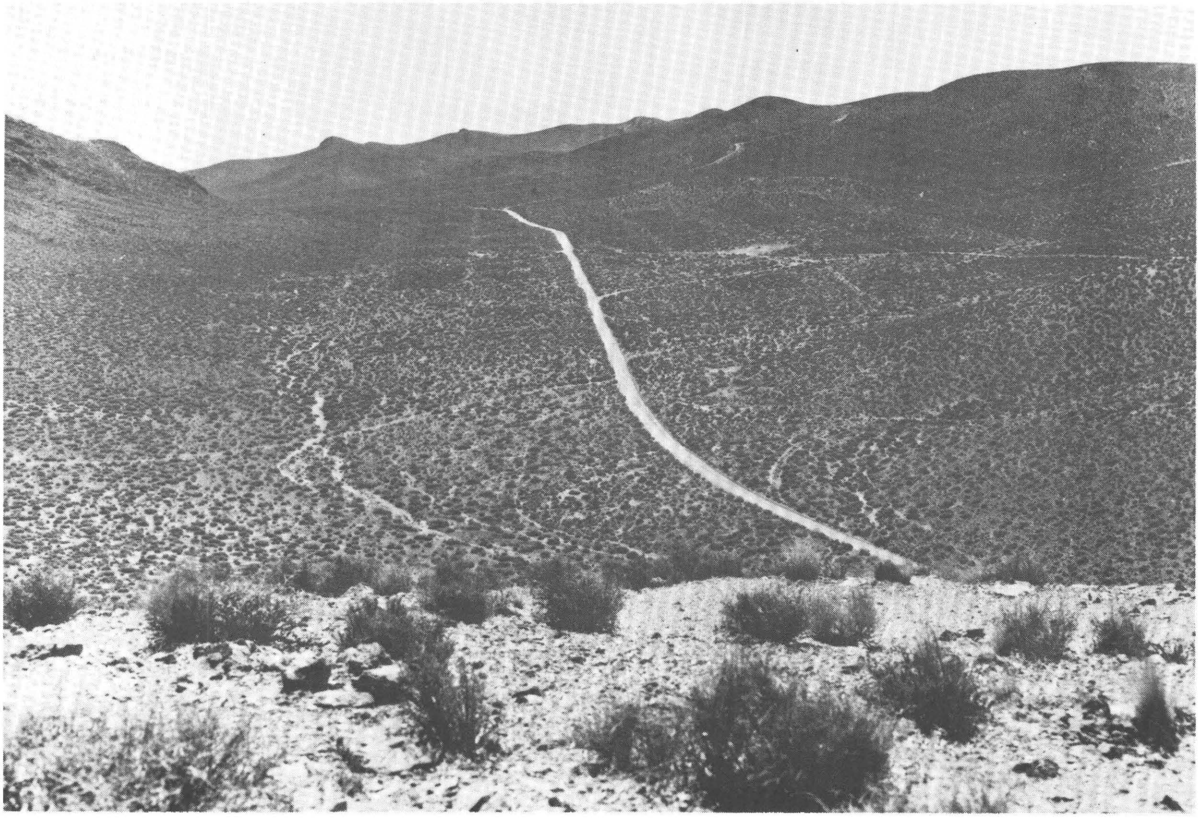
Skidoo townsite

Two periods of recovery (63 and 74 yr) were identified in Skidoo townsite. Photographs of the townsite taken in 1906 and 1907 (fig. 10A) and historical data indicate that 1907 was the time of maximum occupation. A 1916 photograph (fig. 11A) shows the townsite reduced to frame structures, with



A

Figure 10. Skidoo townsite. View is toward the southeast. A, In 1907. B, In 1960 (A and B courtesy of Death Valley National Monument). C, In 1983 (Raymond Turner, U.S. Geological Survey).



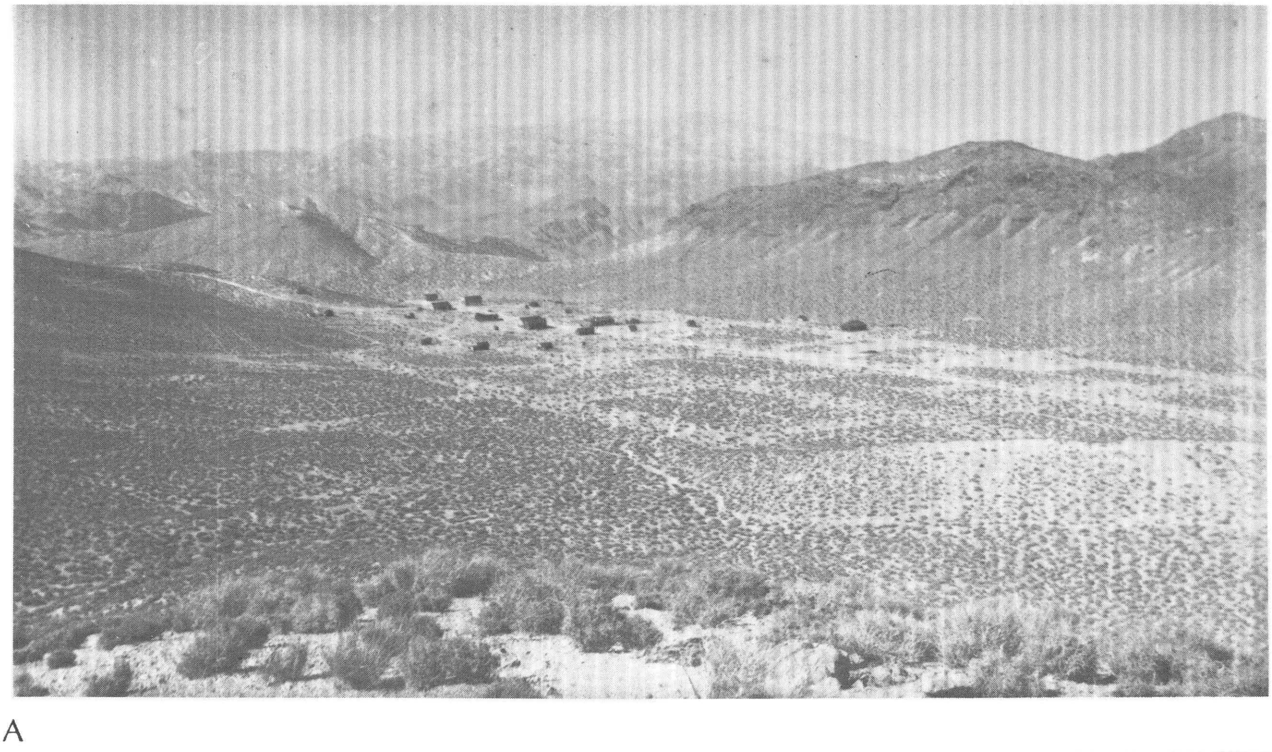
B

C

Figure 10. Continued.

little apparent habitation. The main part of town between 1st and 5th Streets (fig. 9) was active until abandonment in 1917, giving a recovery period of 63 yr to the beginning of the present study in 1981. The section of Montgomery Street east of 6th Street was cleared when the site was originally platted in 1906 but apparently never occupied, and thus had a recovery period of 74 yr to 1981.

Two study sites corresponding to the 63- and 74-yr recovery periods were established on Montgomery Street east of 6th Street and on 1st and 2d Streets between Montgomery and Skidoo Streets (fig. 9). Representative undisturbed sites (controls) for each of the disturbed sites were selected on the basis of proximity to the disturbed site and the absence of obvious disturbances. For the Montgomery Street site, an area



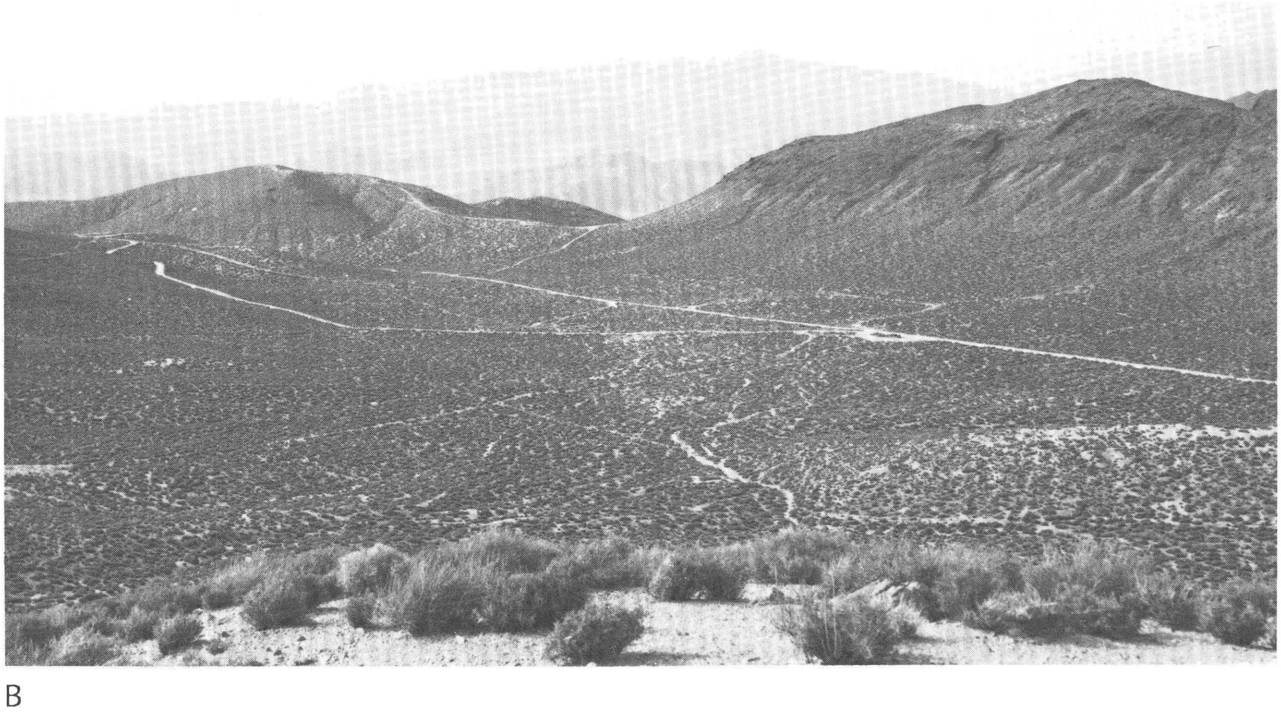


Figure 11. Skidoo townsite. View is toward the northwest. A, In 1916 (courtesy of Arizona Historical Foundation, Hayden Library, Arizona State University). B, In 1983 (Raymond Turner, U.S. Geological Survey).

bounded by Montgomery, Skidoo, 6th, and 7th Streets was selected as its control. An area bounded by Skidoo, Montgomery, 3d, and 4th Streets was selected as the 1st and 2d Streets control (fig. 9).

Residual soil compaction was measured by three methods for all sites. A simple 30° cone penetrometer was used to take 70 measurements of penetration depths. A recording penetrometer (Carter, 1967) was used to record 100 penetration resistance vs. depth curves. A thin-walled soil core sampler was used to determine 10 bulk densities. Undisturbed control sites were no more than 20 m from the disturbed sites.

Density, percent cover, plant volume, and cryptogamic crusts were measured in each disturbed and control site. Belt transects totaling 400 m^2 in area were sampled for density in each site, and cover was measured using 200 m of line intercepts. Thirty individuals of each abundant woody species were measured at each site to calculate biomass. Cover of cryptogamic crusts was estimated at sites as described in the "Methods" section.

The Skidoo Pipeline

Three recovery periods were identified along the pipeline. Where the pipeline was not excavated during the salvage operations of 1917 or 1938, the recovery period can be assumed to be the 73 yr between the pipeline's completion in December 1907 and measurement of soil and vegetation in 1981. Most of the pipeline in easily accessible areas was removed in 1917, and these areas had a recovery period of 63 yr. Remote sections of the pipeline such as Nemo Crest (fig. 13) were removed in 1938, and these areas had a recovery period of 42 years.

The Skidoo pipeline was either laid in shallow open trenches, buried, or constructed atop a berm or frame structure depending on the microtopography of the 2- to 5-m-wide corridor. Often all three construction methods were used within a relatively short distance. This represents a wide variety of disturbance intensity and thus limits measurement suitability. The following criteria were used to select pipeline study sites: (1) Only sites with obvious trench scars over a continuous 0.5 km distance were considered. (2) Dissected surfaces and those showing signs of recent erosion or deposition were avoided where possible. (3) Only sites with relatively continuous lithologies and topography were considered. (4) Only sites with continuous, nonpatchy vegetation assemblages representative of the general area were considered. (5) Sites with signs of recent human or burro use were avoided.

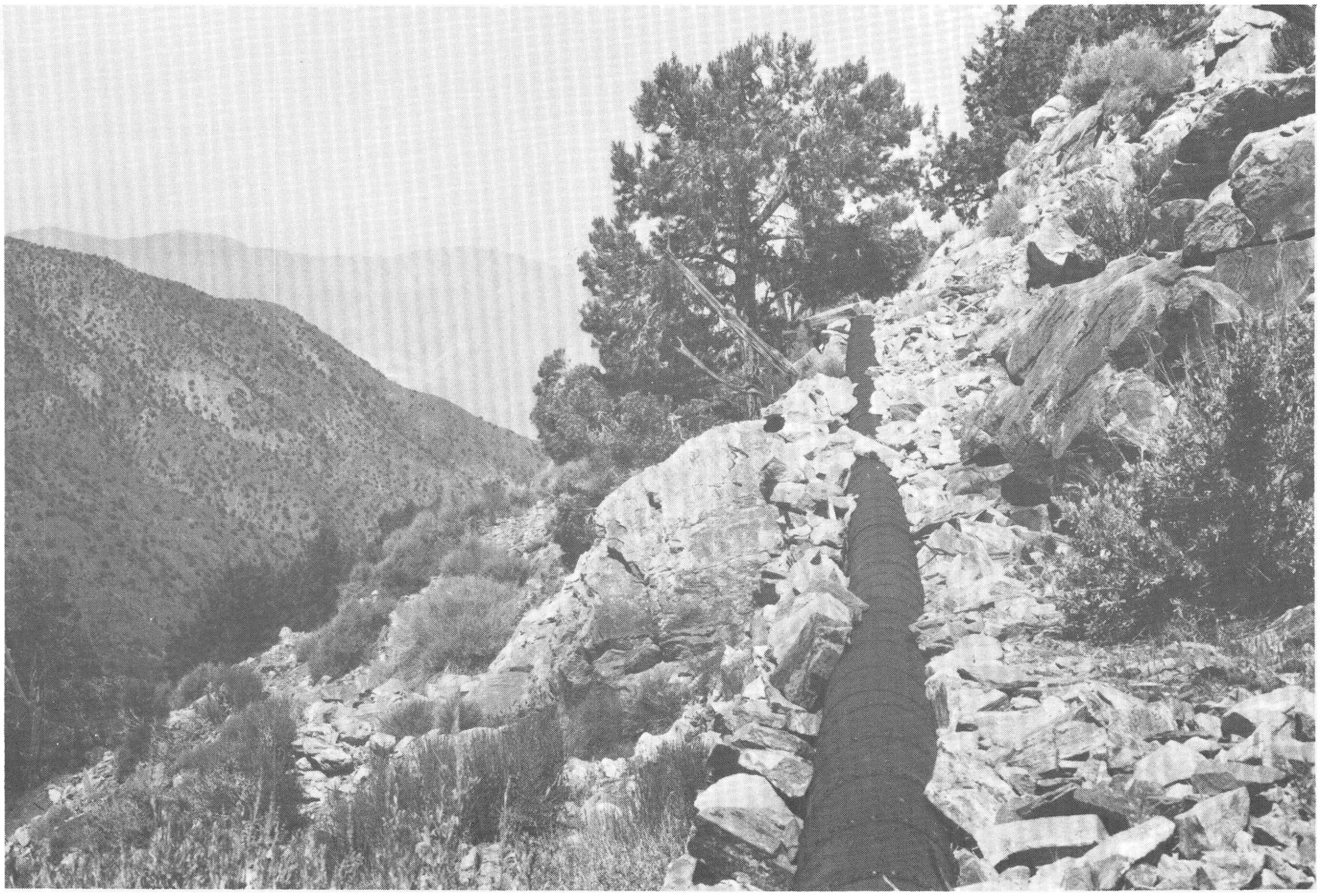


Figure 12. Skidoo pipeline in place west of Birch Spring. The pipeline was not salvaged between Birch Spring and a point north of the crest between Wildrose and Tuber Canyons. Photographed June 1981.

Four study areas were selected, three of which met all the criteria outlined above. The Harrisburg Flats study area lies in a broad valley 8 km south of Skidoo (fig. 1) and had a recovery period of 63 yr. The pipeline trench enters Harrisburg Flats from the north at a bearing of due south and continues down an alluvial fan with a slope of 6°. The vegetative assemblage occupying this rocky slope is dominated primarily by Ephedra, Lycium, Chrysothamnus viscidiflorus, and Haplopappus cooperi. The pipeline crosses Harrisburg Flats, an alluvial flood plain draining to the west, at an elevation of 1,600 m. A 200-m-wide band of eolian sand covers the edge of the Flats between the flood-plain surface and the alluvial fan sloping onto it; this sand dune is dominated by an Ephedra-Hymenoclea salsola assemblage. On the Flats, the assemblage is dominated by Grayia and Chrysothamnus. Cover was measured using 1,300 m of continuous line-intercept data in both disturbed and control sites at the Harrisburg Flats site.

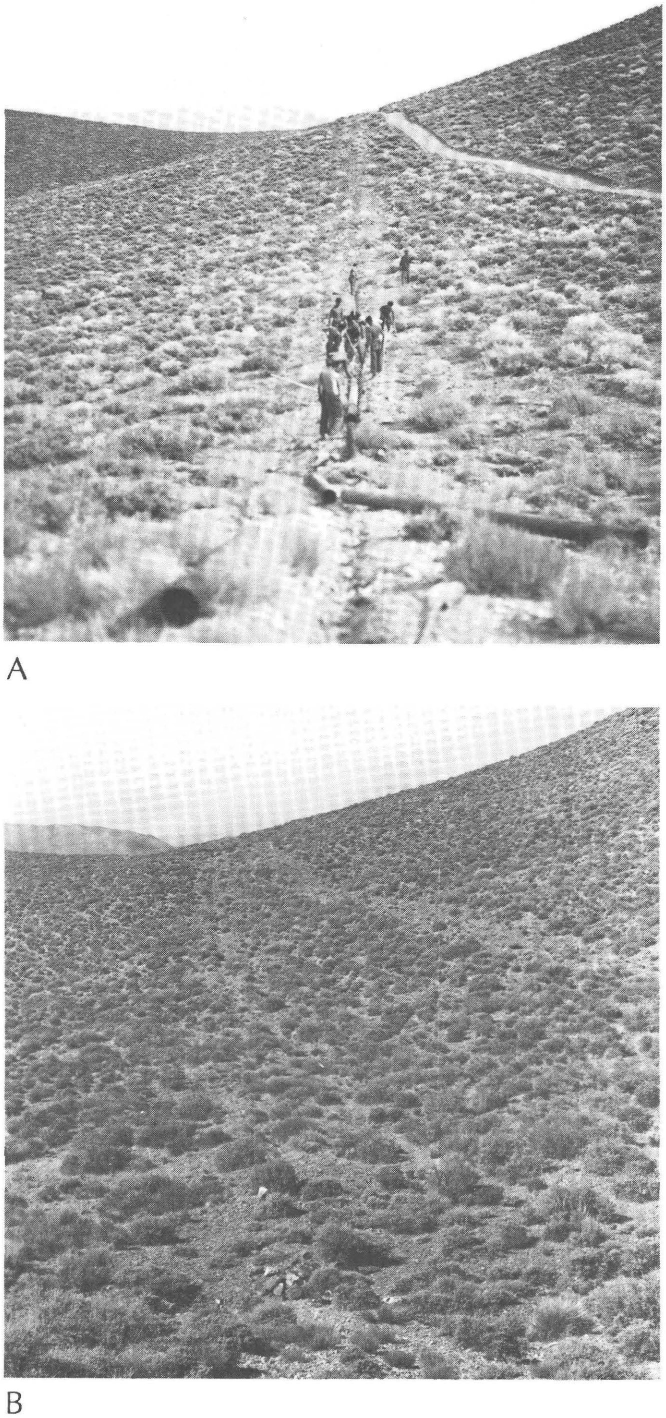


Figure 13. Skidoo pipeline corridor at Nemo Crest. A, In 1938 during salvage operations by the Civilian Conservation Corps (courtesy of Death Valley National Monument). B, In June 1981 (Raymond Turner, U.S. Geological Survey). Measurements were made in both the road and pipeline corridor, as well as upslope and downslope from each.

The Wood Canyon segment (figs. 4, 8) of the pipeline route traverses Wood Canyon at a bearing of N. 11° E., perpendicular to an active ephemeral wash in the bottom of the canyon. The study area ranges in elevation from 1,585 to 1,645 m on the 8° north-facing slope of the canyon. The pipeline in this area was dismantled in 1917, a 63-yr recovery period, and appears to have been above ground only at the top of the slope. Vegetation consists primarily of a Coleogyne-dominated assemblage, with a Grayia-Lycium assemblage occupying a younger surface that bisects the Coleogyne-dominated surface. Cover and density of vegetation in Wood Canyon was measured using 900 m of line-intercept data and 600 m^2 of belt transects in both disturbed and control sites. Belt transects were centered between the edges of the disturbance zone, regardless of the exact location of the pipeline trench within the zone, in order to eliminate edge effects. Transects were split evenly among the three vegetation zones corresponding to debris flows (see section "Primary Plant Succession on Debris Flows in Wood Canyon"); transects were placed to avoid any ecotonal or geomorphic boundaries, such as active washes.

The Nemo Crest study area (fig. 13) lies in a broad, shallowly concave surface between two ridgetops that define the crests of Nemo Canyon to the south and Wood Canyon to the north. The pipeline segment crosses a 10°-15° slope horizontally with a N. 11° E. bearing and was dismantled in 1938, a 42-yr recovery period. Dominated by a Coleogyne assemblage, the Nemo Crest study area was separated into four study sites: an access road last used in 1938, a pipeline trench excavated in 1938, and two controls bracketing the road and pipeline trench. Cover was measured on 250 m of continuous line intercepts in each area. An additional 50 m of pipeline corridor and adjacent control were measured on a 21°-26° slope leading north into Wood Canyon.

The Wildrose Canyon segment of the pipeline (fig. 14) was selected for study based on its dramatic topographical variation as the pipeline traverses the steep north-facing slope of Wildrose Canyon. Vegetation assemblages change along this segment as the elevation increases from 1,625 m at the Wildrose Canyon Road to 2,320 m at the crest between Wildrose and Tuber Canyons. This segment starts in a Coleogyne-Artemisia assemblage, crosses through a relatively homogeneous Artemisia assemblage, and culminates in a Juniperus-Pinus monophylla assemblage. The lower part of the pipeline appears to have been removed in 1917, while upper parts were removed in 1938 or are still intact. Data from this segment are difficult to interpret because of the mosaic of environmental and disturbance gradients present, although generalities about recovery trends can be inferred. Two line-intercept segments, 400 and 900 m long, were measured in both the control and disturbed sites of the Wildrose Canyon segment.

Results

Recovery at Skidoo Townsite

Soil physical properties have recovered considerably during the years since abandonment (table 11; fig. 15). Montgomery Street appears to have been cleared of vegetation with minimal compaction, based on the similarity in soil properties with the adjacent Montgomery control. However, 1st and 2d Streets, abandoned 63 yr, were still significantly compacted. A linear recovery model suggests recovery times of about 90 yr for bulk density and 75 to 80 yr for penetration depth. This suggests that Montgomery Street could have been

Figure 14. Skidoo pipeline corridor across Wildrose Canyon. View is toward the north. Most of the pipeline corridor to the south of Wildrose Canyon road (center) was measured. Photographed June 1981.

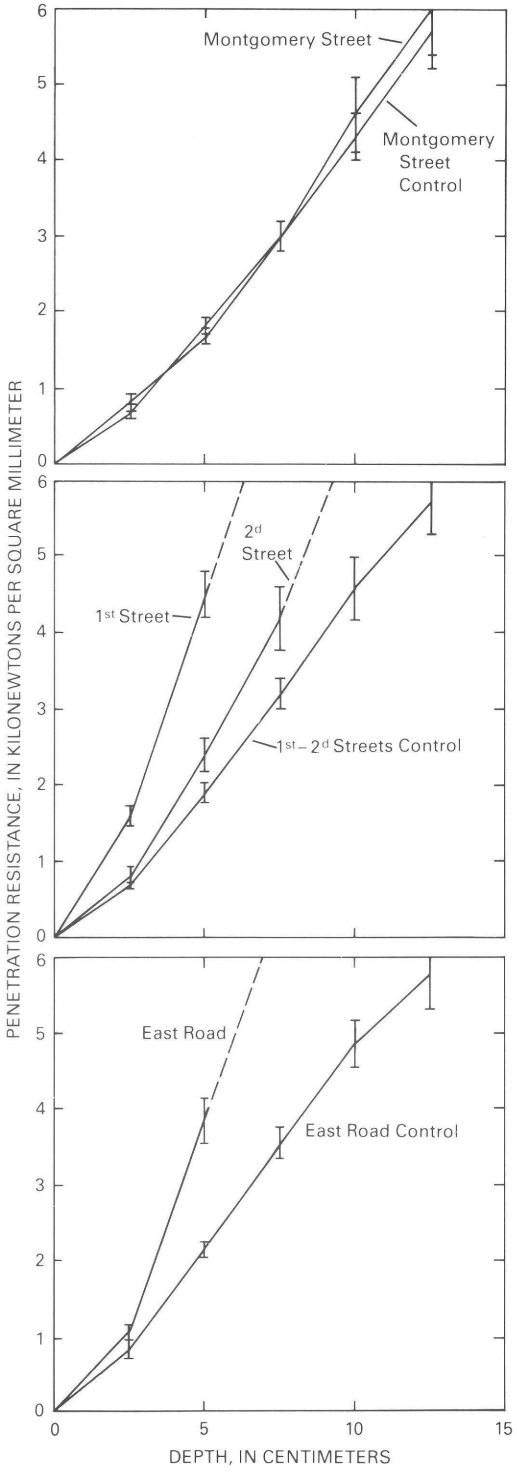


Figure 15. Penetration resistance vs. depth curves for soils at Skidoo townsite. Bars indicate standard error, and dashed lines indicate that the next measurement is off-scale.

compacted to the same level as 1st and 2d Streets because the predicted recovery time (75 to 90 yr) is close to the abandonment time for Montgomery Street (74 yr). However, historical photographs (figs. 10, 11) indicate that no structures ever lined Montgomery Street, which suggests that little use occurred after the vegetation was cleared.

Differences between the 1st and 2d Streets site and the Montgomery Street site appear to be related to the length of recovery period and the intensity and type of disturbance. Total live cover of all perennials in the more severely and more recently disturbed 1st and 2d Streets site represent only 68 percent of the total cover found in the 1st and 2d Streets control (table 12). Total live cover of all perennials in the less-disturbed Montgomery Street site represents 108 percent of the total cover found in the control (table 12). Differences in the total density between the 1st and 2d Street control and disturbed sites are not significant, but the total density in the Montgomery Street site represents 162 percent of the control value.

Grayia, the dominant genus, contributed about 14 percent cover in both controls while contributing only 9.8 percent in Montgomery Street and 5.5 percent in 1st and 2d Streets (table 12). *Ephedra* and *Lycium* had higher densities and cover in Montgomery Street than in the control, whereas the opposite result was found in 1st and 2d Streets. *Chrysothamnus viscidiflorus* contributed 4.2 percent cover and 2,900 individuals/ha in 1st and 2d Streets, but it contributed only 0.6 percent cover and 300 individuals/ha in the control.

Artemisia spinescens, a low, spreading shrub (Wood, 1966), had more than twice the cover and density in Montgomery Street than in the adjacent control. In the more severely disturbed 1st and 2d Streets, the cover and density of *Artemisia* are statistically similar to those of the 1st and 2d Streets control, which suggests that the severity of disturbance affects the colonization ability of this species. Similar differences relating to the degree of disturbance can be seen for *Chrysothamnus nauseosus*, *Hymenoclea*, and *Atriplex* (table 12). Apparently, the colonization ability of these species is enhanced by compaction.

The biomasses of the dominant species illustrate further differences among sites. Although the mean biomass for *Grayia* was lower in disturbed than control sites (table 13), high variability renders any difference among means statistically meaningless. However, *Chrysothamnus*, *Lycium*, and *Artemisia* appear to have higher biomasses in disturbed than control sites.

Differences in the cover of cryptogamic crusts between disturbed and control sites indicate a recovery time of 110 yr for complete reestablishment (table 14). The assumption of 0 percent cover at the time of abandonment can be justified by the physical process of blading and the observed lack of cryptogam recovery on recently disturbed surfaces (fig. 16). Trampling from tourists and burros has probably reduced the cover from what it would be in a more isolated area (see Anderson and others, 1982b), but it can be assumed that both disturbed and control sites were equally affected. There is no clear evidence that compaction affects the reestablishment of cryptogamic crusts.

Recovery Along the Skidoo Pipeline

At Harrisburg Flats (fig. 1), recovery of the Skidoo pipeline corridor was measured with a 1,300-m continuous line-intercept that crossed three distinct vegetation assemblages (table 15). A *Grayia*-*Chrysothamnus* assemblage exists on essentially level ground that is flooded periodically. The last flooding occurred during the storms of February 1976 that caused the Wood Canyon debris flows (see section "Primary Plant Succession on Debris Flows in Wood Canyon"). Evidence for flood damage could be seen on aerial

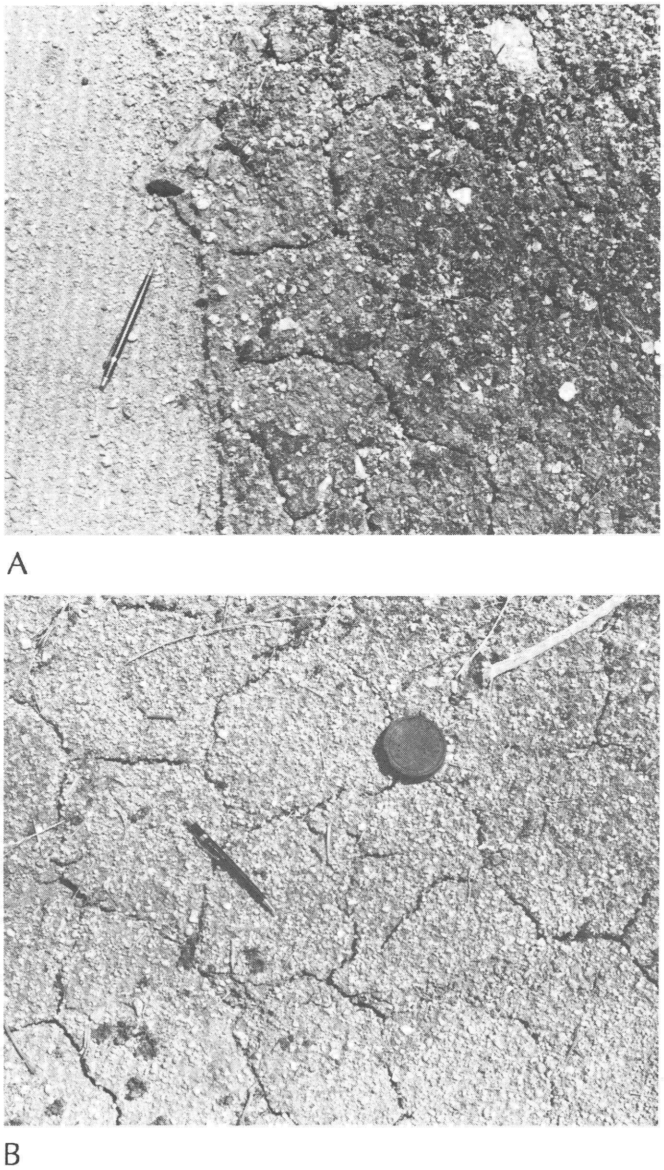


Figure 16. Cryptogamic crusts at Skidoo townsite. A, Fully developed crust truncated at left by an active road. B, Typical crust in 1st Street.

photographs and in fine-grained sediments that were plastered around the bases of shrubs. Hence, the geomorphic surface supporting this assemblage is periodically disturbed and therefore geomorphically unstable. Sand dunes north of this area, which are dominated by Hymenoclea and Ephedra, are also unstable. The third assemblage, dominated by Ephedra and Chrysothamnus, occurs on a moderately sloping rocky surface dissected by small drainages.

The 665 m of pipeline corridor along Harrisburg Flats is dominated by Chrysothamnus, with a large contribution of cover by Grayia (table 15). Parts of this corridor appeared to be less disturbed than others, suggesting that perhaps not all the vegetation was stripped during either construction of the pipeline or its removal in 1917. Species more abundant in the pipeline than in the control were Chrysothamnus, Dalea fremontii, Atriplex, and Ephedra. The dune-area measurements showed little difference between pipeline and control except for greater cover of Grayia, Chrysothamnus, and Atriplex in the pipeline corridor. This perhaps had more to do with the exposure of the underlying, more-stable substrate than with the successional process. On the rocky slope, Haplopappus and Hymenoclea had a higher cover in the pipeline corridor, whereas Ephedra, Chrysothamnus, Lycium, and Grayia had much higher cover in the control. Of the three segments, only the pipeline corridor on the rocky slope had a total cover less than the adjacent control.

These results suggest that substrate and stability affect the distribution of individual species. Chrysothamnus appears to readily colonize disturbed sites, whether natural or human caused, in fine-grained soils, whereas species such as Hymenoclea and Haplopappus act as colonizers when the substrate is rocky. However, Chrysothamnus was well established (6.1 percent cover; table 15) on the rocky slope in the main small drainages that dissect the main slope. Consequently, microtopographic and grain-size variability may control revegetation at local scales.

In Wood Canyon, three segments of the pipeline corridor were studied on old debris flows (debris flows A, B, and C; fig. 8); the pipeline on these segments was probably dismantled in 1917. On debris flow A, an assemblage dominated by Acamptopappus and Chrysothamnus characterized the pipeline corridor, whereas Coleogyne, Lycium, and Ephedra characterized the control (table 16). Total cover in the pipeline corridor was much less than the cover in the control. On flow B, Acamptopappus dominated the pipeline corridor and was highest in the control even with only half the cover it had in the corridor. Ephedra and Tetradymia spinosa also had a higher cover (but not density) in the pipeline corridor, whereas Grayia, Lycium, and Coleogyne had a much lower cover than in the adjacent control (table 16). The calculated biomasses on these flows reflect the differences found in cover (table 17). Differences between the pipeline corridor and control were less obvious for flow C because both were dominated by Coleogyne. In an anomaly not observed at any other site, Coleogyne had a higher density in the disturbed area and statistically identical values for cover (table 16) and biomass (table 17). The equal cover of Coleogyne in the pipeline segment and control can be attributed to relatively less disturbance in this segment because the pipe was probably aboveground. All other shrubs in the control were less numerous in the pipeline corridor except for Haplopappus, Chrysothamnus nauseosus, C. teretifolius, C. viscidiflorus, Acamptopappus, and Hymenoclea. Machaeranthera tortifolia, an herbaceous perennial, had a much higher density in the pipeline corridor.

At Nemo Crest, the Skidoo pipeline, salvaged in 1938, and an abandoned road segment were bracketed by two controls (table 18). The species dominant in the control areas, Coleogyne, Grayia, Ephedra, and Lycium, all had a lower cover value in the road and pipeline, while Acamptopappus, C. viscidiflorus, and C. nauseosus had a greater cover than both adjacent controls. The total cover was much lower in the disturbed sites than in the undisturbed sites (table 18).

On a short (50 m) segment on a 30° slope north of Nemo Crest, Artemisia tridentata and grasses contributed the greatest cover in the pipeline corridor. Artemisia, Ephedra, Grayia, and Coleogyne had much lower cover values in the pipeline corridor than in the adjacent control, which had three times as much total cover (table 19).

Cover of perennial vegetation was measured along four segments of the Skidoo pipeline corridor in Wildrose Canyon. Segment A of the pipeline was built on a rocky, gently sloping alluvial fan and passes through an assemblage dominated by Coleogyne and Ephedra with 28.7 and 12.9 percent cover, respectively. Since the dismantling of the pipe in 1917, Coleogyne has recovered to 10.4-percent cover, and the entire pipeline assemblage contains 40 percent of the total cover of the control. Segment B of the pipeline was constructed on a steep slope that reaches a maximum of 30°, at the base of the divide between Tuber and Wildrose Canyons. The corridor is now an open pipeline trench probably dating from 1938 and has less than half the total cover of the control. Artemisia, Coleogyne, and Ephedra have a much lower cover in the pipeline corridor, whereas Chrysothamnus viscidiflorus and grasses have a lower cover in the control area (table 20). Segment C passes through another A. tridentata-Coleogyne assemblage on higher slopes with essentially the same conditions as segment B.

Segment D, however, has the longest time of any segment to recover because the pipe was still in place 74 yr after construction. Again on steep slopes, the total cover was similar in the pipeline corridor and control. However, A. tridentata contributed greater cover in the pipeline corridor than control, while Coleogyne contributed greater cover in the control (table 20). Other species with a greater cover in the pipeline corridor were Eriogonum fasciculatum and Salvia dorii (table 20).

Discussion

Measurements in Skidoo and along the Skidoo pipeline corridor show that recovery follows a pattern similar to the pattern of primary succession observed in Wood Canyon. The species invading denuded areas generally were predictable, and some (especially Chrysothamnus viscidiflorus) were observed to be colonizers on debris flows. At Skidoo, C. viscidiflorus appeared to be the most important colonizer. This species often was found in the center and along the edges of active roads, which suggests that it has an ability to colonize under high-stress conditions. A summer-flowering species, C. viscidiflorus has a low growth habit and produces large quantities of seeds (Young and Evans, 1974, p. 132). The germination rate for this species must be high because a large number of seedlings were observed in disturbed sites. C. viscidiflorus has increased after disturbance in a variety of Great Basin Desert plant assemblages (Young and Evans, 1974, p. 131), and both it and C. nauseosus produce growth earlier in the spring and in greater biomass when competing vegetation is removed (McKell and Chilcote, 1957). Other species observed to be colonizers include Artemisia spinescens and A. tridentata, Atriplex, and Chrysothamnus nauseosus. The presence of colonizers that are similar in life-history strategy with the colonizers on debris flows in Wood Canyon suggests that secondary succession may be a viable model for revegetation and recovery of desert plant assemblages.

The role of cryptogamic crusts in the recovery pattern at Skidoo is uncertain. Relatively little is known about the relationships between cryptogamic crusts and vascular plants. Several papers have concluded that the success of cryptogamic crusts does not affect the success of vascular plants (Kleiner and Harper, 1972; Anderson and others, 1982b). However, cryptogams have been found to increase infiltration and decrease soil erosion (Fletcher and Martin, 1948; Loope and Gifford, 1972; Anderson and others, 1982a), and their role in nitrogen fixation is well documented (see Anderson and others, 1982a). Anderson and others (1982b) compared the cryptogamic crusts in range exclosures, with recovery periods between 14 and 38 yr, with those in areas being grazed in southern Utah. They found that cryptogamic cover increased 4-15 percent during the first 14-18 yr of exclusion and only 1 percent during the next 20 yr. They concluded that "reestablishment of cryptogamic crust occurs in at least 14-18 years and possibly sooner."

A comparison of the Utah study with the findings from Skidoo suggests that the colonizing ability of cryptogams is very weak compared with that of vascular plants. Cryptogamic crusts were completely eliminated in heavily disturbed areas of the Skidoo townsite, and total recovery, based on a linear recovery model, was estimated to be 110 yr. Grazing in southern Utah reduced the cover of cryptogamic crusts to a value between one third and one tenth of that found in ungrazed sites, yet recovery was estimated to take as little as 14 yr. Evidently, any surviving cryptogamic crusts considerably increase the rate of recovery of the crusts, whereas the superior vagility of vascular plants decreases the relative importance of survivors in affecting their rate of recovery. This hypothesis is also supported by the greater extent of recovery shown by vascular plant cover vs. the recovery shown by cryptogamic crusts at Skidoo townsite (tables 12, 14).

PRIMARY PLANT SUCCESSION ON ALLUVIAL TERRACES IN GOLD VALLEY AND RECOVERY OF GOLD VALLEY TOWNSITE

The Black Mountains on the east side of Death Valley provide a contrast in vegetation with the Panamint Range to the west, mainly because of the lower elevations in the eastern range. Plant assemblages on the eastern slope of the Black Mountains are dominated by Larrea, the most ubiquitous plant in the Mojave Desert (Johnson, 1976, p. 138). Vegetation growing on alluvial terraces in Gold Valley in the Black Mountains (fig. 1) displays a comparable primary succession sequence to that found in Wood Canyon in the Panamints. The abandoned townsite of Gold Valley, built on one of these alluvial terraces, provides a direct comparison between a primary succession sequence and revegetation of a disturbed site.

Gold Valley ranges in elevation from 960 to 1,320 m in the valley and up to 2,060 m at Funeral Peak. Gold Valley townsite is at the southern end of the valley at an elevation of 1,310 m and a slope of 4° (fig. 17). The townsite is approximately 12 km by rough dirt road from the more heavily used Greenwater Valley road, and hence access to the area is limited. Hunt and others (1966, p. B7) estimate a mean annual rainfall for this area of 125 to 250 mm; a more likely range would be 150 to 200 mm, as estimated from Kurzius (1981, p. 12-21).

The discovery of copper and gold deposits in Gold Valley caused a mining boom in 1906. The townsite of Willow Spring, founded in August 1906, was abandoned in 1907 when copper could not be profitably mined. Gold discoveries in the south end of Gold Valley caused a second boom in April 1907, at which time the town of Gold Valley (fig. 17) was founded. By December 1907, Gold Valley consisted of a dozen tent houses and several buildings (Latschar, 1981, p. 640). The abandonment of Greenwater townsite to the north in early 1908 caused an additional influx of miners, and by March 1908, Gold Valley had a population of 70 (Latschar, 1981, p. 642). In May, 25 tons of gold ore were shipped and a large store was built, indicating a high optimism in the town's future (Latschar, 1981, p. 642). However, the isolation of the area and the high cost of mining forced closure of most of the mines in the autumn of 1908. Latschar (1981, p. 643) reports that most miners left Gold Valley during late 1908 and early 1909. Apparently, no attempts have been made to revive mining in Gold Valley, and the townsites were not reoccupied.

The geology of the area is complicated as a result of the intense tectonic activity that the Black Mountains have undergone since the Mesozoic. Drewes (1963, p. 69) reports that the gold mined at Gold Valley came from the Proterozoic Noonday Dolomite and Johnnie Formation south of the townsite. These blocks were thrust upon Precambrian metasedimentary rocks and early Tertiary intrusive rocks in early Tertiary time (Drewes, 1963, p. 70). To the north of the townsite, Precambrian metasedimentary rocks are separated from intrusive and extrusive Tertiary volcanic rocks by a fault zone (plate 1 in Drewes, 1963). Tectonism in the Black

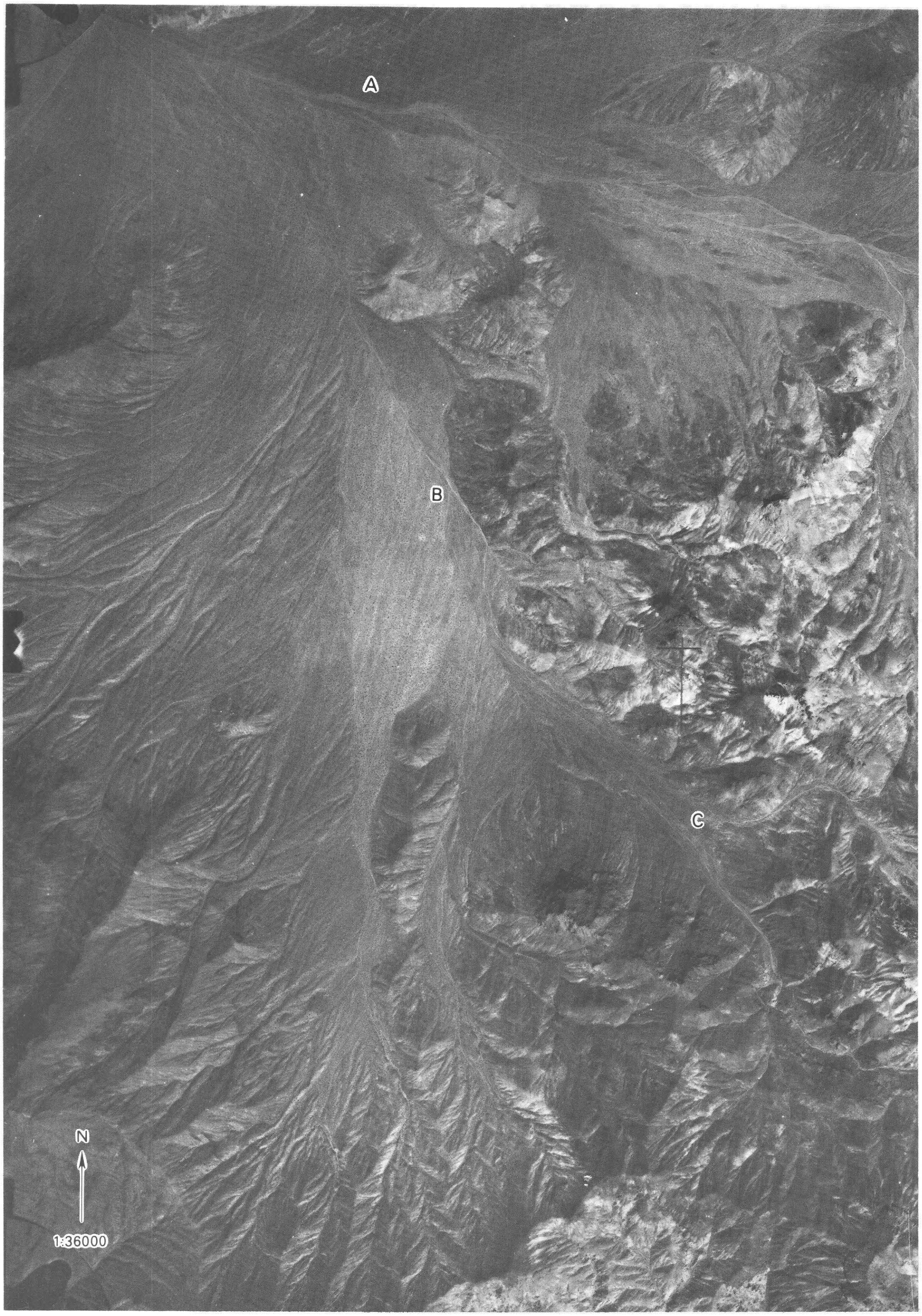


Figure 17. Aerial photograph of Gold Valley showing the location of study sites. A, terrace sequence A; B, terrace sequence B; C, terrace sequence C and Gold Valley townsite. Photographed March 1976 (National Park Service photograph number DEVA 8-11).

Mountains has continued through the Quaternary, with the rate of displacement on the Black Mountains fault system increasing since the late Tertiary (Drewes, 1963, p. 71).

Tectonism apparently has affected alluvial deposition in Gold Valley. Drewes (1963, plate 1) and Denny (1965, plate 4) depict the alluvium in Gold Valley as "unweathered gravel in modern washes," yet a detailed field examination revealed a series of alluvial terraces along all major drainageways, culminating in truncated alluvial fans with a stage IV carbonate horizon. The terraces possibly formed in response to tectonic uplift; Denny (1965, p. 32) speculated that more than 30 m of displacement has occurred along the range-front faults in "the last few thousand years." The fan at the mouth of Willow Creek, which drains Gold Valley (fig. 1), is cut by six normal faults (Drewes, 1963, pl. 1); these faults occur in both old and young gravels (Denny, 1965, p. 33). However, the drainages in Gold Valley are separated from these faults by the 5-km-long bedrock channel of Willow Creek, thus eliminating knickpoint migration in alluvium as the cause of terrace formation. An alternative explanation for the terraces in Gold Valley is that they might have formed in response to climatic fluctuations. However, terraces per se are not well developed at Wood Canyon, Skidoo, or the Greenwater district townsites, which presumably would have undergone the same climatic shifts.

The vegetation assemblages present in Gold Valley are similar to the Larrea-Ambrosia and Larrea-Lycium-Grayia assemblages of Beatley (1976, p. 30-32). Gold Valley townsite vegetation is part of a broad ecotone between Mojave Desert and Great Basin Desert assemblages (Beatley, 1976, p. 44-46). Larrea, Coleogyne, Ephedra, Grayia, and Lycium are the most abundant species, with Ambrosia dumosa (burrobush) abundant at lower elevations. A list of species found in Gold Valley appears in table 47. The assemblages vary in composition on different terrace surfaces within the valley, which suggests a primary plant succession sequence.

Methods

Three sites for the study of vegetation assemblages on alluvial terraces were established at elevations ranging from 990 to 1,310 m over a distance of 2 km. These sites, labeled terrace sequences A, B, and C (fig. 17), consisted of alluvial terraces at different heights above the modern drainage. Valley cross sections were measured with hand level and stadia rod at each terrace sequence. Soil profiles were described and, generally, vegetation was measured using 200 m of belt transects and 400 m of line intercepts.

Gold Valley townsite was built on one of the terraces in terrace sequence C. For this study the townsite was separated into east and west halves because of different intensities of disturbance. Bulk densities, penetration depths, and shear strengths were measured in both halves of the townsite, a nearby undisturbed control, and the active road. Spatial constraints required several transects in terrace sequence C and the Gold Valley townsite to be shorter than the usual 50-m interval. Surfaces for measurement were limited by the smaller size of the terraces located near the top of the alluvial fan and by the relatively small size of the townsite (see tables 25, 27).

Terrace Sequences A and B

The vegetation assemblages on three alluvial terraces and the channel flood plain were measured at terrace sequence A (fig. 18). These terraces were labeled on the basis of height above the channel flood plain as TA$_0$ (channel flood plain), TA$_1$, TA$_2$, and TA$_3$ (highest). The composition of the parent material appeared to be the same for all terraces, and the depth to ground water appeared to be large. The soil developed on TA$_0$ consists of 55 cm of essentially unweathered alluvium overlying a buried stage IV carbonate horizon (table 21). Terrace TA$_1$ has a stage I carbonate horizon, with discontinuous to continuous pebble coatings, but no B horizon. Terrace TA$_2$ displays a cambic B horizon and a stage II carbonate horizon. Finally, terrace TA$_3$ has an argillic horizon with an underlying stage II-III carbonate horizon (table 21).

Because absolute dating for these terraces could not be obtained, a soil chronosequence was developed and age estimates were obtained by correlation with soils of known age in other areas. The soils on the terraces have formed in alluvium dominated by felsic volcanic rocks at a slope of 4° and aspect of N. 60° W. Some limestone and (or) dolomite from the Noonday Dolomite and Johnnie Formation was present as clasts. The rate of carbonate influx in dustfall is not known but is probably similar to that in Wood Canyon.

The terraces of terrace sequence A increase in age with height above the drainage (fig. 19). Terrace TA$_0$, the channel flood plain, has no soil development and is estimated to be less than 100 yr old. Terrace TA$_1$, which has a soil with no cambic or argillic horizon but with a stage I carbonate horizon, is early or middle Holocene in age. Terrace TA$_2$, which has a soil consisting of a B horizon and a stage II carbonate horizon, is latest(?) Pleistocene in age. Finally, terrace TA$_3$, which has a well developed B$_{2t}$ horizon and a stage II-III carbonate horizon, is late(?) Pleistocene in age.

Each terrace supports a distinct assemblage of vegetation (table 22). Hymenoclea, with a cover of 12.8 percent and density of 7,400 individuals/ha, dominates the assemblage on TA$_0$ with Dalea fremontii and Ephedra adding some additional cover. Eriogonum inflatum has a high density (2,800/ha) and is located predominantly between individuals of Hymenoclea. This assemblage is not homogeneous because Larrea forms patches of several individuals. However, these patches generally appear to be on channel bars of older age than the channel flood plain. These bars were neither continuous enough nor distinctly different from the channel flood plain to assign them to a terrace other than TA$_0$.

Larrea dominated the assemblage on terrace TA$_1$, with Ephedra, Ambrosia, and Lycium adding significant cover. The high (3,200/ha) density of Ambrosia is indicative of the small sizes of the individuals of this species (table 22). On terrace

TA$_2$, Ambrosia assumes dominance, and Lycium, Larrea, and Grayia contribute significant cover. Hymenoclea and E. inflatum are insignificant to the assemblage on TA$_2$, and Ambrosia has almost twice as high a density on terrace TA$_2$ as on TA$_1$ (table 22).

Terrace TA$_3$ supports an Ambrosia-Larrea assemblage with few other species well represented, an exception being Lycium. The density of Ambrosia (15,000/ha) is higher than the total density for each of the other terraces (table 22). E. inflatum and Hymenoclea appear locally where erosion of the terraces has exposed carbonate horizons. Acamptopappus sphaerocephalus also forms large patches in areas locally disturbed. The sides of this terrace, which are actively eroding, support a diverse group of species including Hymenoclea, Acamptopappus, Salazaria mexicana, Dalea, E. inflatum, and Ephedra with scattered Larrea and Ambrosia individuals.

A directional change has apparently taken place from an assemblage dominated by Hymenoclea to an assemblage dominated by Ambrosia and Larrea. The percentage similarities of terraces TA$_0$, TA$_1$, and TA$_2$ compared with terrace TA$_3$ were 6, 71, and 69 percent, respectively, for cover, and 21, 41, and 53 percent, respectively, for density. The total density of plants on terrace TA$_3$ was double the density of each of the other terraces, and the total cover on TA$_0$ was slightly less than the total cover of each of the other terraces.

Two terraces were identified along the channel draining the southern part of Gold Valley, and these constitute terrace sequence B (fig. 17). These terraces occur at an elevation of 1,140 m. The soil developed in the channel floodplain TB$_0$ had a very weak stage I carbonate horizon consisting of discontinuous, powdery carbonate coatings on the bottoms of pebbles. Terrace TB$_1$, higher than terrace TB$_0$ (fig. 19, table 21), has a soil with a stage I carbonate horizon. These carbonate horizons would suggest that TB$_0$ is late Holocene and TB$_1$ is middle or early Holocene in age.

The assemblage on terrace TB$_0$ is dominated by Hymenoclea and Ephedra, with Grayia and Lycium adding significant cover (table 23). Herbaceous perennials were well represented, with Eriogonum inflatum contributing the highest density of these species (2,900/ha). In contrast, Grayia and Larrea dominate the assemblage on terrace TB$_2$, with Thamnosma and Ephedra adding significant cover. The herbaceous perennials have decreased significantly compared with their density on TB$_0$ (table 23), and two shrubs found on terrace TB$_0$, Eriogonum fasiculatum and Dalea, were not found on TB$_1$. The total density and cover on terrace TB$_1$ are considerably lower than they are on terrace TB$_0$, and the percentage similarities of the vegetation on TB$_1$ and TB$_0$ are 41 and 35 percent for cover and density, respectively.

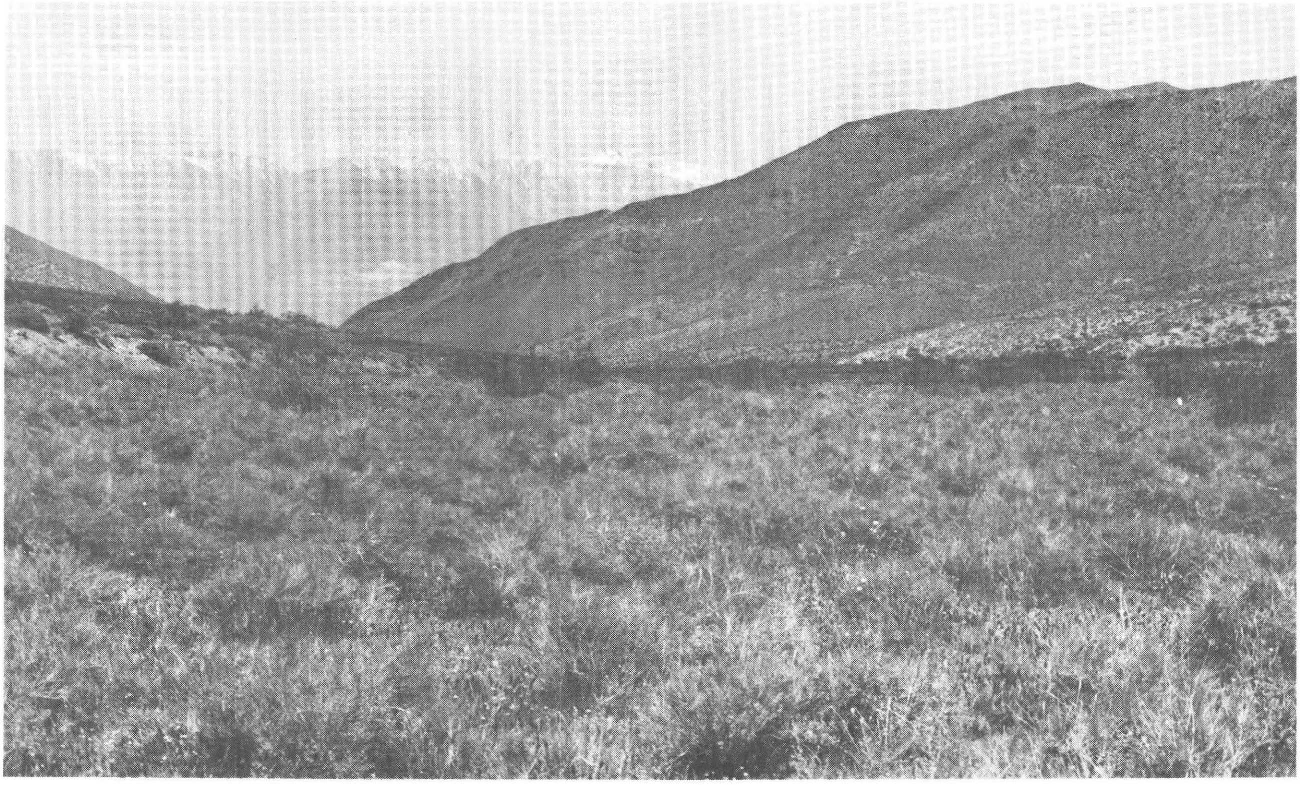
Terrace Sequence C and Gold Valley Townsite

Five terraces were identified at terrace sequence C, and four of these were of large enough areal extent for vegetation measurements (figs. 20, 21). The presence of Gold Valley townsite on one of these terraces provides an excellent contrast between primary plant succession and recovery after disturbance. The lowest terrace in terrace sequence C (TC$_0$) is the bottom of a drainage (fig. 21). The soil present on TC$_0$ is complex owing to its polygenetic development (table 24). Stage II-III carbonate horizons in this soil probably represent gully-bed cementation (Lattman, 1973) because they occur preferentially in lenses of coarse sand and gravel. These lenses were neither parallel with the ground surface nor laterally continuous. Pedogenic carbonate consisted of discontinuous coatings of carbonate on the bottoms of pebbles (stage I; table 24). Exhumed stage IV carbonate horizons appeared at various locations on the terrace. Terrace TC$_{1/2}$ refers to channel-bar deposits 25 to 50 cm higher than TC$_0$ (fig. 21); the area of TC$_{1/2}$ was too small for measurement.

Terrace TC$_1$, approximately 1 m above terrace TC$_0$ (fig. 21), is characterized by weak stage I carbonate horizons (table 24). The carbonate occurs as continuous coatings on the bottoms of pebbles. This terrace appears to be inset against terrace TC$_2$, which has stage I carbonate horizons with continuous pebble coatings and no B horizon. Terrace TC$_3$ formed the highest terrace in the area, and its soil has a stage II carbonate horizon overlying a buried soil with a stage IV horizon (table 24). Terrace TC$_4$ appeared as a remnant among the other terraces and has a well-developed pavement, an argillic horizon, and a stage II-III carbonate horizon. The soil on TC$_4$ is probably correlative with the exhumed soil characterized by a stage IV carbonate horizon.

A chronosequence can be developed from the soils on these terraces. Although terrace TC$_0$ is in a drainageway, the recurrence time between flow events is large enough to allow a soil to develop. The soil on terrace TC$_1$ shows a greater degree of development than that on TC$_0$, and hence TC$_1$ is an older terrace than TC$_0$. Similarly, terrace TC$_2$ is older than TC$_1$, and terrace TC$_3$ is older than TC$_2$. The differences in ages among these terraces are probably thousands of years. Terrace TC$_0$ is late Holocene in age, while terraces TC$_1$, TC$_2$, and TC$_3$ range from early into middle Holocene in age. The age of terrace TC$_4$ is more uncertain but may be middle Pleistocene.

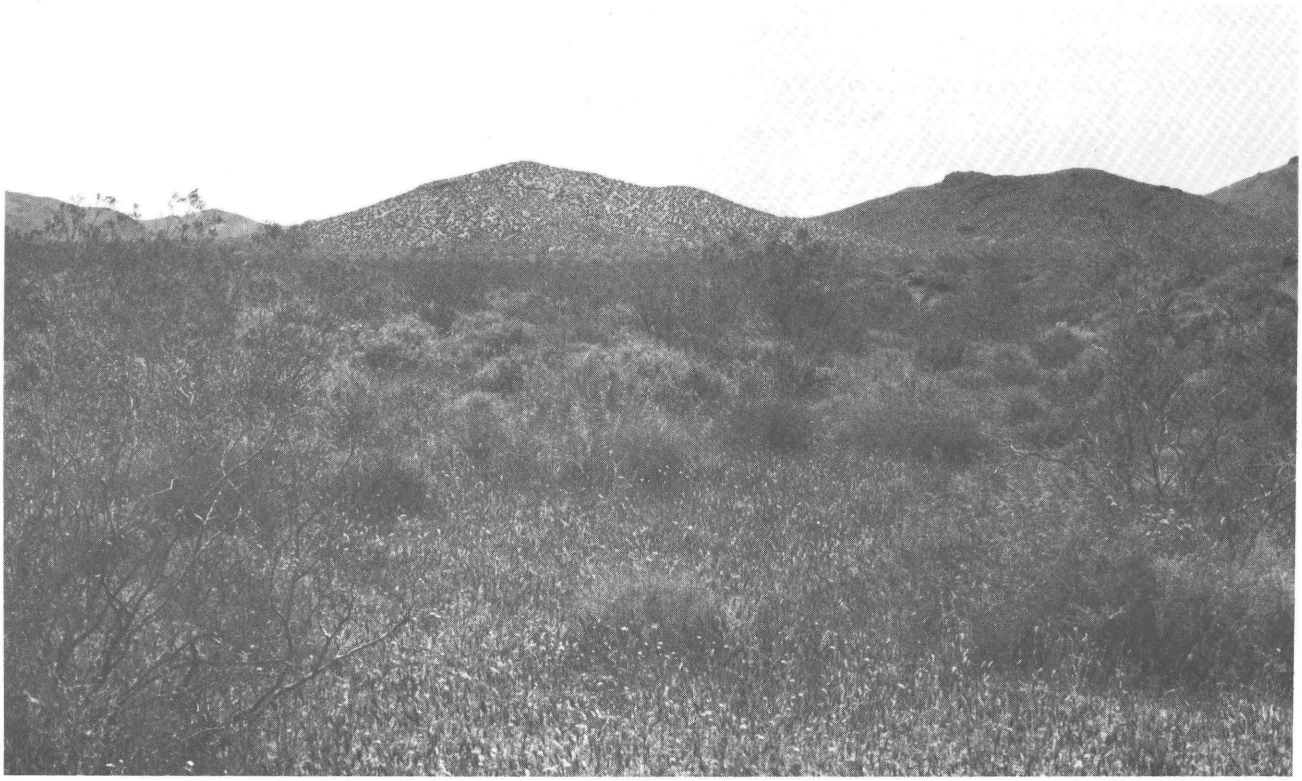
The vegetation on these terraces follows a primary succession similar to that observed on the other terrace sequences in Gold Valley. The vegetation on terrace TC$_0$ is dominated by Hymenoclea and Coleogyne (table 25), with Coleogyne apparently related to the outcroppings of stage IV carbonate horizons. Eriogonum fasciculatum and Ephedra are also abundant on TC$_0$. The vegetation on terrace TC$_1$ is dominated by Grayia, Coleogyne, and Lycium, with Hymenoclea and Ephedra contributing significant cover (table 25). Terrace TC$_2$ supports an assemblage dominated by Ephedra, Coleogyne, Lycium, and Grayia, with Larrea contributing an additional 2.2-percent cover (table 25). Terrace TC$_3$ is dominated by Coleogyne and Larrea with Lycium and Ephedra adding significant cover. The vegetation on terrace TC$_4$ was not measured because of disturbance and its small area; however, the undisturbed vegetation appeared to be mostly Coleogyne and Larrea.



A

B

Figure 18. Terrace sequence A in Gold Valley. The foreground of each photograph shows the surface of the respective terrace. A, Terrace TA_0 (active wash), showing a Hymenoclea assemblage. View is toward the northwest. B, Terrace TA_1, showing an



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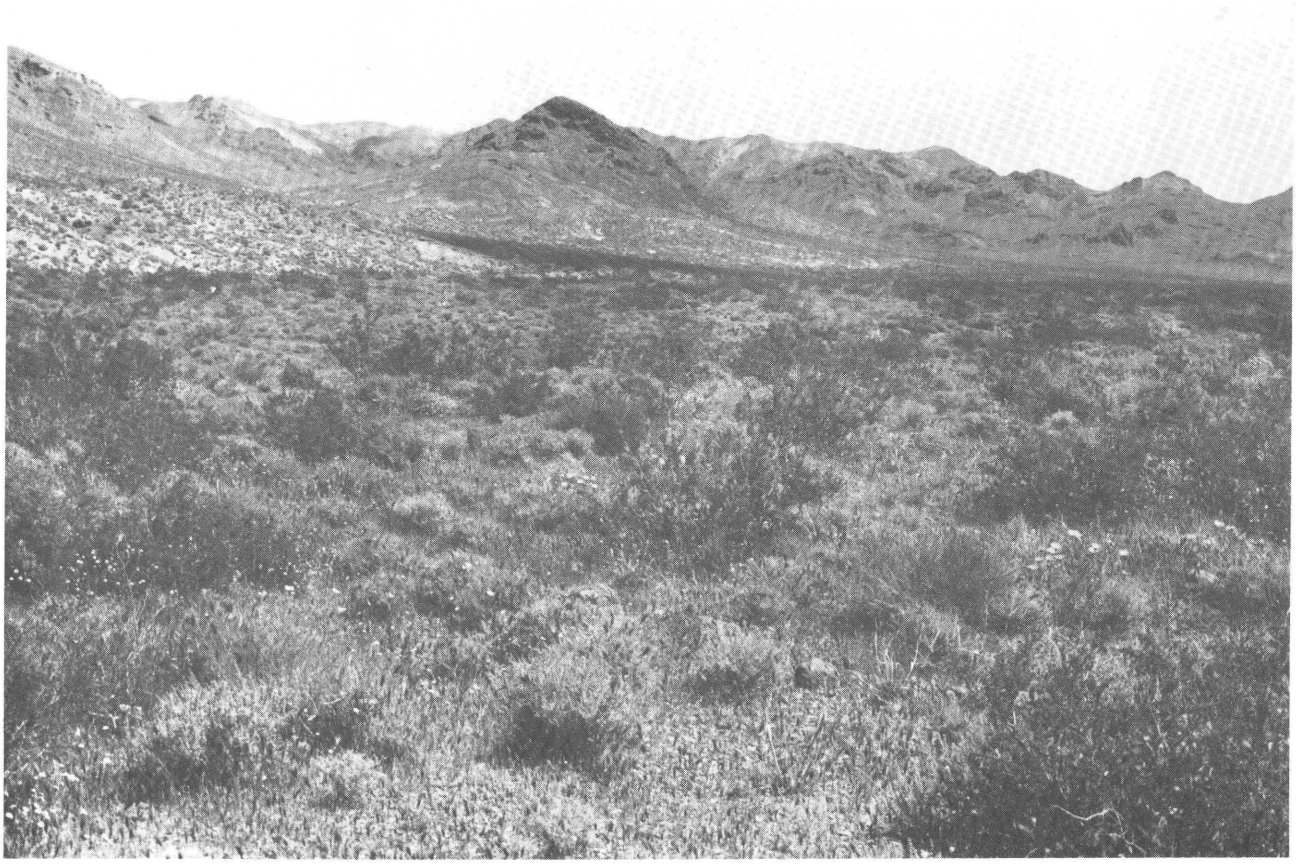


D

assemblage with Larrea, Grayia, and Lycium. View is toward the northwest. C, Terrace TA_2, showing a Larrea-Ambrosia assemblage. View is toward the south. D, Terrace TA_3, showing an Ambrosia-Larrea assemblage. View is toward the northeast.

Gold Valley townsite was built on terrace TC_2 (figs. 20, 21) and shows some recovery of soil and vegetation. The soil bulk density and peak shear strength were greater and the penetration depth was less in the townsite than on undisturbed soil on terrace TC_2 (table 26). The soil penetration resistances (fig. 22) indicate residual compaction on both sides of the townsite. The recovery times estimated from a linear model of recovery range from 90 to 120 yr for the western townsite, and 90 yr for the eastern townsite (table 26). The vegetation in the west half of the townsite is dominated by Ephedra, Hymenoclea, Coleogyne, and Lycium, while the east half of the townsite is dominated by Ephedra, Grayia, and Lycium, with Coleogyne also significant (table 27).

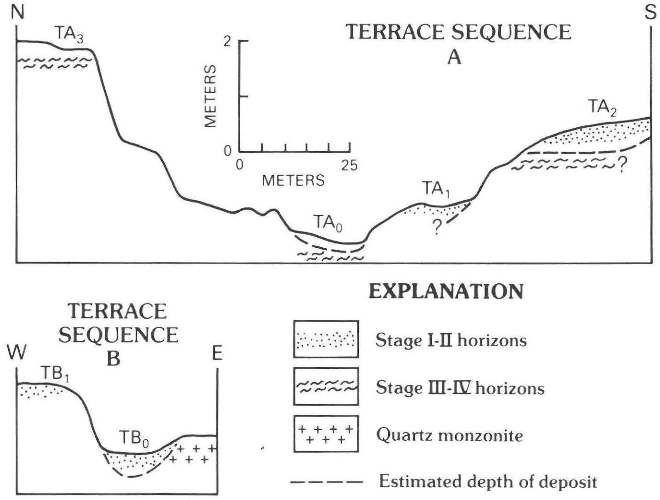


Figure 19. Cross sections of terrace sequences A and B in Gold Valley.

Percentage similarity values, calculated for all sites, indicate a high degree of similarity in vegetation between the townsite and terrace TC_2. The PS values for cover and density are 63.3 and 45.5 percent between TC_2 and the western townsite, 70.1 and 74.4 percent between TC_2 and the eastern townsite, and 70.0 and 58.1 percent between the eastern and western townsites, respectively. However, the PS values for cover and density are 46.1 and 29.0 percent between TC_3 and the western townsite, 37.8 and 44.1 percent between TC_3 and the eastern townsite, and 57.4 and 51.1 percent between TC_2 and TC_3. Therefore, while the similarity is high between the townsite and undisturbed vegetation on the same terrace (TC_2), the percentage similarity is lower when the townsite is compared with an older terrace (TC_3).

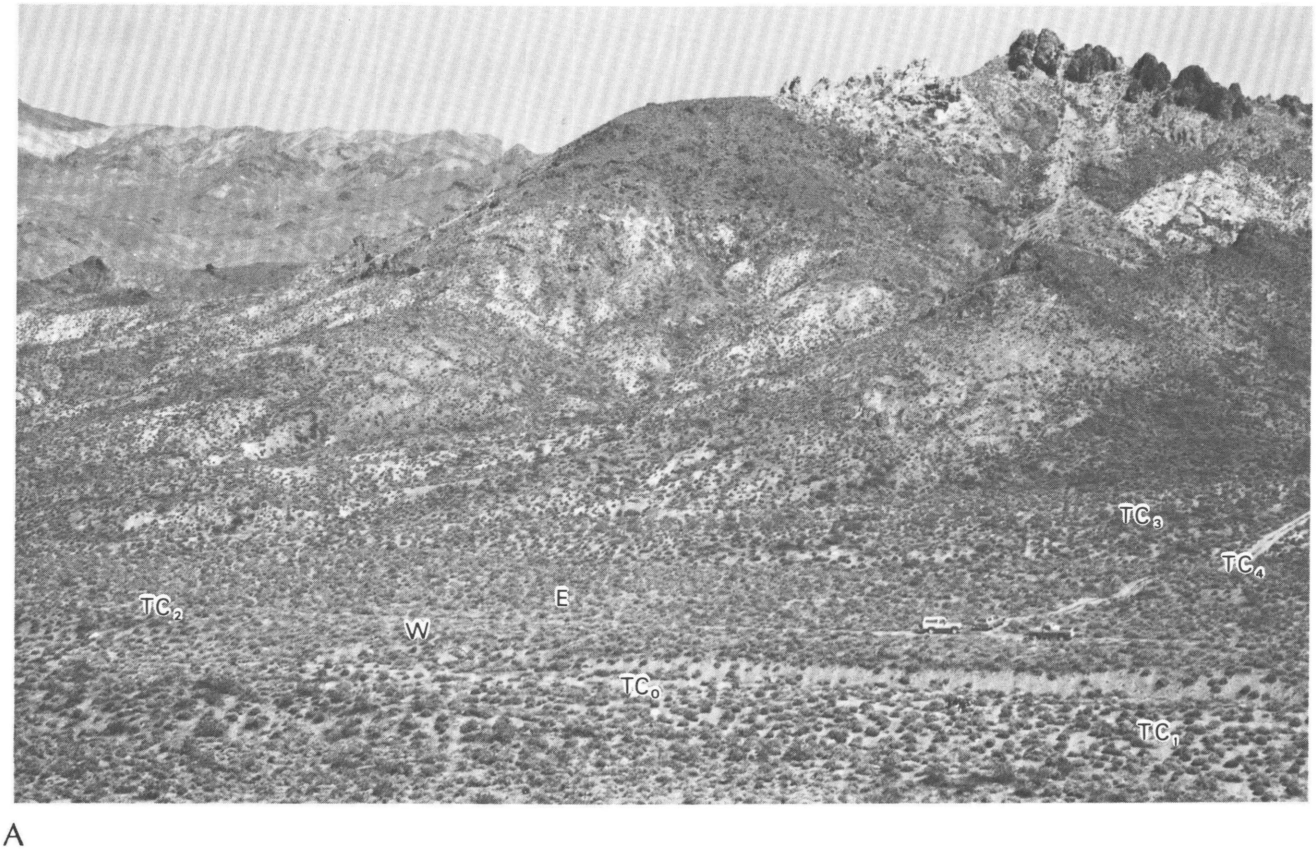
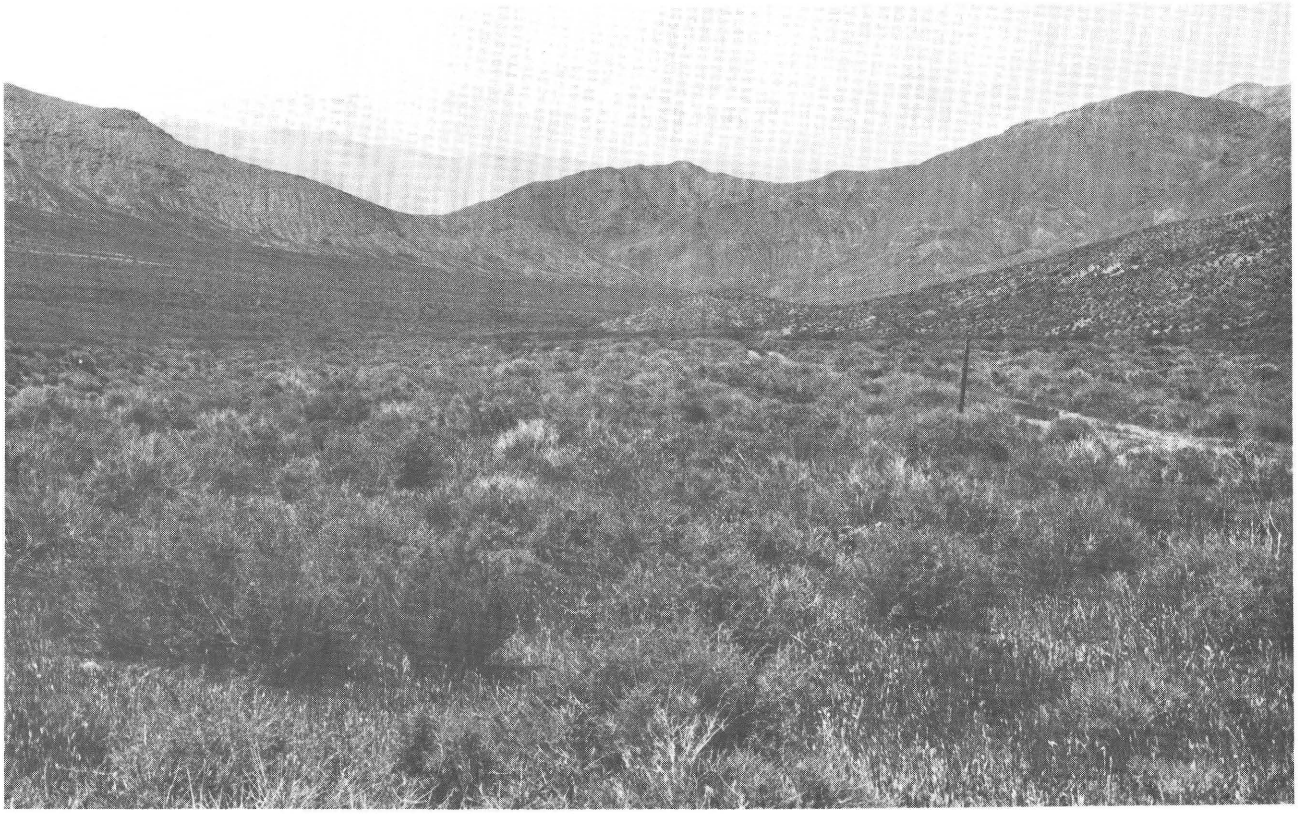
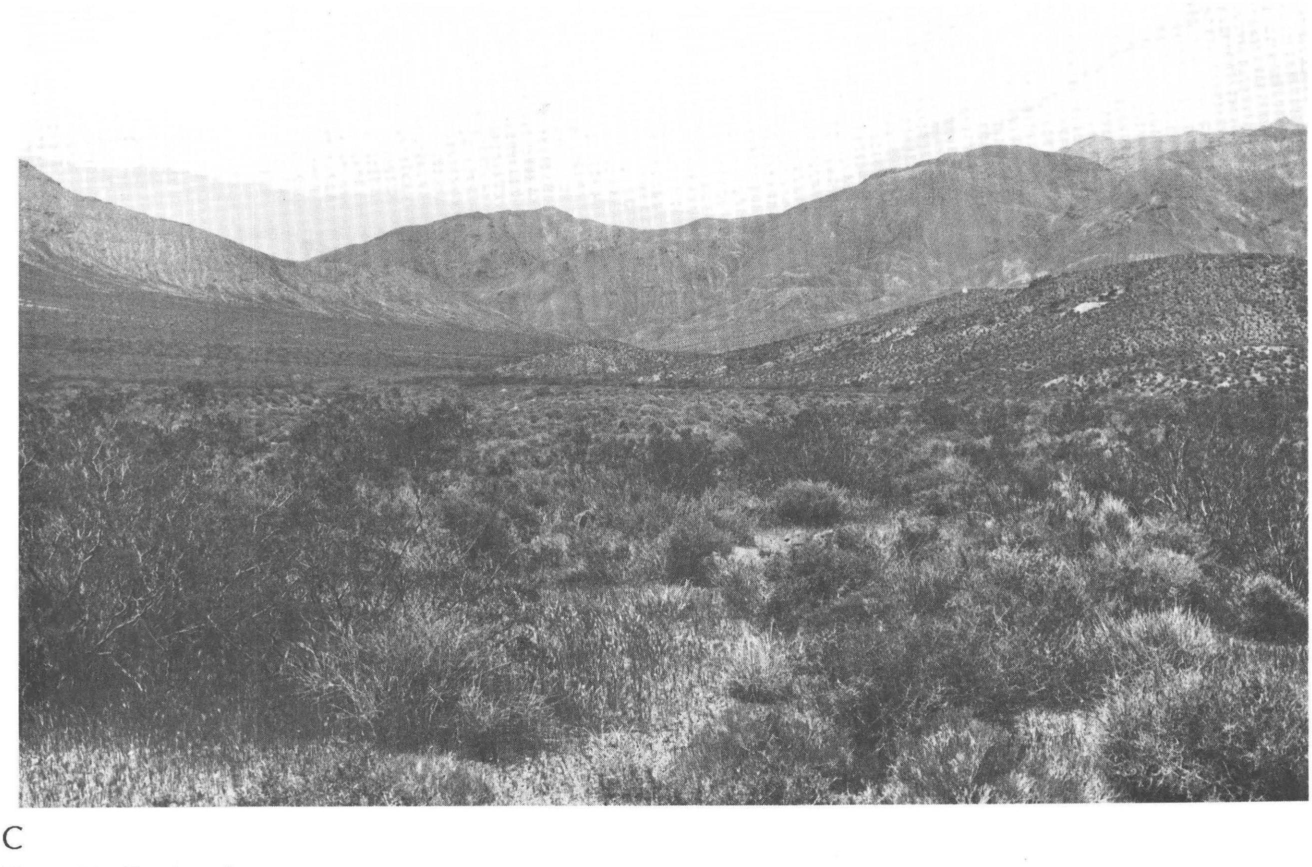


Figure 20. Gold Valley townsite and terrace sequence C. The foreground of each photograph shows the surface of the respective terraces. A, View is toward the northeast; the terraces and the eastern (E) and western (W) townsite are labeled. B, Townsite location on terrace TC_2; view is toward the north. C, Terrace TC_3, showing a Larrea-Coleogyne assemblage; view is toward the north.



B



C

Figure 20. Continued.

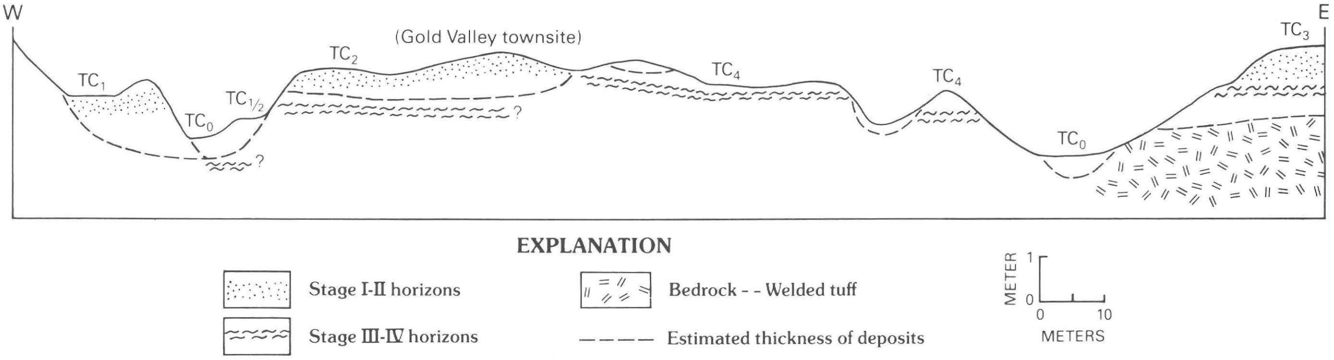


Figure 21. Cross section of terrace sequence C and townsite in Gold Valley.

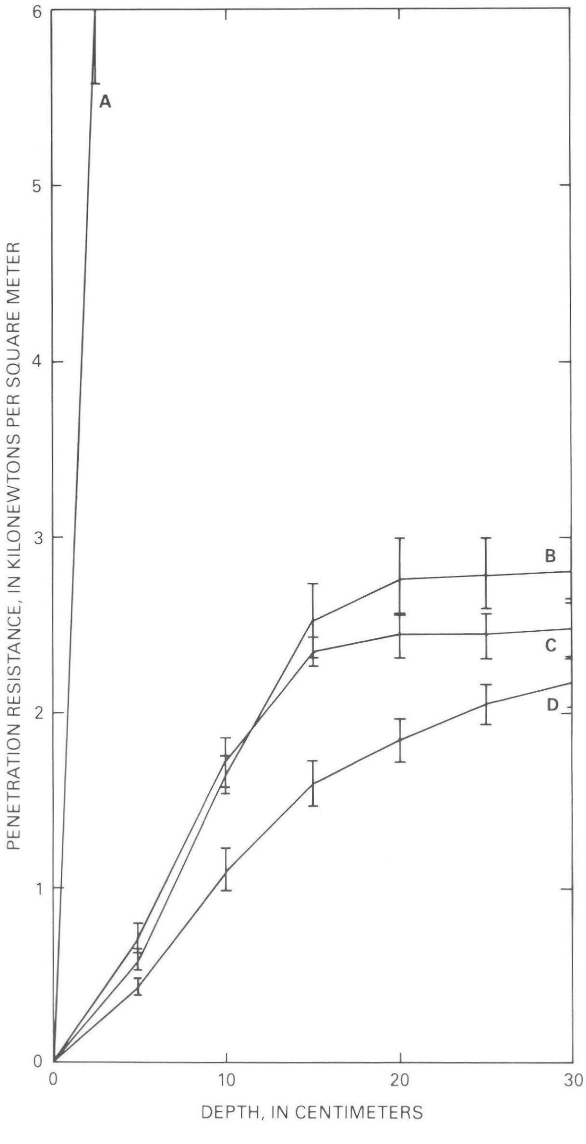


Figure 22. Penetration resistance vs. depth curves for soils at Gold Valley townsite. A, active road; B, western townsite; C, eastern townsite; D, terrace TC_3 control. Bars indicate standard error.

Discussion

Differences in the species composition of vegetation on alluvial terraces in Gold Valley provide evidence for primary plant succession in Larrea-dominated assemblages. The alluvial terraces are distinguished at three sites by height above the modern channel, and they are separated in age by thousands of years on the basis of soil morphology (table 28). The stages of succession, which are completely gradational, are the following for all terrace sequences: (1) The colonizing assemblage is dominated by Hymenoclea. This assemblage probably persists for decades. (2) Hymenoclea is slowly replaced by species such as Ephedra, Dalea, Eriogonum fasciculatum, and Ambrosia. (3) Larrea, Ephedra, Lycium, Grayia, Coleogyne, and (or) Ambrosia assume dominance in the assemblage, the composition of which varies with elevation. This stage appears to be representative of surfaces that are several thousand years old. (4) Larrea, Ambrosia, and (or) Coleogyne assume dominance, with other species declining in importance. (5) Coleogyne or Ambrosia attains higher coverage than Larrea, and few other species are present in the absence of local natural disturbances.

Geomorphic processes exert controls on primary succession in Gold Valley. The observation that drainages have soils and are mantled with vegetation in terrace sequences B and C indicates that floods rarely occur in Gold Valley. Discharges in the drainages would scour the channel bed, thus destroying any vegetation on the channel bottom; however, no denuded channel was observed in Gold Valley. Hence, the channel bottoms are probably stable for decades or perhaps centuries. Older terraces, formed in response to tectonic or climatic factors, are probably relatively stable in the current climatic regime.

The oldest stages of primary succession are unstable, as illustrated by the oldest terraces in Gold Valley. Runoff and erosion occur on these terraces because desert pavements and stage IV carbonate horizons inhibit infiltration of rainfall. Hence, eroded areas are common on these terraces, and Hymenoclea, Eriogonum inflatum, Acamptopappus, and (or)

Dalea occur in discrete patches in the disturbed areas. The erosion is episodic, and older eroded areas support assemblages with Ephedra, Lycium, and Grayia. Therefore, a climax assemblage must be arbitrarily defined as an assemblage on a terrace of finite, although great, age (middle Pleistocene in Gold Valley).

Composite plant assemblages in Gold Valley are difficult to explain except by episodic erosion and life-history strategies. Coleogyne contributes 7.0 percent cover and 1,600 individuals/ha density to the assemblage on TC_0, but it also dominates the older terrace surfaces. Either Coleogyne has a widely variable life-history strategy or else it has an affinity for stage III carbonate present at shallow depth. Regardless of the cause for Coleogyne's appearance on younger surfaces, terraces with exhumed soils are a composite of primary and secondary succession sequences. This composite illustrates that the distinction between primary and secondary succession is ambiguous where a well-developed calcic horizon is present in the soil.

The vegetation in Gold Valley townsite suggests that revegetation occurs at a faster rate than the primary succession model would suggest. The western townsite, which still has compacted soil, supported an assemblage dominated by Ephedra, Hymenoclea, and Coleogyne that is comparable to the assemblage on terrace TC_0 of the upper terrace sequence. The eastern townsite was apparently less disturbed than the western townsite and supports an assemblage with more Grayia and Lycium. However, it appears that the stages through which succession proceeds are similar in composition in primary succession and revegetation. This indicates that secondary succession is a viable model for recovery of vegetation in disturbed sites.

RECOVERY OF GREENWATER, KUNZE, AND FURNACE TOWNSITES

> You must know just about exactly where Greenwater was before you can find its ghost....Once Greenwater is found, though, evidences of its swift flowering and swifter demise may be seen scattered through hundreds of acres of blackbrush. And in the hills, the great waste dumps look freshly mined though more than half a century has passed since the final work was done there. Thus they may remain a thousand years more.... (Weight, 1969, p. 17).

The towns of Greenwater, Furnace, and Kunze (the Greenwater district) were all built in 1906 and abandoned in 1908 during the mining boom that also led to the establishment of Skidoo and Gold Valley (fig. 1). Observations and measurements in the Greenwater district townsites indicate revegetation patterns similar to those found in the other townsites. All three townsites in the Greenwater district were built on alluvial fans with similar parent material, elevation, slope, and exposure. A well-documented history and the large areal extent of the Greenwater district facilitated a highly detailed study of the recovery of vegetation in these disturbed sites.

History of the Greenwater District

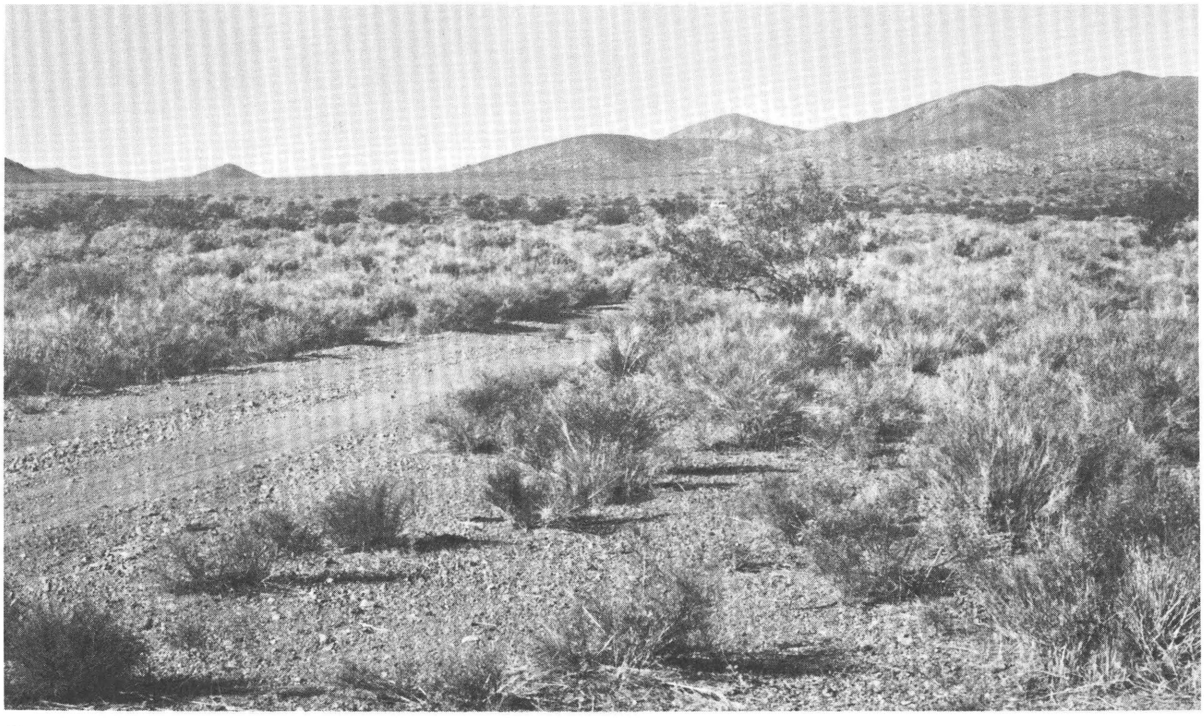
In 1905, copper mineralization on the east slopes of the Black Mountains attracted thousands of prospectors (Latschar, 1981, p. 508). In response to the boom, Furnace townsite was established in January 1906, while rival townsites named Kunze (also irregularly called Greenwater) and Ramsey were established nearby. In the winter of 1906-1907, Kunze and Ramsey were abandoned in favor of a merged camp named Greenwater, which became the commercial center of the district because of its greater potential for expansion.

The population of these townsites rose and fell with the fortunes of the mines, reaching a maximum in early to mid-1907. Kunze had a maximum population of about 1,000 before abandonment. The maximum population of Furnace was estimated to be over 1,000 (Weight, 1969, p. 22), whereas the population of Greenwater was between 700 and 1,000 at the height of the boom. Contemporary newspaper accounts (Latschar, 1981, p. 548) indicate that Furnace's maximum population was only 500, and that the maximum population of the entire Greenwater district was 2,000 in the spring of 1907.

The Greenwater boom was short lived and has been called "a monumental stock fiasco" (Paher, 1973, p. 14) and "the monumental mining stock swindle of the century" (Weight, 1969, p. 31-32). More than $100 million was invested in claims over a four-month period of 1906 to 1907. No ore was found that could be profitably mined, despite surface exposures described as "fantastic," or that would have made Greenwater worthy of the title "Greatest Copper Camp on Earth" (Weight, 1969). Only 100 miners remained at Greenwater by September 1907. The few remaining miners were concentrated around two persistent mines, one just south of Kunze and the other west of Furnace. The population of the entire district was estimated to be 50 in February 1908 (Latschar, 1981, p. 566). Although the former deputy sheriff (and later State senator) Charles Brown reported staying at Greenwater until 1909 (Weight, 1969, p. 26), all three townsites were effectively abandoned by mid-1908. All buildings were quickly scavenged for the scarce wood and metal. Work continued at the two mines until 1910 with a small number of miners involved, and small-scale attempts at reviving the district in later years failed (Latschar, 1981, p. 573).

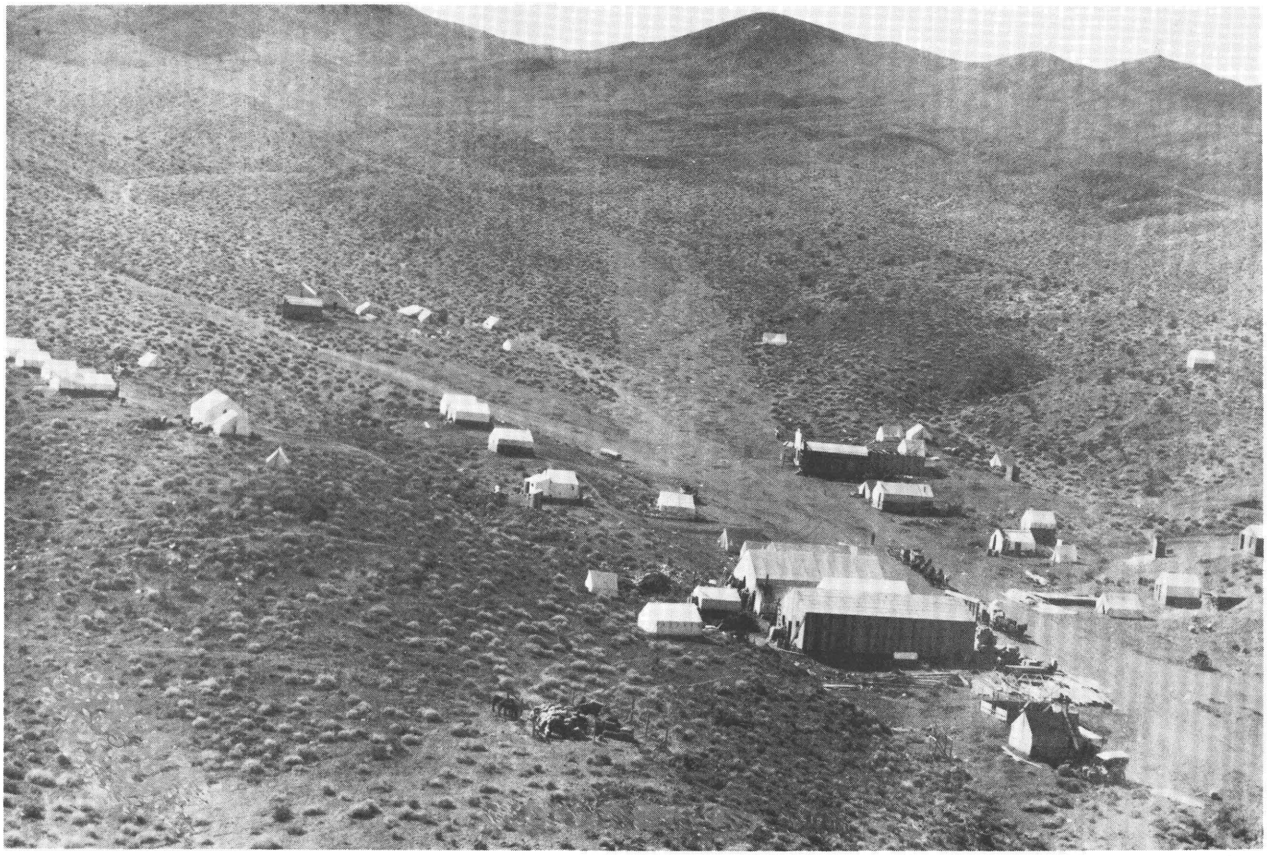
The disturbed areas of the Greenwater district represent the combined effects of trampling, vehicle use, construction of buildings, clearing of vegetation, grading of house pads, occasional fires, and limited livestock grazing. Based on wood pieces, cellars, and garbage found at the site, combined with historical photographs (figs. 23, 26) and modern aerial photographs (figs. 27-29), the use history of the site can be reconstructed. Streets were cleared of vegetation and houses were built (figs. 23, 25), although some areas were cleared and not used (area in back of town; fig. 24). Automobiles were common and driven throughout the townsites (figs. 25, 26). Horses were also used (fig. 25), which suggests that some livestock grazing must have occurred. The effects of grazing were probably limited; Weight (1969, p. 8, 24) reports that Greenwater had feedlots and that hay wagons supplied the town. Level pads for houses were excavated in the slopes, and outhouse holes were dug through the soil caliche; bottle hunters in subsequent years dug readily identifiable pits in the townsite. Evidence for cutting of "greasewood" (probably Larrea) is present only in limited areas of the townsites, and

A



B

Figure 23. Main Street in Greenwater townsite. The foregrounds of the two photographs are probably not identical. A, In 1906 (courtesy of the Mojave River Valley Musuem). B, In 1981.



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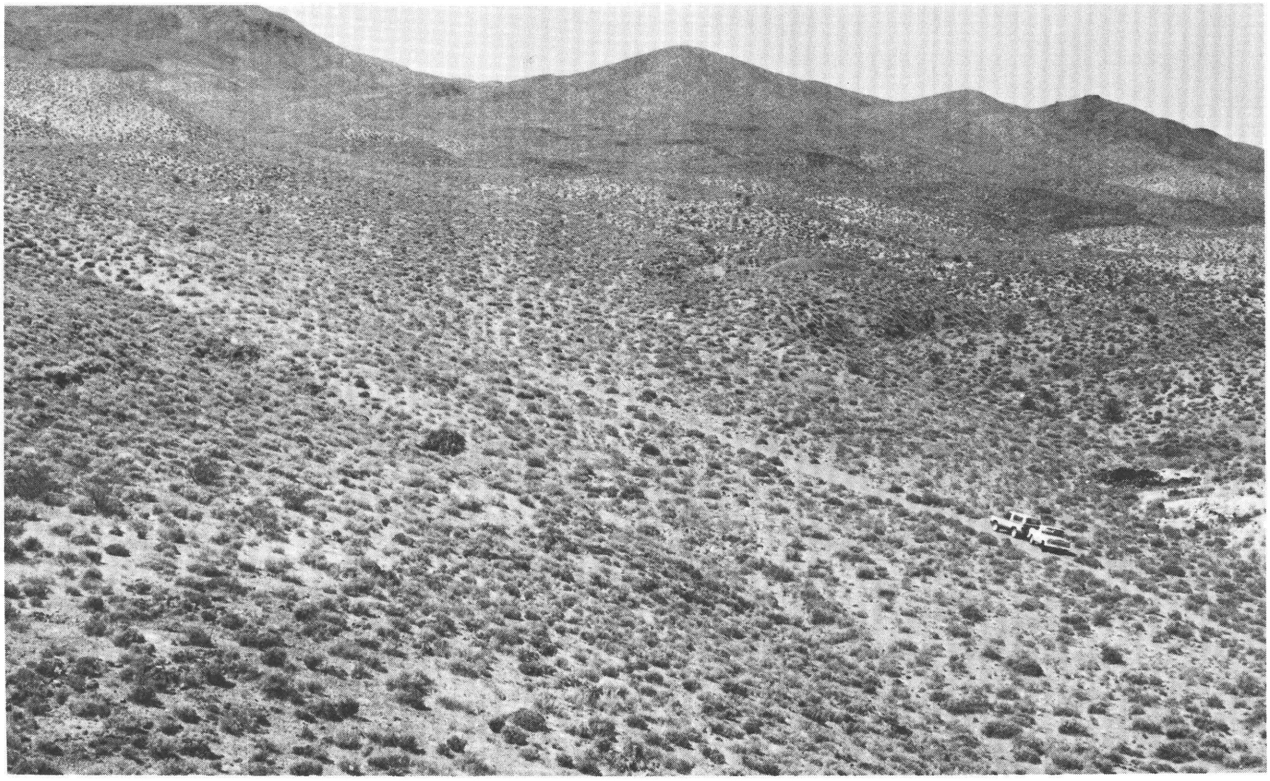

B

Figure 24. Hilltop views of Kunze townsite. View is toward the south-southwest. A, In 1906 (courtesy of the Nevada Historical Society). Photographs taken later in 1906 show a more extensive development of the townsite before it was moved to Greenwater in the winter of 1906-1907. B, In 1983 (Raymond Turner, U.S. Geological Survey).

given the ubiquitous growth of Larrea throughout the Greenwater Valley, the report of "scarce greasewood" (Latschar, 1981, p. 538) seems exaggerated.

The Setting of the Townsites

The Greenwater district lies near the apex of an east-facing bajada on the west side of the Greenwater Valley (fig. 1). Greenwater was built on a broad alluvial fan at an elevation of 1,340 m and a general slope of 4° (fig. 27). Kunze, located 2.4 km west of Greenwater, was built on a fan embayment at 1,430 m elevation and 5° slope (fig. 28). Furnace was built on dissected alluvial deposits at 1,429 m elevation and 11° slope (fig. 29). Ramsey townsite was not located.

Meteorological data for this area are nonexistent. The nearest stations, at noncomparable sites, are Furnace Creek, approximately 45 km northwest, and Shoshone, California, approximately 40 km southeast. Hunt and others (1966, p. 7-9) estimated an average annual precipitation of about 130 mm and a mean annual temperature of 13-15 °C for the area.

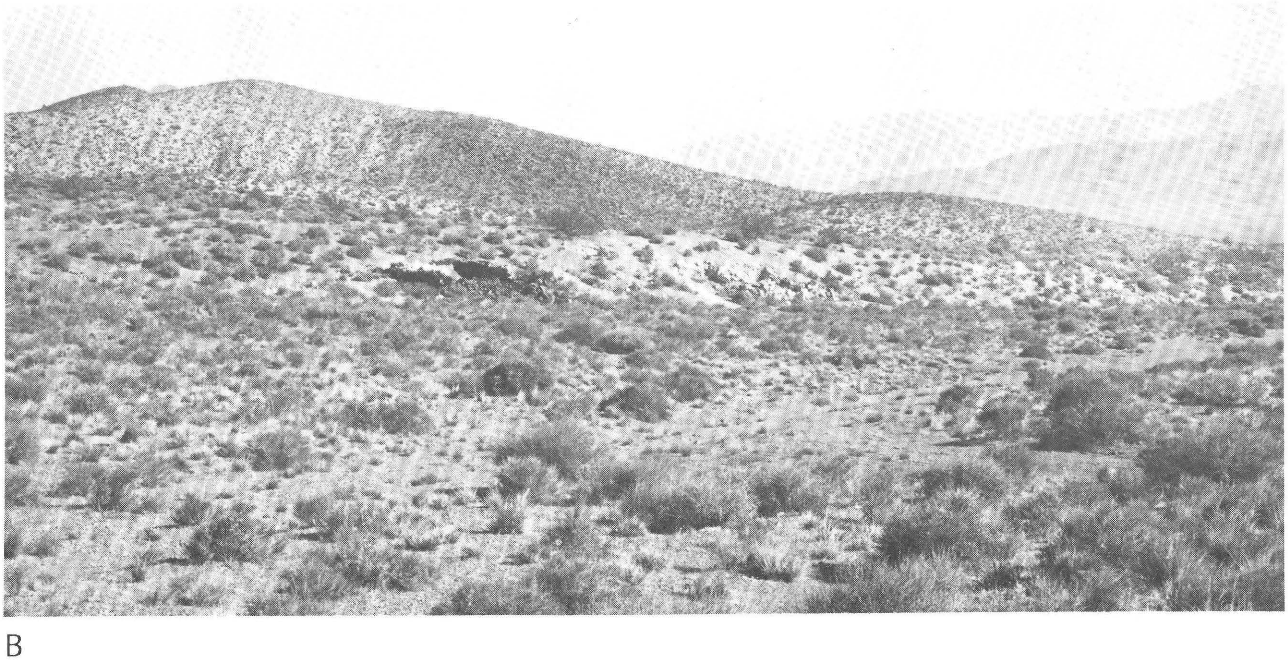

Figure 25. Main Street in Furnace townsite. View is toward the north. A, In 1906 (courtesy of the Nevada Historical Society). B, In 1983 (Raymond Turner, U.S. Geological Survey).

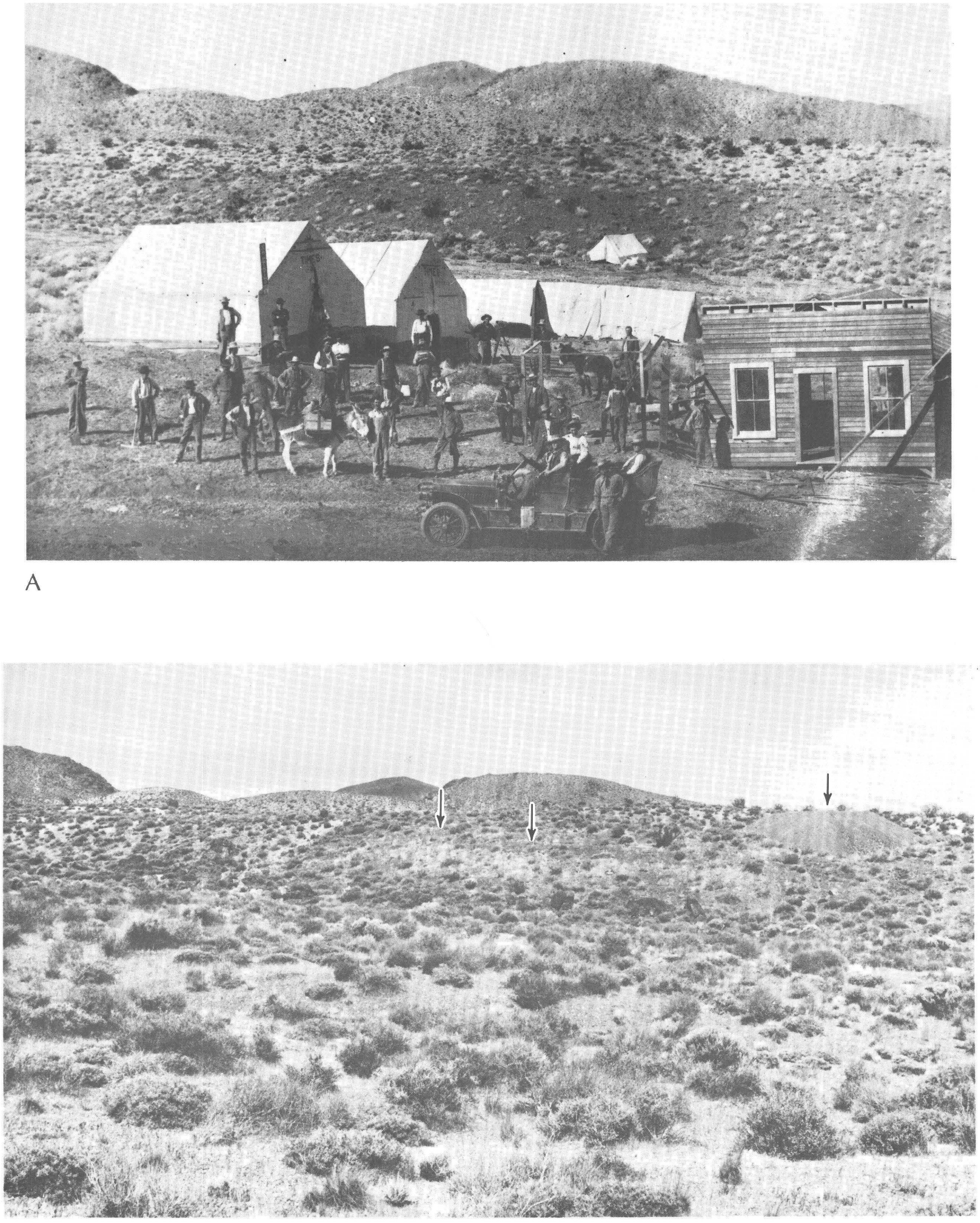

Figure 26. Locale of the Greenwater Times office at Kunze townsite. View is toward the northwest. A, In 1906 (courtesy of the Nevada Historical Society). B, In 1983 (Raymond Turner, U.S. Geological Survey). Note the lack of Larrea behind where the buildings stood (double arrows) and the mine tailings (single arrow) that were deposited sometime after the 1906 photograph was taken.

Temperature extremes of below 0 °C to above 27 °C were reported while the townsites were occupied, as was the occurrence of occasional winter snow (Weight, 1969, p. 27), which was also documented by us in December 1981 and March 1982.

The alluvial deposits underlying all three townsites were derived from Tertiary rhyolite and rhyodacite source materials (plate 1 in Drewes, 1963). Drewes mapped the alluvial deposits at Furnace as cemented Quaternary gravels and the deposits at Greenwater as Quaternary gravels, implying that the alluvial surface at Furnace is older. Kunze, built in a periodically flooded drainage, has the youngest alluvial deposits.

The gently undulating topography at Greenwater townsite represents a complex history of deposition, as reflected by the degree of soil formation on different surfaces. The soil in the western part of Greenwater is oldest and is characterized by the presence of an argillic horizon and a patchy stage IV calcic horizon (table 29); this soil occurs on the tops of low ridges. In the eastern part, soils on ridges have less developed profiles and are generally characterized by stage II to stage III calcic horizons (control C, table 29). Soils developed in swales east of the townsite are younger still and are characterized by well developed stage I carbonate horizons (control D, table 29). The youngest soil at the Greenwater townsite occurs in a drainage east of the townsite and is characterized by a weak stage I carbonate horizon.

Furnace townsite was built on the tops of dissected ridges similar to those at Greenwater. The soil at Furnace is characterized by a stage I carbonate horizon (table 29) overlying a buried stage IV carbonate horizon. The soil developed in the drainage at Kunze has a stage I carbonate

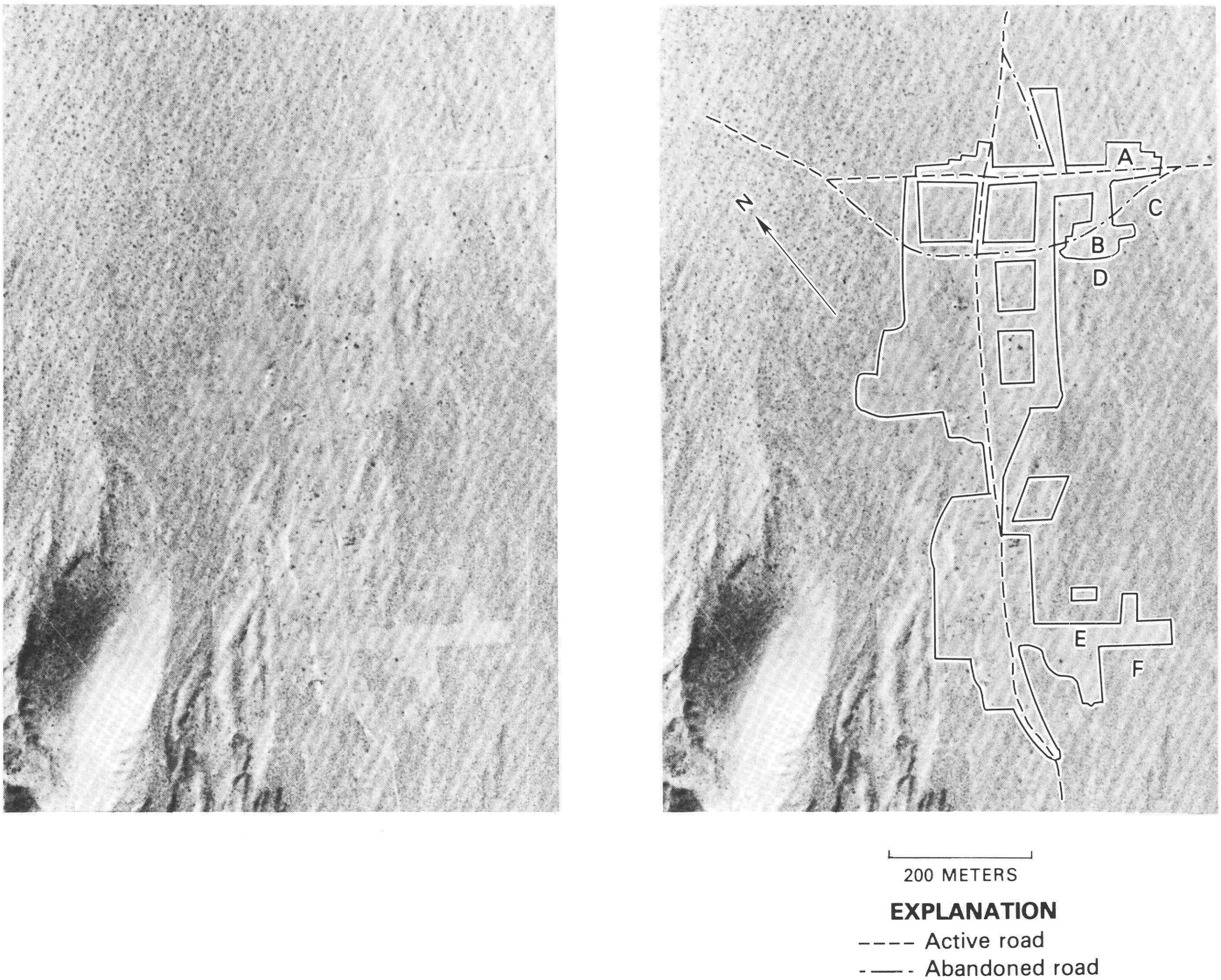

Figure 27. Aerial photograph of Greenwater townsite, showing the location of study sites: A and B, lower Greenwater townsite; C and D, lower controls; E, cleared area; F, upper control. Photographed November 1948 and enlarged four times (photograph number IF-3-61).

horizon. The soils at Kunze and Furnace are probably correlative with the soil in control D at Greenwater. Surface texture of all townsite soils is in the range considered most susceptible to compaction (Webb, 1983).

The vegetation at all three sites is representative of the Larrea-Lycium-Grayia assemblage of Beatley (1976, p. 31) near the ecotone with the higher elevation Coleogyne assemblage. The highest elevation parts of the Greenwater townsite (labeled E and F in fig. 27) are part of this ecotone boundary. Thirty-two perennial species are found in the Greenwater area (table 47), and a similar flora occurs at Furnace and Kunze. In the lower elevation Greenwater sites, the dominant species are Larrea, Lycium, Menodora spinescens, and Ephedra. In the upper elevation Greenwater sites, the dominant species are Menodora and Lycium, with large contributions from Grayia, Ephedra, Haplopappus cooperi, and H. laricifolius. At Furnace, Menodora, Larrea, and Lycium dominate. At Kunze, the vegetation has been altered substantially by human occupation, but site elevation and vegetation on surrounding hills suggest a similarity with the Furnace site. The young age of the soil at Kunze and possible disturbance from flooding would imply that the undisturbed vegetation at other sites in the Greenwater district is not analogous to the vegetation at the Kunze townsite prior to occupation.

Methods

Study-Site Selection

Several study sites were established to determine recovery (figs. 27-29). At Greenwater, the study sites consisted of a section of townsite with graded house pads (labeled A in fig. 27); a section cleared but with less evidence of use (labeled B); two control sites with different soils (table 29) on slightly different topography for comparison with A and B (labeled C and D); a cleared but probably unused site 600 m upslope from C and D (labeled E); and a control adjacent to E (labeled F). In addition, the vegetation within house-pad areas and Larrea individuals were measured in the general townsite and compared with measurements at controls C and D. Soil in an abandoned road crossing townsite B was measured for residual soil compaction. Sites A, B, C, D, and the general townsite are in a vegetation assemblage with significant Larrea in the undisturbed site, whereas sites E and F are in an ecotonal boundary site generally devoid of Larrea.

At Kunze, a study site was located in the main portion of the townsite, but no suitable control site was located (fig. 28); the townsite is within a Larrea assemblage, but spatial heterogeneity in species composition, topographic irregularities, and the general small size of comparable,

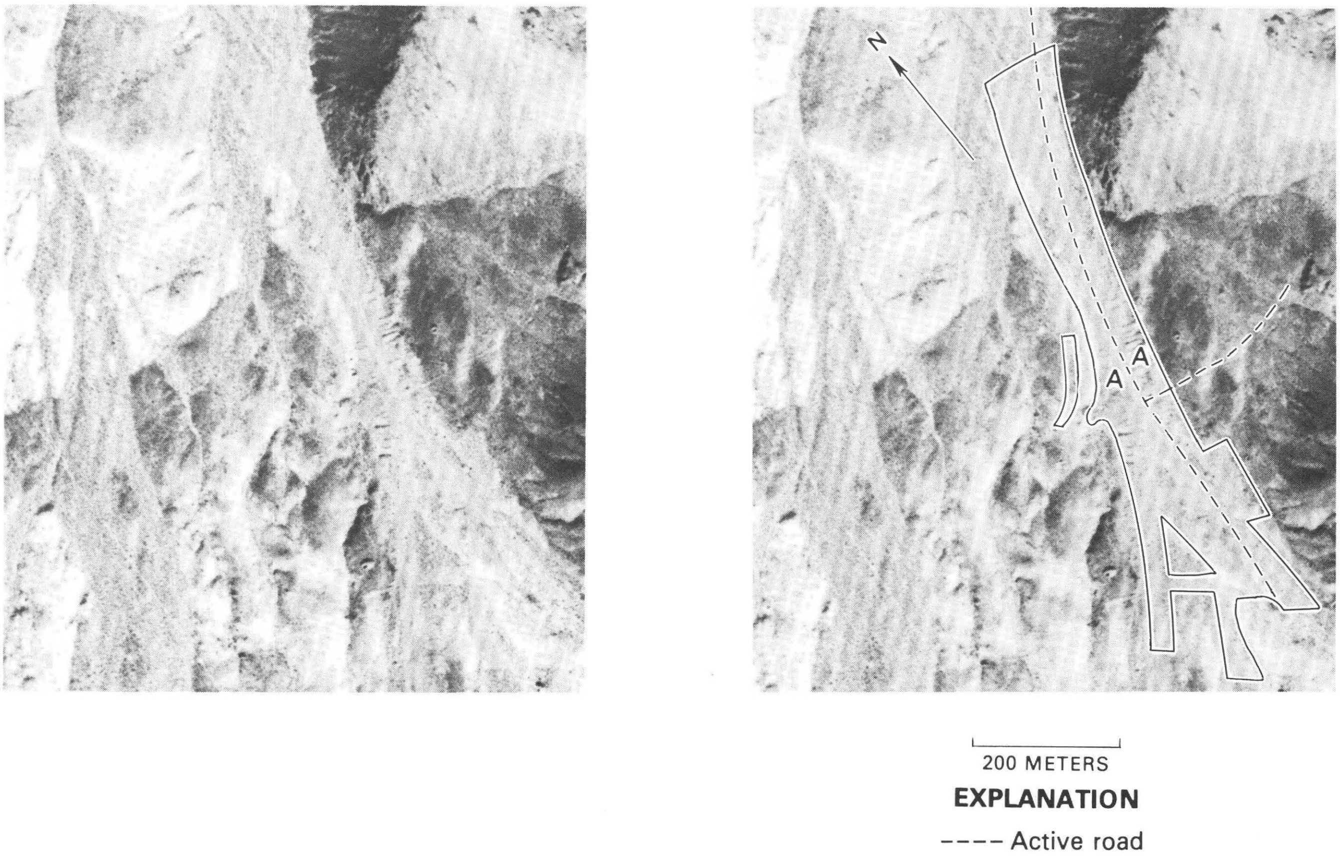

Figure 28. Aerial photograph of Kunze townsite, showing the location of the study site. A, townsite. Photographed November 1948 and enlarged four times (photograph number IF-3-61).

undisturbed sites precluded measurement of a control site. At Furnace, study sites were located in a portion of the townsite (labeled A in fig. 29) and a control site situated in an unused city block (labeled B).

Soil and Vegetation Measurements

Soil compaction was measured with a simple 30° cone penetrometer. Other soil measurements were not performed because of the high gravel content of the soil (table 29). The soil was air-dry at the time measurements were taken. The Shapiro-Wilk W-test (Shapiro and Wilk, 1965; Mark, 1978) was used to test the hypothesis that penetration depths are normally distributed; in general, the hypothesis that the distribution of penetration depths was normal could not be rejected at the 95-percent confidence level.

Vegetation measurements included density, percent cover, and dimensions of individual plants. Densities were obtained from 400-m² belt transects, and percent cover was determined from 400 m of line intercepts in each study area. Shrub heights and minimum and maximum diameters were measured on 30 individuals of each abundant woody species in order to calculate volumes; at Greenwater, 50 Larrea individuals selected throughout the townsite were compared with 50 individuals in control C. Shrub biomass was estimated for each species for which shrub volume data could be collected.

Results

Recovery of Compacted Soils at Greenwater and Furnace Townsites

Soil penetration resistance measurements revealed residual compaction in an abandoned road and all disturbed sites except sites B and E (table 30). Hence, plants attempting to colonize most of the disturbed sites faced soils with high density and high strength, whereas plants colonizing the cleared areas faced less harsh conditions. If it is assumed that penetration depth increases linearly with time, a complete recovery time for the compacted soil is estimated to be 100 yr for Furnace, 100 yr for townsite A, and 110 yr for the abandoned road in townsite B.

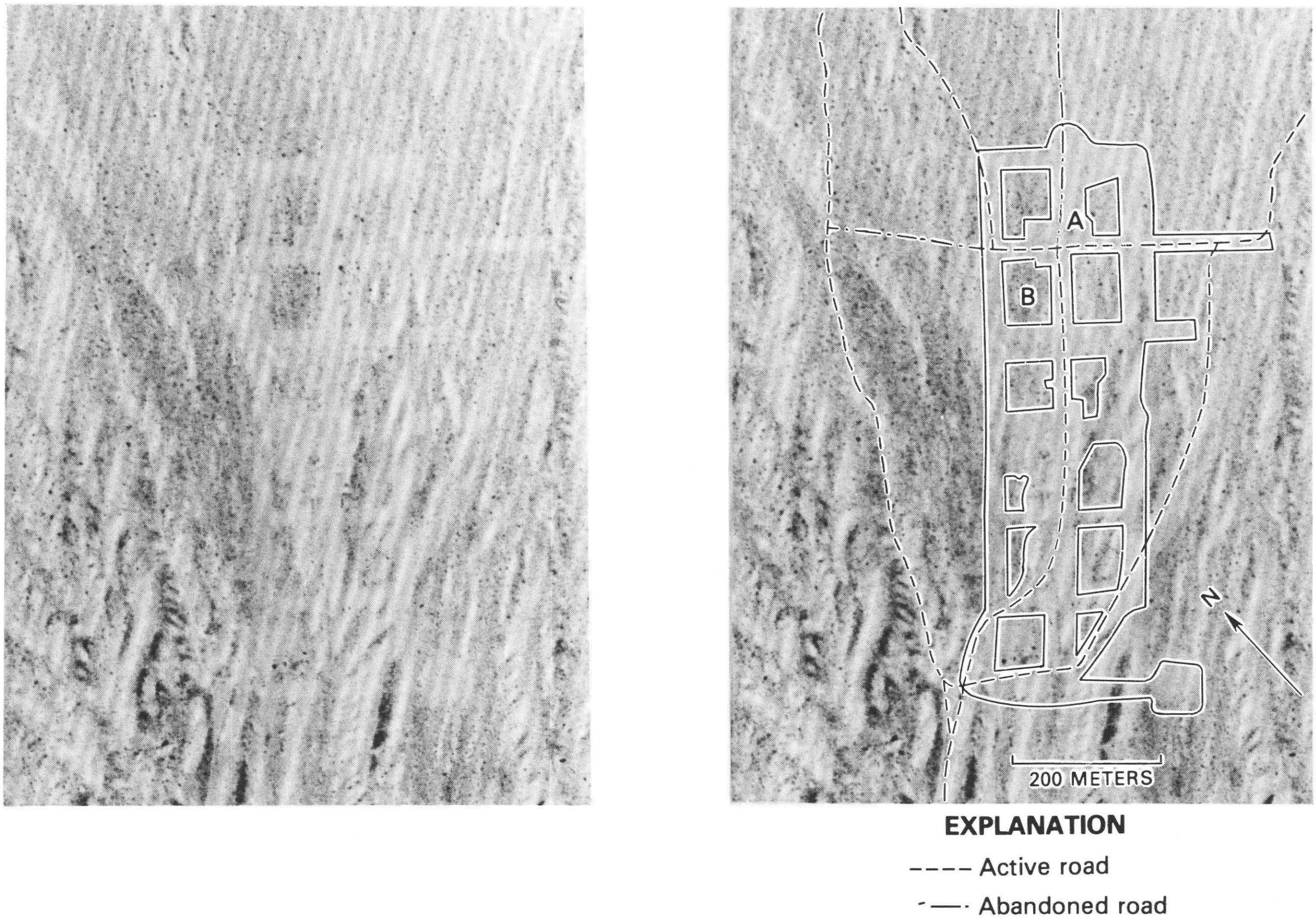

Figure 29. Aerial photograph of Furnace townsite, showing the location of study sites, A, townsite; B, control. Photographed November 1948 and enlarged four times (photograph number IF-3-61).

Recovery of Vegetation at Greenwater Townsite

The cleared areas at Greenwater townsite have undergone substantial revegetation in the 73 yr since abandonment. Total cover is similar between disturbed and control sites, and only minor differences were measured between controls. However, the disturbed sites can be readily distinguished from undisturbed sites because of shifts in species composition, cover, and biomass, as well as the apparent slow reestablishment of Larrea (table 31).

At the lower Greenwater sites, the cover of Lycium, Menodora, and Larrea is much less in the disturbed sites A and B than in either control C or D (table 31, fig. 27). These differences far surpass differences between controls C and D caused by soil differences (table 29). The cover of Ephedra is lower in site A but not in site B, while Grayia cover is lower only in site B. Hymenoclea and Stipa speciosa have a greater cover in sites A and B than in the controls (table 31). Haplopappus sp. generally had a higher cover in site A than the controls, but this species exhibits a high spatial variability and tends to clump. Only minor differences were measured between controls, with the lower cover of Lycium and higher cover of Haplopappus sp. in control D the most important. No consistent differences in species cover were observed between sites A and B, despite the lack of compaction in site B (table 30). The density of vegetation in sites A and B was roughly similar to the density of vegetation on 16 house pads distributed throughout Greenwater townsite (table 35) with respect to the paucity of Larrea, Lycium, Menodora, and Ephedra.

The disturbed sites in the lower townsite had a higher total density and a lower density of long-lived shrubs than the control sites. Hymenoclea had a much greater density in sites A and B than the controls, whereas the density of Lycium, Ephedra, Menodora, Larrea, and Grayia was lower in all of the disturbed sites (table 31). Generally, Hymenoclea, Stipa, and herbaceous perennials contributed the largest density in the disturbed sites, while woody shrubs contributed the largest densities in the controls.

In the upper Greenwater site, the cover of Menodora, Lycium, and Grayia was lower in the cleared site E (table 30) than control site F (table 32). The cover of Ephedra was similar in both sites, while the cover of Haplopappus sp., Hymenoclea, and Stipa were greater in the cleared site. Total live cover was similar in the two sites, but the cover contributed by shrubs was much lower in the cleared site than in the control (table 32). The densities of Hymenoclea and Stipa were much greater and the densities of other woody shrubs were much less in cleared site E than in control F.

The most striking difference in shrub volumes was between Larrea sizes in disturbed sites vs. controls (fig. 30). Data from both Greenwater and Furnace controls show a similar unimodal distribution of Larrea volumes, whereas a distinct bimodal distribution of volumes was found in the disturbed sites. In each case, the means were not significantly different, yet the volume distributions were obviously different. A possible explanation of this phenomenon may be the decreased competition for water among Larrea individuals left standing after the townsites were constructed. These individuals increased in volume by taking advantage of the excess water not used by other perennials and are represented in the histogram by the peak in the large volumes (fig. 30). Seedlings established after abandonment of the townsite encountered increased competition from established Larrea individuals and other reestablished species or simply grew slowly with respect to the 73-yr abandonment time; this is illustrated by the peak in the smaller volumes (fig. 30).

Larrea in the control sites also showed a strong tendency toward clumping of individuals, whereas individuals in the disturbed sites were usually solitary. The majority of clumped Larrea in the controls may be clonal rings, which indicates that these are very old individuals (Vasek, 1980b). The solitary individuals could be either relatively recent recruits or

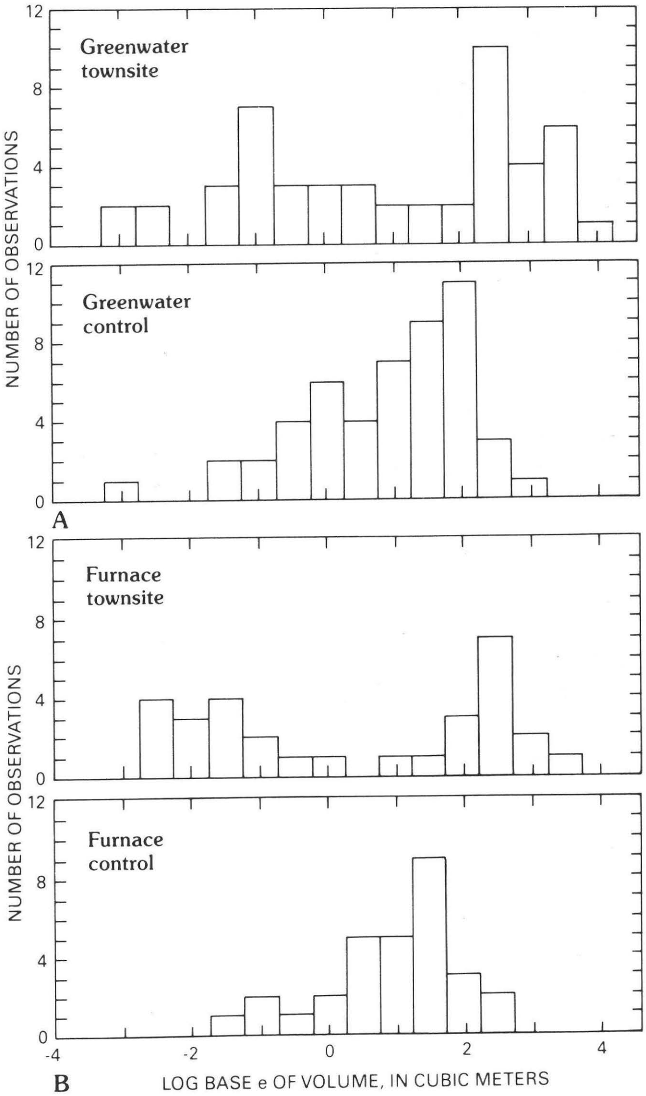

Figure 30. Histograms showing volumes of individual Larrea tridentata. A, In Greenwater townsite (50 individuals). B, In Furnace townsite (30 individuals).

remnants of destroyed clonal rings. Similar patterns can be detected in the distributions for other species, but these differences in distributions are not as striking as those for Larrea between disturbed and control sites.

Fundamental differences were observed in the distribution of biomass among shrub species. Hymenoclea always had a much greater biomass in disturbed than control sites (tables 33-35), while the biomass of species dominant in control sites (such as Menodora, Lycium, and Larrea) was always less than in the disturbed sites. Some species, such as Ephedra, showed little biomass differences between disturbed and control sites, while the biomass of Haplopappus sp. was too variable to allow comparisons. In general, the large errors associated with the biomass calculation (as much as 50 percent) preclude meaningful conclusions except in the cases of obvious large differences, and certainly they prevent a meaningful estimation of total biomass for the sites.

Recovery of Vegetation at Furnace and Kunze Townsites

Furnace and Kunze townsites showed a pattern of revegetation generally similar to the Greenwater townsite but with some important differences. As was the case at Greenwater townsite, the disturbed sites generally supported a higher cover of Stipa and Hymenoclea and a lower cover of Menodora and Larrea than the Furnace control site (table 36). However, the cover of Haplopappus sp. was much lower in Furnace townsite than in the control, whereas generally the opposite was true at Greenwater townsite. Dyssodia cooperi, an herbaceous perennial, contributed a relatively large cover in Furnace townsite compared with the control, whereas little difference between control and disturbed sites was measured at the lower Greenwater townsite.

The total covers in Furnace townsite and control were similar (table 36), although they were lower than at comparable sites at Greenwater. The cover contributed by shrubs at Furnace townsite was the lowest of any of the disturbed sites. In a manner similar with the Greenwater sites, Hymenoclea, Stipa, and herbaceous perennials contributed the greatest density in the townsites, whereas other woody shrubs contributed the greatest density in the Furnace control (table 36).

Shrub volumes followed a pattern similar to that observed at Greenwater townsite. Larrea in Furnace townsite showed a strong bimodal distribution, as discussed previously (see fig. 30B). Some other species, particularly Grayia, also showed an apparent bimodal distribution of volumes in the townsite compared with an apparent unimodal distribution in the control. Statistical comparison of mean volumes revealed a significantly greater volume for Hymenoclea in Furnace townsite than in Furnace control. All other volumes were found to be statistically similar, although the mean volume of Larrea was 70 percent greater in Furnace townsite than in Furnace control.

Biomass calculations revealed patterns similar to those found at Greenwater (table 37). The dry-weight biomass of Hymenoclea was much greater in Furnace townsite than in Furnace control. The biomasses of Menodora and Larrea were much lower in the townsites than in Furnace control, whereas little difference could be discerned between townsites and control for Ephedra and Lycium.

Discussion

The data and observations on vegetation in the Greenwater district can be used to formulate a model for secondary succession. Hymenoclea appears to be the first perennial to colonize recently disturbed sites at Greenwater, with Ephedra and Thamnosma also of importance as colonizers. A lightly used road at Furnace had Hymenoclea on its shoulders and median. Haplopappus, Lycium, and Grayia become established with Hymenoclea within a timespan on the order of the time since abandonment. Menodora and Larrea apparently assume dominance after a much longer time period.

Larrea's response to disturbance affects the interpretation of recovery. Larrea is a highly visible shrub in the Greenwater district, and its presence and absence is easily detected on aerial photographs (figs. 27-29). Its low density is offset by its height, a characteristic of this species (Beatley, 1974). Larrea has a conspicuously low density and cover in Greenwater district townsites, a result not expected based on Larrea's relatively early appearance in primary succession sequences in Gold Valley. However, Larrea is at its upper elevational limits in Greenwater and could be limited by too much precipitation (Beatley, 1974). To test climatic change as an influence in recovery of disturbed sites, pack rat middens were analyzed near Greenwater townsite (see section on "Paleoecological Studies in the Black Mountains").

Little information is available concerning the life-history strategy of Menodora (Beatley, 1976, p. 214-215; Jaeger, 1941, p. 181; Munz, 1974, p. 589). However, Menodora is inferred to be a stress tolerator based on its similarity with Larrea in distribution among control and disturbed sites; its shoot morphology, consisting of short, stout, spiny branchlets; its low, lateral crown spread; and its apparent low palatability. The plant appears to tend toward a more competitive strategy than Larrea as suggested by its phenology and frequency of flowering during periods of maximum potential productivity, by leaf phenology composed of well-defined peaks of leaf production, and by relatively short longevity of leaves.

The species of uncertain importance in the successional sequence are Ephedra, Tetradymia, and Haplopappus sp. Ephedra behaves partly like Hymenoclea in its colonization of disturbed sites through both root-crown sprouting (Vollmer and others, 1976) and seedling establishment. Ephedra has been termed a "long-lived" species (Vasek and others, 1975a), also implying a similar strategy as Larrea, and has been recommended for the artificial reseeding of disturbed sites (Kay and others, 1977c). It has many characteristics of a stress tolerator, including small, ephemeral leaves, photosynthetic stems, and a regenerative strategy of low seed production and vegetative propagation via lateral spreading of the root crown.

However, Ephedra's life-history strategy is more similar to a stress-tolerant competitor than a stress tolerator because of its ability to colonize relatively quickly, its ability to propagate vegetatively, and its shoot morphology.

Haplopappus sp. also appears to have an ambiguous strategy within the townsites, possibly depending upon its viability within the undisturbed assemblage. At Furnace, the cover of Haplopappus was less in the townsite than in the control, whereas in Greenwater townsite Haplopappus usually contributed greater cover in disturbed sites. Haplopappus contributed about three to five times the cover in the controls at Greenwater than in Furnace control, and this observation suggests that the Furnace site is not favorable for its growth. The relative importance of Haplopappus sp. in the undisturbed vegetation at Greenwater indicates a strategy similar to stress-tolerant competitors. Therefore, Haplopappus sp. are in a position somewhere between the stress-tolerant ruderal and the stress-tolerant competitor strategies.

PALEOECOLOGICAL STUDIES IN THE BLACK MOUNTAINS

Plant succession in Death Valley cannot be considered independent of climatic influences. Five of the six townsites studied (including Wahmonie; Webb and Wilshire, 1979) were close to the upper elevation limit of Larrea. According to the primary succession sequence from Gold Valley, Larrea individuals should be in disturbed sites but instead are conspicuously absent. Either a cooling trend during the last several hundred years (LaMarche, 1973) or wetter conditions could explain the low density and cover of Larrea seedlings in disturbed sites, because germination of Larrea is limited by temperature and precipitation (Beatley, 1974).

To test the degree of climatic influence, a series of modern and fossil packrat middens were collected south of Greenwater townsite (fig. 1). This midden series records the extent of change in vegetation assemblages in the Black Mountains during the last 2,000 yr. These changes can be used to infer climatic fluctuations that could have influenced the vegetation assemblages at other sites in the Death Valley area (also see Cole and Webb, 1985).

Methods

A hill near Greenwater townsite (fig. 31) was chosen for the midden study. This hill, composed of rhyolitic volcanic rocks, supports a Larrea assemblage below 1,350 m elevation, and a Coleogyne assemblage starting at a slightly higher elevation. Larrea-dominated assemblages are characteristic of low-elevation Mojave Desert, while Coleogyne-dominated assemblages are characteristic of the higher elevation transition between the Mojave and Great Basin Deserts (Beatley, 1976). The two dominant species are mutually exclusive on this hill, and the upper elevation limit of Larrea and lower elevation limit of Coleogyne are referred to here as the Larrea-Coleogyne limit.

We hypothesized that a change in the Larrea-Coleogyne limit at a given time would reflect the prevalent climatic conditions. Larrea's upper elevation limit appears to be controlled by precipitation because the elevation and latitude limits of Larrea in Nevada coincide with a maximum mean precipitation of 183 mm, and because the viability of Larrea seeds decreases considerably when the mean annual precipitation exceeds 150 mm (Beatley, 1974). Coleogyne assemblages are best developed where the mean annual precipitation exceeds 200 mm (Beatley, 1975). The temperature requirements of the two species overlap (Beatley, 1975); hence, a shift in the Larrea-Coleogyne limit should indicate a change in mean annual rainfall but not necessarily in mean annual temperature or in temperature extremes.

To test this hypothesis, eight fossil and five modern middens were collected between 1,340 and 1,410 m elevation (see bottom of table 38). Exposures ranged from northeast to southeast, and xeric conditions increased in more southerly exposures and at lower elevations. All middens were collected from sites with a similar rhyolitic substrate, a procedure that thus eliminated substrate as a source of variability. Two modern middens—G8 and G15 (table 38)—were collected to represent the most xeric, Larrea-dominated sites on the hillslope; a third modern midden (G7) was collected to represent the most mesic, Coleogyne-dominated sites. One modern and six fossil middens were collected within a 20-m radius at the Larrea-Coleogyne limit, and one modern and two fossil middens were collected at a site 60 m above the limit (table 38).

The contents of the fossil middens were quantified to obtain a statistical analysis of changes with age. Cole and Webb (1985) provide details of the methods used. The concentration of each taxon was quantified as the logarithm of the number of identifiable fossils per kilogram of washed midden matrix. The concentrations were analyzed using principal-components and factor analysis (Gauch, 1982). The input matrix was similar to table 38, except that annuals and species found in less than three middens were excluded. Both methods calculated a matrix of correlation coefficients obtained from comparison of each midden with all other middens. Factor analysis (oblique rotation) differs from principal-components analysis in the selection of reference axes; principal-components analysis selects axes to account for the maximum amount of variance among the middens, whereas factor analysis uses the dissimilar (least correlated) middens to select axes.

Results

The eight fossil and five modern middens collected from the hill south of Greenwater illustrate species composition changes over the last 2,200 yr (fig. 32). Larrea has decreased in fossil concentration during the last 270 yr, but this decrease may not be statistically significant. Coleogyne, however, has become established only within the last few hundred years. It is represented in all five modern middens and fossil midden G6b (270 yr B.P.) and is absent from the seven older middens (table 38). Coleogyne fossils are the most abundant in middens G7 and G11a (table 38), both collected adjacent to Coleogyne individuals at 1,360 and 1,410 m elevation, respectively (table 38). The other three modern middens, more distant from Coleogyne individuals, record seed dispersal 25 to 50 m from the individuals. The absence of older Coleogyne macrofossils, especially from middens G11b and G11c (table 38) indicates that the Larrea-Coleogyne limit was above 1,410 m on this hillside until the last several hundred years. Tetradymia spinosa was not found in any fossil middens but was relatively abundant in three of five modern middens (table 38). Eriogonum fasciculatum and Grayia also increased in concentration during the last 750 yr (fig. 32), but the trends are not as distinct nor are the species as well represented as Coleogyne is in the modern middens.

Principal-components and factor analysis were used to examine trends within the variability of the macrofossil concentrations (fig. 33). The total variance explained with the first two principal-components axes (fig. 33A) was 66 percent, with the total variance explained for individual middens ranging from 44 to 90 percent. Two modern middens representing the most xeric sites on the hillslope, G8 and G15, are clustered with the oldest middens at the bottom of the ordination (fig. 33A) while the other modern middens appear at the top. The arrows on figure 33 illustrate temporal trends from older middens (clustered with modern middens G8 and G15) to modern middens collected at the same site. The factor-analysis (oblique rotation) ordination (fig. 33B), with the most dissimilar middens used as X-axis endpoints, shows clearer temporal trends. Middens G8 and G15 are clustered with the older middens, and a series of nearly straight lines connect these middens with the other modern ones at the lower left (fig. 33B).

The principal-components scores (table 38) indicate the species responsible for the clustering patterns. Larrea and Haplopappus are the most important determinants of the X-axis position because of their high positive values. These species also have the highest fossil concentration for all middens (table 38). However, those species showing high positive values for the Y-axis, such as Eriogonum fasciculatum and Ephedra sp., are near their lower elevation limit on this hillside, while those species with high negative values, particularly Larrea and Ambrosia, are at their upper elevation limit. On the basis of the principal-components scores, the Y-axis appears to reflect site differences resulting from elevation or time, whereas the X-axis reflects the most abundant species, sample variability, and some elevation or time aspects.

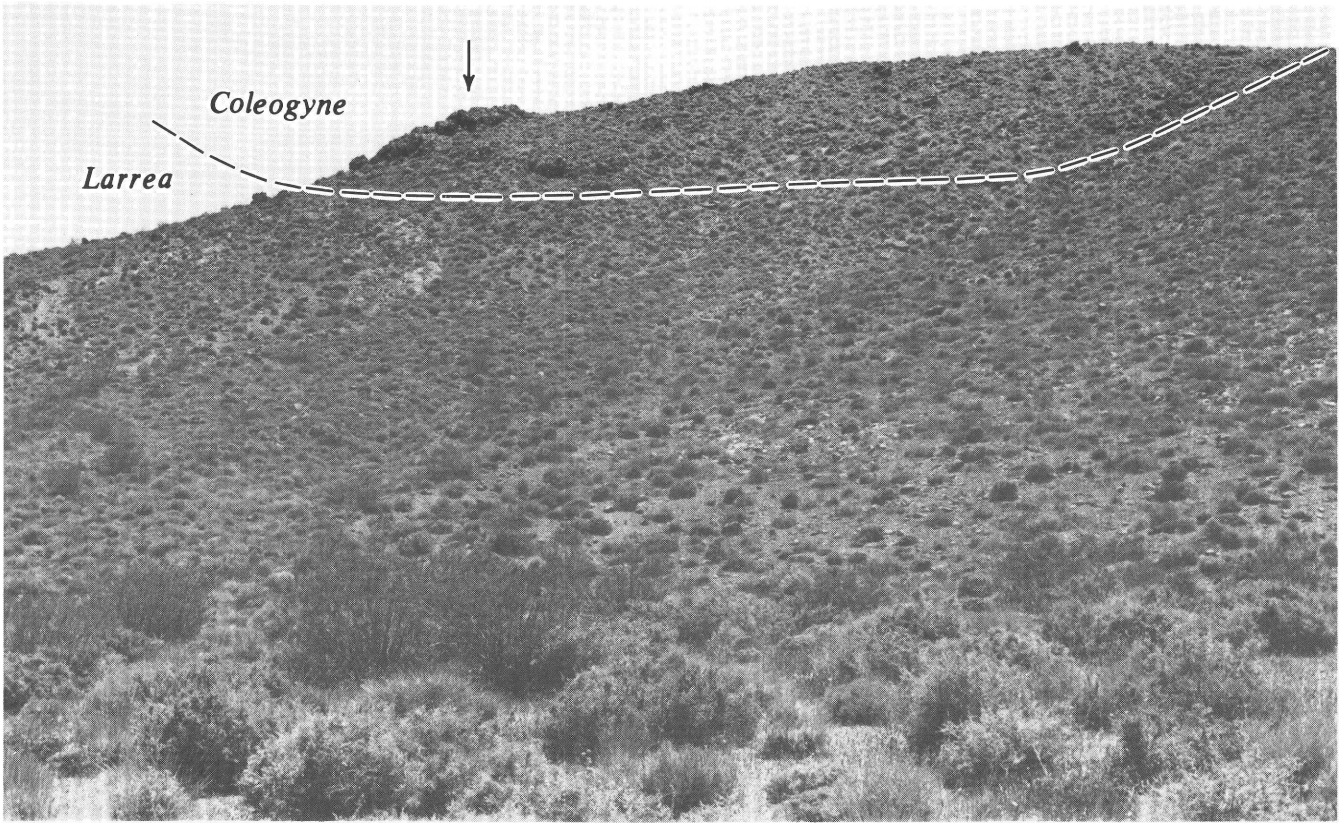

Figure 31. Fossil packrat-midden collection site near Greenwater townsite. Dashed line indicates approximate upper elevation limit of Larrea and lower elevation limit of Coleogyne. Arrow indicates rock outcrop where most of the middens were collected. View is toward the west.

The ordinations suggest that the Larrea-Coleogyne limit has shifted downward in elevation with time. Older middens are less similar to modern middens collected at the same site than to modern middens found at more xeric sites. Coleogyne appears only in middens younger than 270 yr B.P. Because Coleogyne is absent from all fossil middens except G6b and now occurs as low as 1,360 m, its lower elevation limit has decreased a minimum of 50 m within the last several hundred years.

Discussion

Packrat middens collected near Greenwater townsite indicate that climatic fluctuations during the late Holocene have affected species near their elevation limits. Wetter and possibly cooler conditions starting approximately 500 yr ago are probably responsible for the decrease in the lower elevation limit of Coleogyne. This corresponds to the "Little Ice Age" (Flint, 1971, p. 524) and a lowering of the upper treeline in the White Mountains of California (LaMarche, 1973; fig. 32).

The packrat-midden data suggest that germination of Larrea may be restricted in the townsites because of climatic factors. Beatley (1974, p. 259) states that high rainfall is detrimental to the reproduction of Larrea, and that minimum air temperatures were responsible for exclusion of Larrea from closed basins. However, Beatley (1974, p. 245) concludes that upper elevation limits of Larrea are controlled by mean annual precipitation. Larrea may have become established at its current elevation limits prior to the wetter period of the last 500 yr and is now either not reproducing or reproducing at a greatly reduced rate. The destruction of relic stands of Larrea could explain the absence of Larrea from townsites near its upper elevation limits.

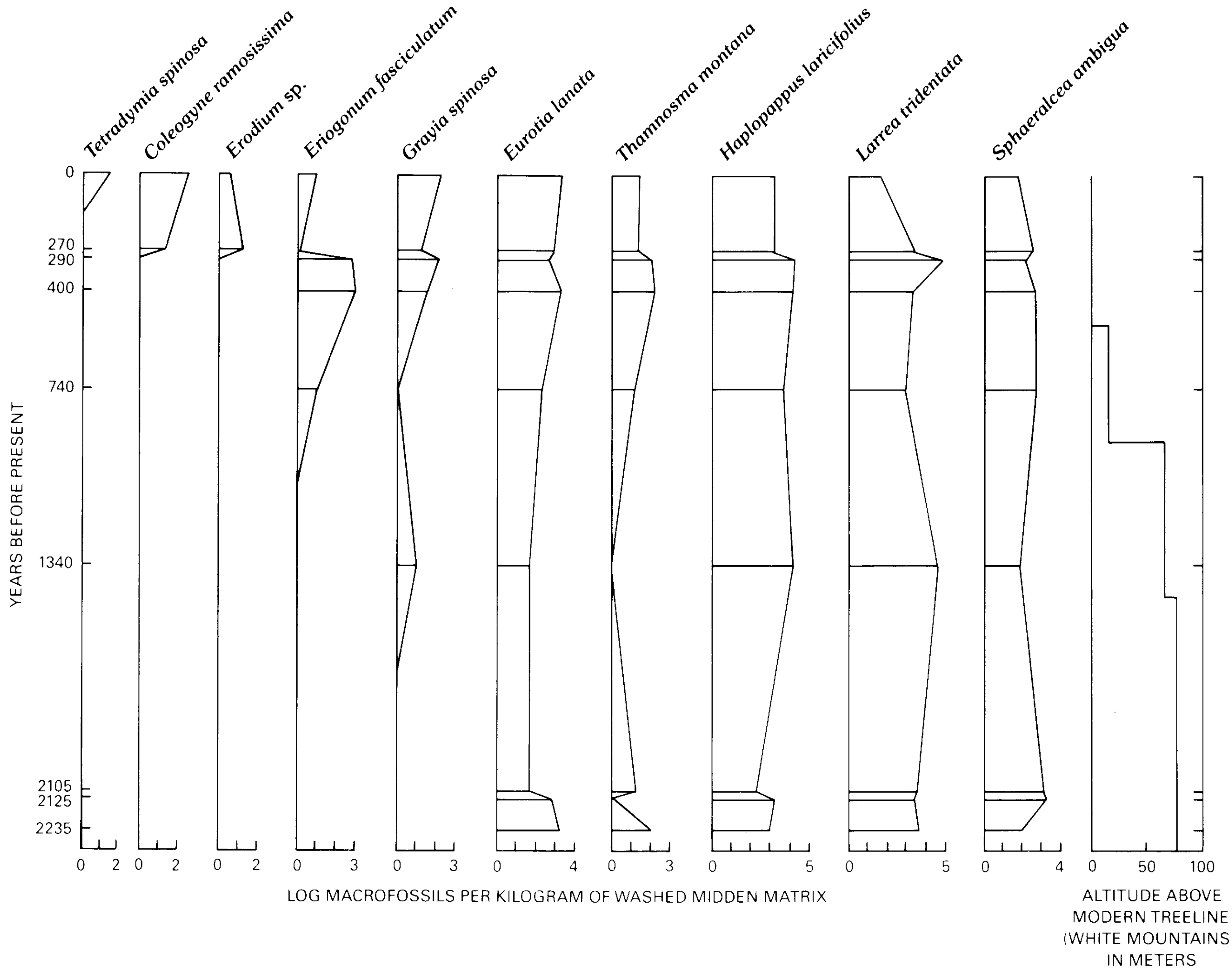

Figure 32. Change in concentration of plant macrofossils with time in middens collected from the vicinity of Greenwater townsite. Treeline data are adapted from LaMarche (1973).

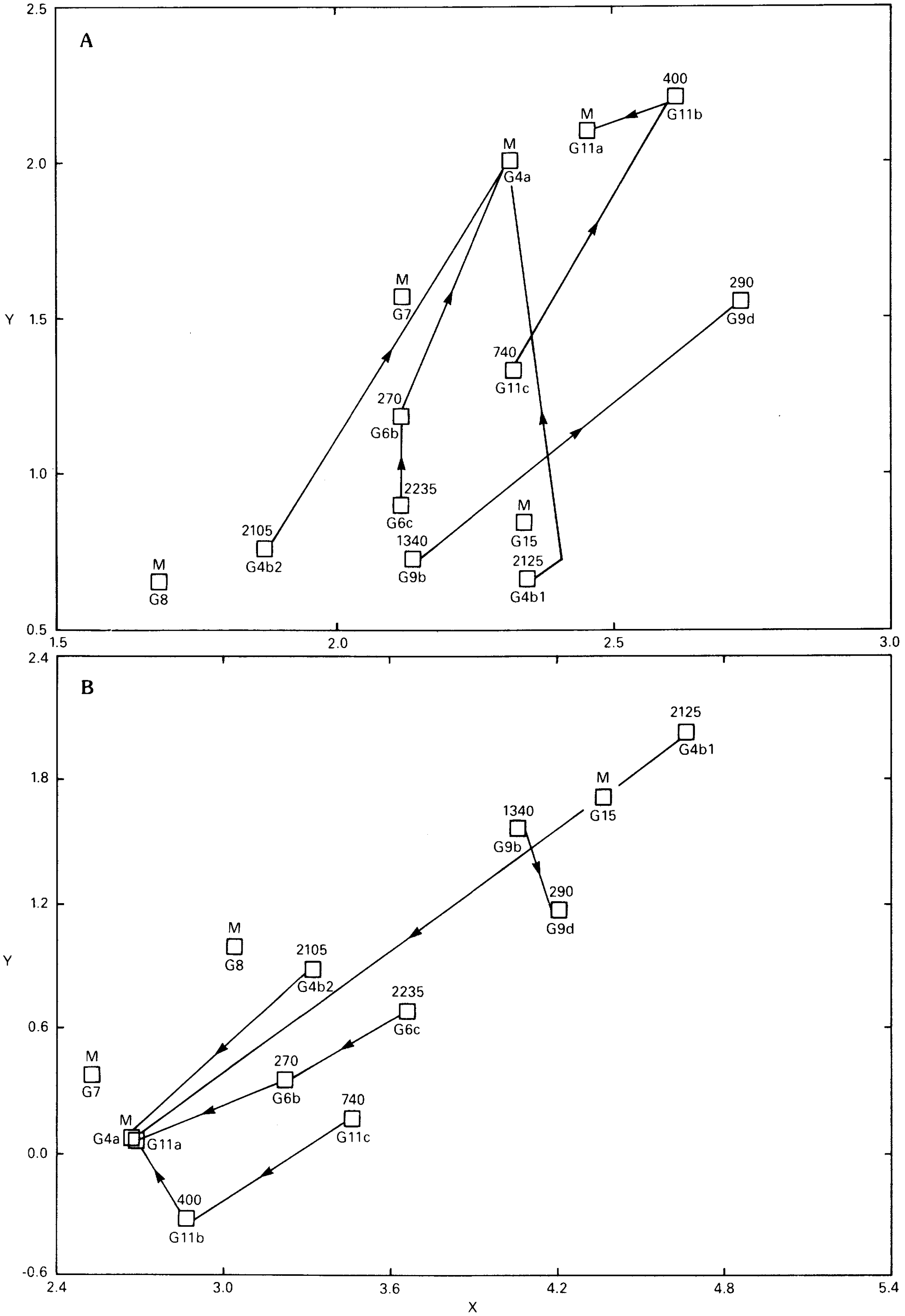

Figure 33. Principal-components analysis and factor analysis of the contents of fossil packrat middens from the vicinity of Greenwater townsite. Number above each data point is the midden age in years before present. M indicates a modern (less than 200 yr B.P.) midden. Code below or to the side of each data point identifies the midden (see table 38). A, Principal-components ordination. B, Factor-analysis (oblique rotation) ordination.

Erodium sp. (probably E. cicutarium) and Bromus fossils were only found in modern middens G4a, G7, and G15, and in the 270 yr B.P. midden G6b (table 38). The absence of Erodium and Bromus fossils in middens older than 270 yr B.P. indicates that these two species have only occurred on this hillside in the last several hundred years. These species are now common throughout the Black Mountains (Schramm, 1982), which indicates that climate is not a factor in their presence/absence in middens. This observation suggests that Erodium and Bromus can be considered exotic to the Greenwater townsite, and it provides additional information on the status of these "introduced" species (Beatley, 1966; Wester, 1981).

A MODEL OF SUCCESSION IN DEATH VALLEY

Definition of Succession

Studies of plant assemblages in Death Valley National Monument indicate sequential, directional changes in species composition take place after disturbance, and thus that plant succession occurs. Succession is a controversial model of change in species composition of plant assemblages, and the term requires a rigorous definition (Egler, 1954; Drury and Nisbet 1973; Horn, 1974; White, 1979), especially when applied to desert plant assemblages (Muller, 1940; Shreve, 1942; Pianka, 1974; Beatley, 1976; Rowlands, 1980). The arguments against the occurrence of succession in deserts are based either on confusion over differing definitions of what succession is or on what the driving forces behind vegetation change are. Most plant ecologists agree that "informally" (Pickett, 1976, p. 107) or in the "widest sense" (Drury and Nisbet, 1973, p. 331) succession implies change in the composition of a vegetation assemblage after a natural or human-induced disturbance. This definition is well established and does not require specification of autogenic or allogenic forces (Drury and Nisbet, 1973, p. 357; Connell, 1980).

We use the term "succession" to depict sequential, directional changes in the species composition of a vegetation assemblage with time. "Primary succession" refers to species composition changes with time occurring on newly created surfaces, where the effect of residuals (MacMahon, 1980) is negligible. "Secondary succession" refers to species composition changes with time occurring on denuded surfaces, where the effect of residuals (including soils) is not negligible. Secondary succession is distinguished from simple revegetation by the requirement that a species composition change must occur. "Simple revegetation" occurs when the colonizers have exactly the same species composition as the predisturbance vegetation.

Primary Succession in Death Valley

The spatial distributions of vegetation on alluvial surfaces in Wood Canyon and Gold Valley are inferred to represent primary succession sequences. The geomorphic processes responsible for the debris flows and the alluvial terraces destroyed preexisting plants and removed residual seeds and organic materials. In order to establish the primary succession sequence, spatially distributed plant assemblages were converted into a hypothetical assemblage that has undergone species composition change with time. Geomorphic processes will continue to episodically destroy patches of vegetation and provide new surfaces for succession to begin again.

Soil chronosequences were used to establish a temporal framework for spatially distributed plant assemblages. Soils forming in arid climates have morphological characteristics that can be used as a basis for relative age dating. The characteristics used as the basis for our chronosequences were desert pavement and varnish, degree of development of B horizons, and degree of development of carbonate horizons. Use of these characteristics allows a distinction of the relative ages for deposits (Bull, 1975; Gile and others, 1981; Hunt and Mabey, 1966), although absolute ages can only be determined from radiometric dating or estimated from correlation with areas that have been radiometrically dated.

Soil chronosequences represent a relative time scale by which the development of vegetation assemblages seen on different surfaces can be linked to discrete times. The processes creating the surfaces, particularly debris flows, are discrete events that leave a deposit that is stable until the next geomorphic event. Consequently, the amount of time since the deposit was formed represents the time over which the assemblage occupying it has developed. Hence, spatial patterns viewed on alluvial fans can be translated into temporal sequences if a chronosequence can be established.

Four primary succession sequences were developed in plant assemblages that are representative of the vegetation found between 1,000 and 2,000 m elevation in Death Valley National Monument (table 39). We use the term "assemblage" to reflect the dominant perennial species, with dominance based on the contribution of the species to ground cover. In Wood Canyon, young debris flows originating in granite were colonized by species such as Lupinus, Atriplex, and Penstemon sp. that were not found on older flows. The assemblages found on flows with increasing age were dominated by Ephedra, Lycium, and Grayia; Coleogyne and Ephedra; and Coleogyne, respectively. Another sequence of debris flows originating from the Kingston Peak(?) Formation showed a succession from an assemblage dominated by Acamptopappus, Grayia, and Lycium to an assemblage dominated by Coleogyne, Lycium, and Ephedra; a wash near these debris flows was lined with Hymenoclea, Chrysothamnus viscidiflorus, and Gutierrezia microcephala.

In Gold Valley, Hymenoclea dominates the assemblages found in drainages that are infrequently scoured by floods (table 39). The assemblages found on terraces of increasing age in the lower part of Gold Valley were dominated by Larrea and Ephedra; Ambrosia, Lycium, and Larrea; and Ambrosia and Larrea. The assemblages found on terraces of increasing age near Gold Valley townsite were dominated by Grayia, Coleogyne, and Lycium; Ephedra, Coleogyne, and Lycium; and Coleogyne and Larrea. The Wood Canyon and Gold Valley plant assemblages are compared in table 39 on the basis of carbonate morphology of soils, the best indicator of relative age, and an estimated geologic age.

Primary succession in Death Valley follows a pattern best described using life-history strategies. Species with a high emphasis on reproduction and growth and a low emphasis on longevity (for example, Hymenoclea, Chrysothamnus) are the dominants in the colonizing stage. These species are replaced by an intermediate group with a wide range in characteristics, but generally have a lower reproductive ability, slower growth, and longer lifespans than the colonizers. With increasing time, species that have lowest reproductive ability, slowest growth, and longest lifespans (for example, Larrea, Coleogyne) dominate.

Recovery of Soil Properties and Revegetation of Abandoned Townsites

Five abandoned townsites and the Skidoo pipeline corridor were measured to determine the recovery of soil properties and vegetation assemblages from human disturbances. Soil compaction was measured to test the hypothesis that compaction would retard the revegetation of townsites. Compaction was present in all but one site; the exception (Greenwater townsite B) probably was not occupied to the same extent as the other sites.

Recovery times were estimated using a linear model of the change in soil physical properties with time. This model was used instead of a more realistic exponential-decay model (Webb and Wilshire, 1979) because the properties at only three points in time—represented by active roads, abandoned sites, and undisturbed sites—could be compared. This model would be expected to predict minimum recovery times, because the rate of change of soil properties decreases as the soil approaches total recovery. The predicted recovery times range from 80 to 120 yr (table 40), and given the uncertainties involved in these predictions, soil compaction in the townsites requires on the order of a century (±50 yr) for total amelioration. Compaction does not appear to be a factor affecting revegetation, because few differences between the vegetation in compacted and that in noncompacted sites could not be attributed to natural variability.

Vegetation assemblages in the townsites were distinctly different from those in the control sites (table 41). Hymenoclea, Stipa, or Ephedra were the dominants in the four townsites in which Larrea was present; Larrea, Lycium, Coleogyne, Menodora, or Grayia dominated the corresponding control sites. At Skidoo, Grayia was the dominant in both control and disturbed sites; consequently, it appears that Skidoo has recovered to a greater extent than the areas dominated by Larrea. However, Grayia contributed less cover in disturbed sites than in control sites at Skidoo, and Chrysothamnus appeared to be an important colonizer there.

Unlike the townsites, the assemblages found in the Skidoo pipeline corridor were not always distinctly different from the adjacent control assemblages (table 42). The greatest differences between pipeline corridor segments and adjacent controls were in the absolute cover contribution of the dominants and in the abundance of species like Chrysothamnus in the pipeline corridor. For example, the Harrisburg Flats pipeline corridor and control were both dominated by Chrysothamnus and Grayia (table 42), but the pipeline corridor had 4.5 percent more cover of Chrysothamnus and 4.0 percent less cover of Grayia than did the control (table 15). In addition, Atriplex canescens contributed 1.4 percent cover in the pipeline corridor, but only 0.3 percent cover in the control. Similar differences were observed in other segments of the pipeline corridor, and the differences were large enough that the pipeline corridor was still conspicuous from a distance in 1981 (figs. 8, 13, 14). Differences appeared to depend somewhat on the length of time since the corridor was dismantled; for example, the segment at Nemo Crest (dismantled in 1938) has not recovered to the extent of the segments in Wood Canyon (dismantled in 1917) despite the close proximity and similarity of undisturbed vegetation. Moreover, the difference between the recoveries of the Wildrose Canyon segments C and D is marked (table 20); segment C was dismantled in 1938, whereas segment D has been left intact since 1906.

Ordinations

Four ordinations using Wisconsin polar ordination and principal-components analysis were generated for townsites in Larrea-dominated assemblages (figs. 34, 35). The two ordination methods were used because Wisconsin polar ordination is more subjective but creates less distortion in ordination graphs than does principal-components analysis. Data from Webb and Wilshire (1979) for the Wahmonie townsite were combined with the data from Greenwater, Kunze, Furnace, and Gold Valley townsites. In general, both methods produced a clear separation among control and disturbed sites. In the ordinations based on cover (fig. 34), the eastern townsite at Gold Valley, the least disturbed of all sites studied, was the only disturbed site not clearly separated from the cluster of control sites. However, the correlation coefficient and PS value between the eastern townsite and the nearest similar control site were only 0.29 and 37.8 percent, respectively, on the basis of cover (table 43). Correlation coefficients and PS values greater than 0.60 and 70 percent, respectively, indicate similar vegetation assemblages (see section on "Reproducibility and Spatial Variability"). The percentages of total variance explained in the principal-components analyses were 59 and 65 percent for the cover (fig. 34A) and density (fig. 35A) ordinations, respectively. The variance explained for each site appears in table 44.

Ordinations using Wisconsin polar ordination and principal-components analysis with cover data were also generated for sites in the Panamint Range (fig. 36). The separation

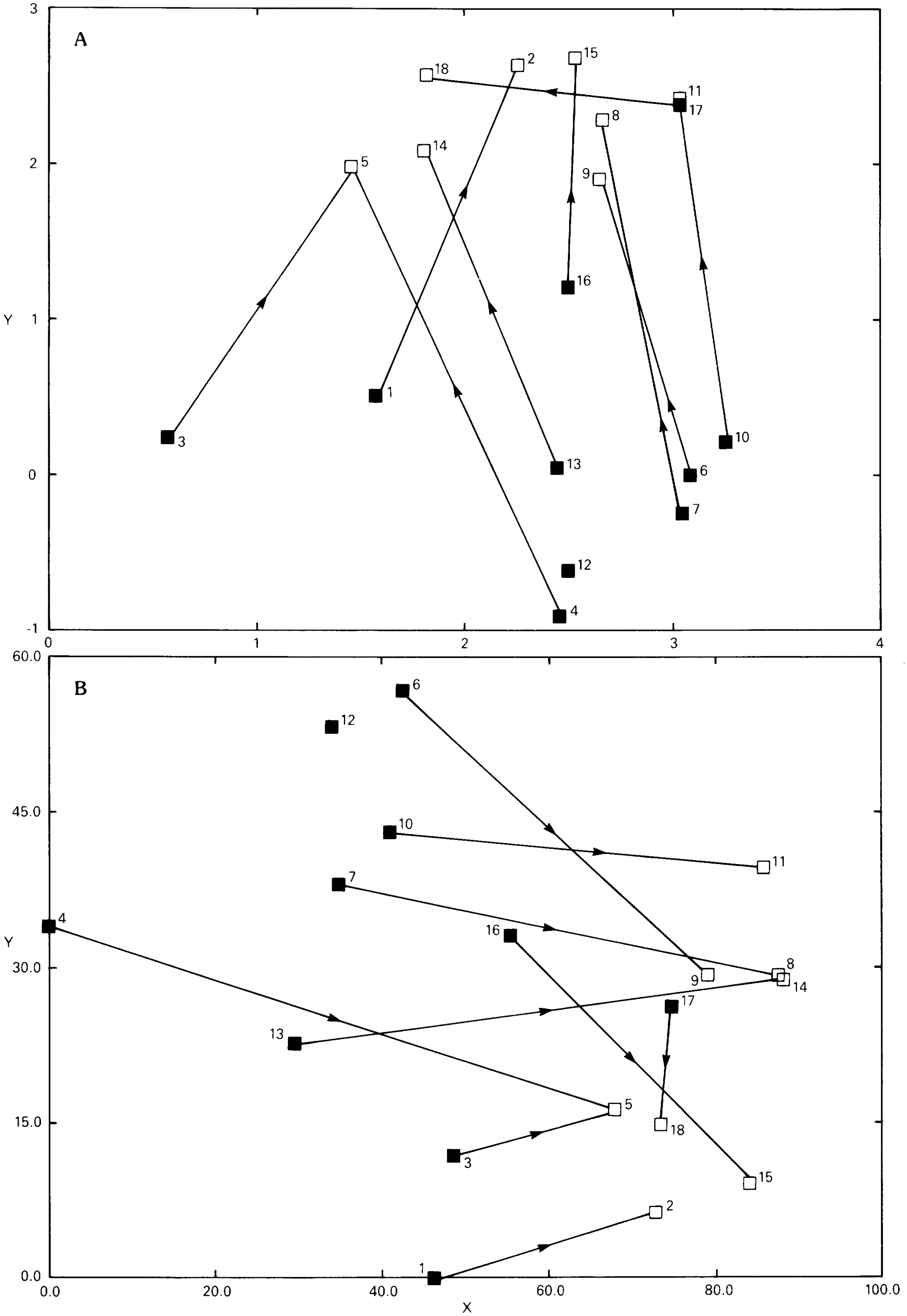

Figure 34. Ordination graphs based on plant cover at townsites in Larrea-dominated assemblages. Dark squares represent disturbance sites; light squares represent corresponding control sites. Site numbers are listed in table 43. A, Principal-components solution. B, Wisconsin polar ordination solution.

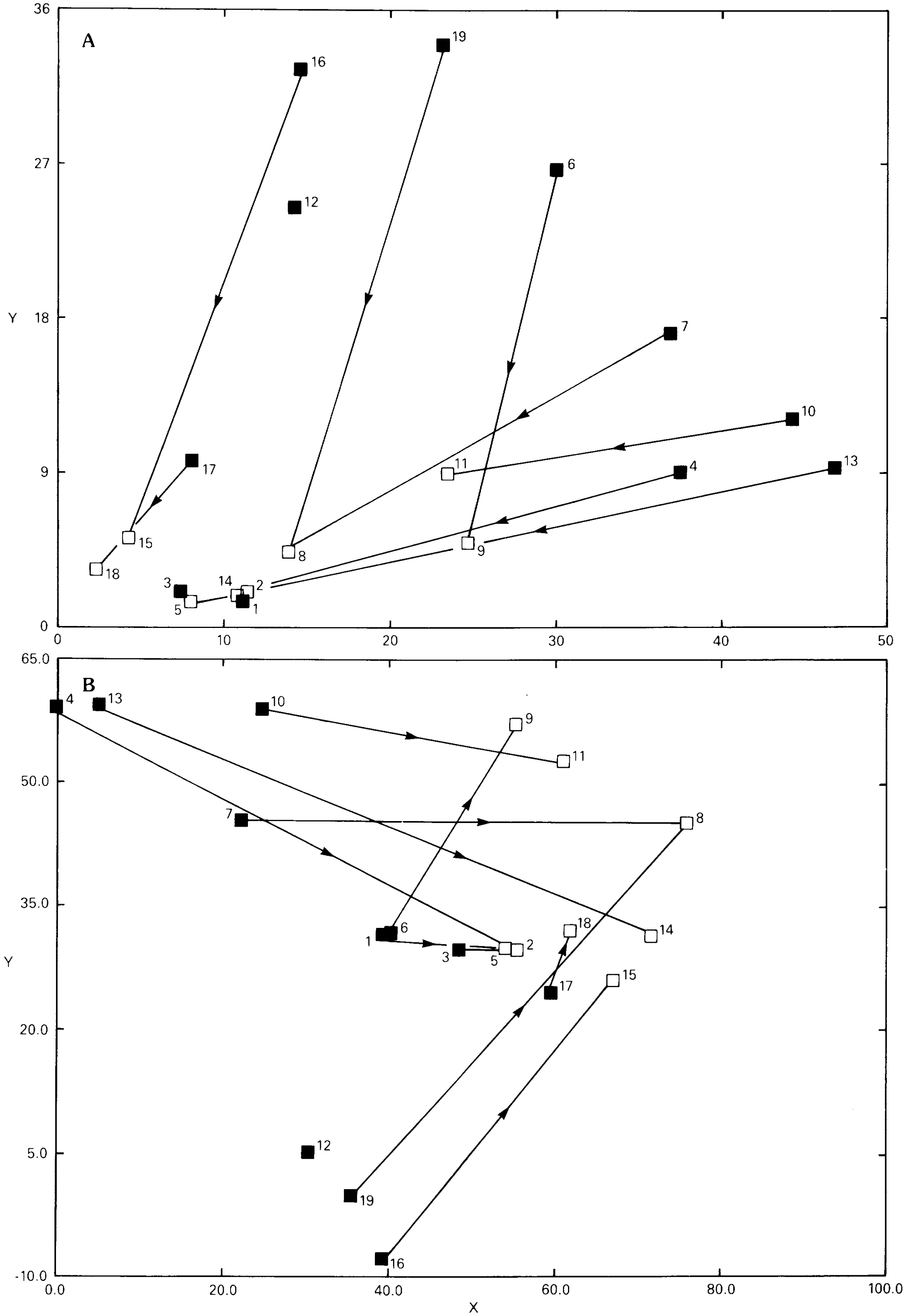

Figure 35. Ordination graphs based on plant densities at townsites in Larrea-dominated assemblages. Dark squares represent disturbed sites; light squares represent corresponding control sites. Site numbers are listed in table 43. A, Principal-components solution. B, Wisconsin polar ordination solution.

between control and disturbed sites is not clear in these graphs as a result of large environmental gradients; assemblages range from Grayia-dominated to Artemisia tridentata-dominated (with Pinus and Juniperus). The principal-components solution first axis (X) apparently reflects variability resulting from disturbance, whereas the second axis (Y) apparently reflects variability resulting from environmental gradients. The assemblages represented change in composition from Grayia-Ephedra-dominated to Coleogyne-dominated to Artemisia-Coleogyne-dominated from bottom to top in the principal-components ordination (fig. 36). The correlation coefficients (table 45) indicate that the assemblages at Skidoo, Harrisburg Flats, and Wood Canyon are unrelated to those in Wildrose Canyon; this is reflected in the clustering patterns shown in figure 36A. Only 48 percent of the total variance is explained by the first two axes, and the variance explained for individual sites (table 46) suggests that addition of a third axis would improve the distinctions.

Comparisons and Contrasts Between Primary and Secondary Succession

The primary succession sequences provide a framework for predicting future changes in vegetation assemblages in the townsites. The stage of primary succession at a given site appears to be related to the degree of soil development, which is a function of time. Primary succession in assemblages other than those studied can be assumed to be qualitatively similar to the primary succession sequences in Wood Canyon and Gold Valley, given comparable environmental settings.

Revegetation of abandoned townsites, when viewed in the context of primary succession sequences, appears to represent the first stage of secondary succession. The species colonizing townsites—especially Hymenoclea and Chrysothamnus viscidiflorus—are also the colonizers in primary succession sequences. Moreover, the occurrence of species in townsites (table 41) are in general agreement with the sequences of primary succession (table 42). Therefore, secondary succession appears to be a viable model for the process of revegetation and can be used to describe the rate of recovery.

Application of primary and secondary succession models helps to explain variability in the patterns observed in Skidoo and along the Skidoo pipeline corridor. Skidoo townsite and many segments of the Skidoo pipeline corridor have comparable environmental settings with the debris flows in Wood Canyon. At Skidoo, the granitic alluvial substrate with a weak stage I carbonate horizon (table 10) supports an undisturbed assemblage dominated by Grayia, Ephedra, and Artemisia. At Wood Canyon, debris flows 2 and B, with a comparable parent material and soil morphology (compare tables 6 and 10), support assemblages generally dominated by a combination of Acamptopappus, Lycium, Grayia, and Ephedra. Coleogyne, abundant on hillslopes around Skidoo, is not present in either the disturbed or control sites at Skidoo. This finding suggests that the undisturbed vegetation at Skidoo is in an early primary succession stage, and it also could explain the fast recovery of Skidoo when compared with other townsites.

The assemblages found at Harrisburg Flats can be similarly compared. The substrate at Harrisburg Flats lies on a low slope and occasionally is flooded, which indicates both a young geologic age and an adaptation of the vegetation assemblages to periodic disturbances. Coleogyne is present on hillslopes surrounding the Flats. The undisturbed vegetation assemblage is dominated by Grayia and is also comparable with debris flows 2 and B in the primary succession sequence observed in Wood Canyon. Similar arguments can be developed to compare the undisturbed assemblages at Nemo Crest and Wildrose Canyon (segment A) with debris flows 3, A, and C.

A general trend was observed in the comparison of primary and secondary succession sequences in the Panamint Range. Recovery of vegetation on disturbed sites depends on the age of the geomorphic surface and thus on the stage of primary succession of the undisturbed vegetation. For example, all the sites at Skidoo and at Harrisburg Flats plot in close proximity on the ordination graphs (fig. 36), and the correlation coefficients between disturbed and control sites at Skidoo and Harrisburg Flats average 0.85. In contrast, recovery appears to require much longer timespans on older surfaces because differences in vegetation assemblages are greater between disturbed and undisturbed sites where soils are better developed. The correlation coefficients between disturbed and control sites are 0.41 for Wood Canyon flow A, 0.68 for Wood Canyon flow B, 0.85 for Wood Canyon flow C, and average 0.34 for the two disturbed-control comparisons at Nemo Crest. Wood Canyon flow C would be expected to have a similar correlation coefficient to flow A, based on the similar ages of these flows; this anomaly could, in part, result from the lesser disturbance of vegetation resulting from emplacement of an aboveground pipeline.

Similar comparisons could not be performed using the ordinations for townsites with Larrea. Disturbed sites were generally devoid of Larrea, and more than a few scattered individuals would be expected in disturbed sites given the appearance of Larrea in the early primary succession stages in Gold Valley. Townsites with Larrea in the surrounding vegetation were built near the upper elevation limit for this species, and germination and survival of Larrea would be expected to be affected by climatic fluctuations. Hence, the climatic shift responsible for the changes recorded in packrat middens could be responsible for the low amount of germination of Larrea in townsites. Consequently, correlation coefficients between disturbed and control sites in these townsites would be expected to be consistently higher if the townsites studied were well below the upper elevation limit of Larrea.

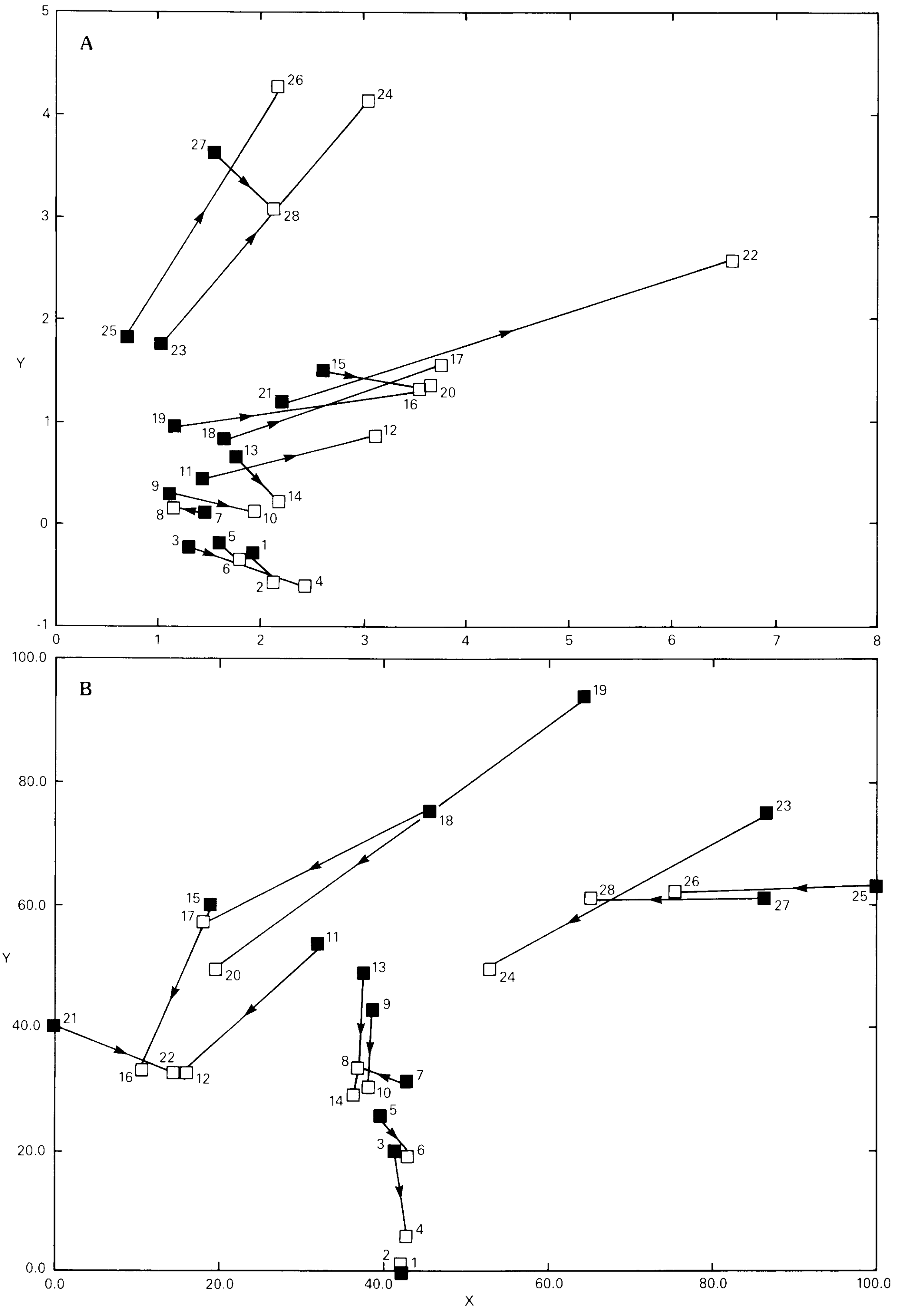

Figure 36. Ordination graphs based on plant cover at sites in the Panamint Range. Dark squares represent disturbed sites; light squares represent corresponding control sites. Site numbers are listed in table 45. A, Principal-components solution. B, Wisconsin polar ordination solution.

Life-History Strategies and Succession

The pattern present in the successional sequences can be interpreted using the life-history strategies of Grime (1979; see section on "Life-History Strategies"). However, this approach involves a degree of circular reasoning because independent life-history strategy data are scarce for most Mojave Desert species, and thus classification for these species relies heavily on their behavior in disturbed areas. Based on published literature, Larrea and Hymenoclea are archetypal stress tolerators and stress-tolerant ruderals, respectively. The successions in all areas begin with Hymenoclea or other species with apparently similar strategies (for example, Lupinus, Chrysothamnus sp.). Grayia, Lycium, and Ephedra eventually dominate, with Coleogyne and Larrea of importance locally. Coleogyne and (or) Larrea eventually become dominant, with Ambrosia dominating at lower (<1,300 m) elevations. Succession in Death Valley could be viewed as temporal changes in the life-history strategies of the dominants from stress-tolerant ruderals to stress-tolerant competitors to stress tolerators.

Not surprisingly, this pattern is similar to the model proposed by Grime (1979) for "unproductive habitats." Until further life-history strategy data are collected to allow for an independent classification, this apparent support for Grime's model should be considered tentative. The use of Grime's classification framework to describe succession in different assemblages is limited by the difficulty in grouping life-history strategies unique to each species and by possible ecotypic variation. For example, species such as Ambrosia and Coleogyne do not possess all the characteristics of stress tolerators (table 1) but assume dominance on the oldest surfaces; similarly, the occurrence of Ephedra and Haplopappus in successions is not consistent in all sites (table 41). However, Grime's approach is useful for regional comparisons of succession because it accounts for physiological and reproductive characteristics and allows a finer resolution to strategy type than do other frameworks.

The classification of a species according to Grime's approach requires a balance between the generalization necessary to group different ecotypes within a species and the resolution necessary to group different species into a particular strategy. This balance may be achieved by ranking the attributes that are most important in a given succession (Noble and Slayter, 1980). In plant successions in Death Valley, species with relatively high growth rates and reproductive capacity are most important in colonization, whereas species that emphasize maintenance of individuals at the expense of reproduction (leading to extreme longevity with few replacements) and greater adaptation to environmental stress are most important as the succession progresses.

The Forces Behind Succession in Death Valley

A combination of allogenic and autogenic forces cause succession in Death Valley, and their relative importance varies as the succession progresses. In any seedling establishment, there is a change in microenvironment that may or may not be beneficial to germination and survival (McCormick, 1968, p. 9). Pioneering species may actually create a more hostile environment for successive species (Drury and Nisbet, 1973; Connell and Slayter, 1977; Connell, 1980). However, the majority of changes occurring on a newly created surface must be beneficial to species in subsequent successional stages. Nutrient additions and concentration in the soil (Garcia-Moya and McKell, 1970), reduction in evaporation around shrubs (Wallace and others, 1980), and even shading and frost protection for seedlings (Turner and others, 1966) are examples of beneficial changes. Therefore autogenesis, often denied in desert plant assemblages (Shreve, 1942; Rowlands and Adams, 1980), is an important force behind succession.

Autogenic factors in Death Valley plant assemblages are most important in the colonization stage because the species composition changes through several stages in the absence of significant pedogenesis. After creation of a new substrate, stress-tolerant ruderals such as Hymenoclea and Chrysothamnus are the first species to be established. With increasing time, individuals of species such as Ephedra or Acamptopappus become established that apparently outlive the initial colonizers. Competitive interactions and, to a limited extent, site modifications are probably the most important forces in these initial stages. Stress tolerators such as Larrea and Coleogyne assume dominance through competitive superiority, which is manifested as the soil develops.

The forces behind secondary succession appear to be primarily autogenic given the slow rate of soil formation in deserts. Depending on the degree of disturbance, the first plants to colonize a barren site will be either colonizers from the surrounding vegetation, species germinating from the surviving seedbank, and (or) individuals regenerated by root-crown sprouting. Stress-tolerant ruderals, especially those that produce large numbers of seeds and have highly efficient dispersal mechanisms, will colonize a disturbed site despite the existing seedbank and control soil moisture (Wallace and others, 1980). Colonization from the existing seedbank will favor species occupying the site prior to disturbance, but such colonization requires minimal soil disruption. In sites without significant disturbance of the soil, root-crown sprouting, which occurs for many common Mojave and Great Basin Desert species, may be the dominant form of revegetation.

The importance of seedbank revegetation and root-crown sprouting depends on the composition of the predisturbance vegetation, which in turn depends on the site's primary succession stage. In the townsites, blading and compaction appeared to destroy most root-crowns, and thus some combination of seedbank revegetation and invasion revegetation resulted, depending primarily on the life-history strategies of the species and the degree of disturbance.

Autogenic forces such as competition become less important with increasing time. The stress caused by the arid climate is continuous and does not decrease as succession proceeds. Nutrient additions are offset by withdrawals and are limited by the potential productivity of litterfall at a site. Although moisture loss through evaporation on a barren surface would be expected to be high, the level of moisture may not increase once shade is provided because of transpiration by colonizers. Available moisture thus decreases as a surface becomes colonized, and competition for the moisture, severe in the initial stages, slows as species which are competitively superior and longer lived gain dominance (Wallace and others, 1980).

Allogenic processes become more important in the later stages of succession. The probability of severe disturbances, such as floods or debris flows, increases with time. Accumulating quantities of carbonate and clay in soils change the soil chemistry and water-retention capacity. With substantial time, stage IV carbonate horizons develop that limit root growth and alter soil hydrologic properties. Climate changes such as the Pleistocene-Holocene change can completely alter the species composition of a site, and the occurrence of climatic fluctuations may alter successional sequences if the important species are near environmental limits.

In addition to the successional changes occurring on a newly created substrate, other environmental factors also cause vegetation change, and these factors may account for discrepancies in our model. Geomorphic processes such as episodic erosion or deposition; evolutionary changes, as exemplified by ecotypic variation; the natural disturbance regime, such as periodic fire or grazing; climatic fluctuations; and human influence have all significantly affected the vegetation patterns present today. Each geomorphic surface formed at a discrete time, and each vegetation assemblage has its own history of change in which succession is the major part.

The process of recovery is linked with the history of the ambient vegetation assemblages. Comparison of a recovering vegetation assemblage to the predisturbance assemblage would be meaningless if some environmental factor were to cause widespread change. Also, primary succession continues as recovery progresses, which again leads to change from predisturbance conditions. Therefore, a definition of when a disturbed site is recovered must use ambient, not predisturbance, vegetation assemblages as its basis.

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TABLES 1— 47

Table 1. Application of the life-history classification framework of Grime (1979) to desert species

[Based on Grime, 1979, table 6, p. 48-49]

	Criteria for classification			
	Stress tolerators	Stress-tolerant competitors	Stress-tolerant ruderals	Ruderals
Longevity	Long-lived	Long- to short-lived	Short-lived	Annuals
Growth form	Shrubs and trees	Shrubs and trees	Shrubs to subshrubs	Herbs
Leaves:				
Production time	Favorable conditions	Mainly seasonal	Seasonal	Seasonal
Longevity	Evergreen or xerophytic deciduous	Deciduous	Deciduous	Deciduous
Morphology	Small leathery, needle-like, xerophytic	Small to relatively large, xerophytic	Varies	Varies; often mesomorphic
Palatability	Low	Low to high	Low to high	Often high
Reproduction:				
Phenology of flowering	Flowers whenever conditions are favorable	Mainly seasonal	Mainly seasonal	Seasonal
Seed production	Small	Small	Large	Large
Regeneration strategy	Expansion from root crown; persistent seedling bank	Expansion from root crown; persistent seedling bank	Persistent seed and seedling bank	Persistent seed bank
Physiology:				
Growth rate	Slow	Slow to intermediate	Fast	Fast
Proportion of production devoted to reproduction	Low	Low	Medium to high	High
	Tentative life-history classification of selected Mojave Desert species			
	Artemisia tridentata *Coleogyne ramosissima* *Juniperus osteosperma* *Larrea tridentata* *Pinus monophylla*	*Acamptopappus shockleyi* *Ambrosia dumosa* *Grayia spinosa* *Ephedra nevadensis* *Lycium andersonii* *Tetradymia* sp.	*Atriplex canescens* *Chrysothamnus nauseosus* *Chrysothamnus viscidiflorus* *Eriogonum inflatum* *Eriogonum fasciculatum* *Gutierrezia microcephala* *Haplopappus cooperi* *Hymenoclea salsola* *Oryzopsis hymenoides* *Salazaria mexicana* *Stipa speciosa* *Thamnosma montana*	*Bromus rubens* *Eriogonum* sp. *Erodium cicutarium* *Salsola iberica*

Table 2. Regression coefficients of dry-weight biomass for Mojave Desert shrubs

[Values are in kilograms per cubic meter. NTS, Nevada Test Site (R.B. Hunter, written commun., 1981). Values are ±1 standard error of the mean. CDCA, California Desert Conservation Area (P.G. Rowland, written commun., 1981). e, estimated. The number of shrubs sampled was much smaller for the CDCA coefficients. Additional information and data are contained in Wallace and Romney (1972, p. 251-252)]

Species	NTS	CDCA
Acamptopappus shockleyi	3.1 ± 0.2	2.8
Artemisia spinescens	4.1 ± 0.2	4.0
Artemisia tridentata	1.8 ± 0.1	1.8
Chrysothamnus viscidiflorus	3.2 ± 0.2	3.3e
Coleogyne ramosissima	5.2 ± 0.3	4.8
Ephedra nevadensis	1.4 ± 0.2	4.3
Grayia spinosa	2.3 ± 0.1	4.3
Haplopappus cooperi	3.2 ± 0.4	2.8
Hymenoclea salsola	3.2 ± 0.2	1.5
Larrea tridentata	1.3 ± 0.1	2.1
Lycium andersonii	2.2 ± 0.1	2.0
Menodora spinescens	8.3 ± 0.5	8.4
Oryzopsis hymenoides	1.1 ± 0.3	2.5
Stipa speciosa	1.1 ± 0.3	2.9
Thamnosma montana	1.7 ± 0.1	3.0

Table 3. Density and cover of perennial vegetation as field tested in Gold Valley, showing variability by different operators viewing transects fixed by each operator

[Density in number per hectare; cover in percent. All values are ±1 standard error of the mean]

Operator--------------	A		B		C	
Species	Density	Cover	Density	Cover	Density	Cover
Shrubs:						
Grayia spinosa	1,500 ± 100	5.6 ± 1.0	1,400 ± 100	7.0 ± 1.4	1,400 ± 100	5.8 ± 1.3
Larrea tridentata	300 ± 100	5.3 ± 1.0	300 ± 0	5.6 ± 1.1	300 ± 100	5.9 ± 1.1
Thamnosma montana	500 ± 200	2.5 ± 1.0	500 ± 200	2.7 ± 1.0	500 ± 200	2.7 ± 1.0
Ephedra nevadensis	1,200 ± 300	2.4 ± 0.7	1,000 ± 300	3.5 ± 0.9	1,000 ± 300	2.9 ± 0.7
Lycium andersonii	500 ± 0	1.8 ± 0.4	400 ± 100	2.5 ± 0.6	500 ± 100	1.9 ± 0.3
Salazaria mexicana	700 ± 200	1.5 ± 0.5	500 ± 100	1.5 ± 0.5	600 ± 200	1.2 ± 0.6
Acamptopappus shockleyi	1,300 ± 500	1.3 ± 0.5	1,200 ± 400	1.4 ± 0.7	1,200 ± 500	1.2 ± 0.6
Hymenoclea salsola	400 ± 200	0.2 ± 0.1	300 ± 100	0.2 ± 0.1	300 ± 100	0.3 ± 0.1
Ambrosia dumosa	200 ± 100	0.2 ± 0.1	100 ± 100	0.1 ± 0.1	100 ± 100	0.1 ± 0.1
Haplopappus cooperi	100 ± 0	0.1 ± 0.1	100 ± 0	0.0	200 ± 100	0.0
Tetradymia spinosa	0	0.1 ± 0.1	0	0.0	100 ± 100	0.1 ± 0.1
Subtotal	6,700 ± 700	21.0 ± 2.0	5,800 ± 600	24.5 ± 2.5	6,200 ± 700	22.1 ± 2.2
Herbaceous perennials:						
Mirabilis bigelovii	300 ± 100	0.1 ± 0.1	100 ± 100	0.1 ± 0.1	100 ± 100	0.1 ± 0.1
Dyssodia cooperi	100 ± 0	0.0	100 ± 100	0.0	100 ± 100	0.0
Eriogonum inflatum	200 ± 200	0.0	400 ± 400	0.0	500 ± 400	0.1 ± 0.1
Subtotal	600 ± 300	0.1 ± 0.1	600 ± 400	0.1 ± 0.1	700 ± 400	0.2 ± 0.1
Grass:						
Stipa speciosa	2,100 ± 600	1.8 ± 0.4	1,900 ± 500	2.1 ± 0.5	2,400 ± 500	3.3 ± 0.7
Total live	9,400 ± 1,000	22.9 ± 2.1	8,300 ± 900	26.7 ± 2.5	9,300 ± 900	25.6 ± 2.4
Dead	400 ± 200	2.9 ± 0.6	600 ± 100	1.6 ± 0.4	1,000 ± 100	3.0 ± 0.4
Total	9,800 ± 1,100	25.8 ± 2.3	8,900 ± 900	28.3 ± 2.6	10,300 ± 1,000	28.6 ± 2.4

Table 4. Density and cover of perennial vegetation as field tested in Gold Valley showing variability by different operators viewing the same transect

[Density in number per hectare; cover in percent. All values are ±1 standard error of the mean]

Operator --------------	A		B		C	
Species	Density	Cover	Density	Cover	Density	Cover
Shrubs:						
Hymenoclea salsola	6,000 ± 600	10.4 ± 1.6	5,700 ± 600	11.6 ± 1.8	5,500 ± 700	12.0 ± 1.8
Ephedra nevadensis	2,900 ± 500	5.4 ± 1.0	2,900 ± 600	6.6 ± 1.0	3,100 ± 400	7.5 ± 1.7
Grayia spinosa	800 ± 200	2.9 ± 0.7	800 ± 200	3.2 ± 0.7	800 ± 200	3.3 ± 0.8
Lycium andersonii	300 ± 100	2.4 ± 0.8	300 ± 100	2.3 ± 0.8	400 ± 100	2.5 ± 0.9
Thamnosma montana	500 ± 100	2.1 ± 0.5	500 ± 100	2.2 ± 0.5	600 ± 200	2.1 ± 0.5
Eriogonum fasciculatum	600 ± 200	1.8 ± 0.6	500 ± 200	1.7 ± 0.7	600 ± 200	2.0 ± 0.7
Tetradymia stenolepsis	100 ± 0	0.6 ± 0.4	100 ± 100	0.8 ± 0.4	100 ± 0	0.9 ± 0.5
Ambrosia dumosa	300 ± 200	0.5 ± 0.2	400 ± 300	0.5 ± 0.3	300 ± 200	0.5 ± 0.3
Dalea fremontii	100 ± 0	0.3 ± 0.2	100 ± 0	0.3 ± 0.2	100 ± 0	0.3 ± 0.2
Salazaria mexicana	100 ± 100	0.2 ± 0.2	100 ± 100	0.2 ± 0.2	100 ± 100	0.2 ± 0.2
Larrea tridentata	0	0.1 ± 0.1	0	0.1 ± 0.1	0	0.1 ± 0.1
Haplopappus cooperi	0	0.1 ± 0.1	0	0.1 ± 0.1	0	0.1 ± 0.1
Subtotal	11,700 ± 900	26.8 ± 2.6	11,400 ± 1,000	29.6 ± 2.5	11,600 ± 900	31.5 ± 3.0
Herbaceous perennials:						
Sphaeralcea ambigua	400 ± 200	0.2 ± 0.2	400 ± 200	0.2 ± 0.2	400 ± 200	0.3 ± 0.1
Eriogonum inflatum	2,900 ± 700	0.2 ± 0.1	3,400 ± 800	0.1 ± 0.1	4,100 ± 900	0.2 ± 0.1
Dyssodia cooperi	300 ± 200	0.0	300 ± 100	0.0	300 ± 100	0.0
Castilleja chromosa	100 ± 100	0.0	200 ± 100	0.0	300 ± 200	0.0
Machaeranthera tortifolia	100 ± 100	0.0	100 ± 100	0.0	100 ± 100	0.0
Mirabilis bigelovii	100 ± 100	0.1 ± 0.1	100 ± 100	0.0	100 ± 0	0.1 ± 0.1
Subtotal	3,900 ± 800	0.5 ± 0.3	4,500 ± 800	0.3 ± 0.2	5,300 ± 1,000	0.6 ± 0.2
Grass:						
Stipa speciosa	600 ± 300	0.2 ± 0.2	600 ± 400	0.1 ± 0.1	900 ± 400	0.3 ± 0.1
Total live	16,200 ± 1,200	27.5 ± 2.6	16,500 ± 1,300	29.9 ± 2.6	17,800 ± 1,400	32.4 ± 3.0
Dead	2,400 ± 300	5.1 ± 0.4	1,800 ± 200	4.3 ± 0.5	2,700 ± 200	4.4 ± 0.6
Total	18,600 ± 1,200	32.6 ± 2.6	18,300 ± 1,400	34.2 ± 2.6	20,500 ± 1,400	36.8 ± 3.0

Table 5. Comparison of vegetation data from Wahmonie townsite and control areas

[Data from Webb and Wilshire (1979) and Beatley (1979, 1980)]

Site	Percent similarity						
	1	2	3	4	5	6	7
1	--	46	33	38	34	32	33
2	34	--	23	14	70	80	80
3	49	7	--	19	28	14	13
4	70	2	28	--	14	4	5
5	29	84	4	2	--	54	57
6	15	94	7	-25	62	--	90
7	-12	97	5	-26	84	96	--

1. Streets and avenues (Webb and Wilshire, 1979, p. 297).
2. Southwest control (Webb and Wilshire, 1979, p. 297).
3. Old Main Road (Webb and Wilshire, 1979, p. 299).
4. Townsite (Webb and Wilshire, 1979, p. 299).
5. Northeastern Control (Webb and Wilshire, 1979, p. 299).
6. Site 66 (Southwest Control), 1963 (Beatley, 1979; 1980, p. 157-158).
7. Site 66 (Southwest Control), 1975 (Beatley, 1979; 1980, p. 157-158).

Table 6. Soil and site descriptions for debris flows in Wood Canyon

[Abbreviations used: Texture: k, cobbly; g, gravelly; ls, loamy sand; sl, sandy loam; s, sand; scl, sandy clay loam. Color: Munsell notation (hue value/chroma). Carbonate: Stages follow nomenclature of Gile and others (1981, p. 67). See Soil Survey Staff (1975) for further details]

Debris flow 1

Age: 5 yr
Source material: cobbles and grus of granite
Exposure and elevation: 8-10° WNW., 1,750 m
Number of descriptions: 2

Depth (cm)	Horizon	Texture	Dry color	Carbonate
0-7	A	kgls	10 YR 6/3	---
7-50+	C	kgls	10 YR 6/3	---

Debris flow 2

Estimated Age: late Holocene
Source Material: cobbles and grus of granite with minor metasedimentary rocks
Exposure and elevation: 8-10° WSW., 1,750 m
Number of descriptions: 2

Depth (cm)	Horizon	Texture	Dry color	Carbonate
0-6	A	kgsl	10 YR 5/3	---
6-12	C_1	kgls	10 YR 5/3	---
12-25	C_2	kg(s-ls)	10 YR 5/3	---
25-50	IIC_{3ca}	kgs	10 YR 6/3	stage I
50-65+	IIC_{4ca}	kgs	10 YR 6/3	stage I

Debris flow 3

Estimated Age: middle Holocene
Source Material: cobbles and grus of granite
Exposure and elevation: 8-10° WSW., 1,750 m

Depth (cm)	Horizon	Texture	Dry color	Carbonate
0-5	A	kgsl	10 YR 5/3	---
5-15	C_1	kgsl	10 YR 5/3	---
15-65+	C_{2ca}	kgsl	10 YR 6/3	stage I

Debris flow 4

Estimated Age: late Pleistocene
Source Material: cobbles and grus of granite
Exposure and elevation: 10° SW., 1,830-1,860 m
Continuous exposure

Depth (cm)	Horizon	Texture	Dry color	Carbonate
0-5	A	kgsl	10 YR 6/4	stage I
5-12	B_1	kgsl	10 YR 5/6	stage I
12-90	IIB_{2tca}	kgls*	7.5 YR 5/6	stage I
90-175	IIC_{ca}	---	---	stage III

*clay skins on pebbles

Exposed profile in wash in Wood Canyon

Source Materials: granitic and metasedimentary rocks
Exposure and elevation: 2° W., 1,720 m
Continuous exposure

Depth (cm)	Horizon	Texture	Dry Color	Carbonate
0-5	A	gls	10 YR 5/3	---
5-15	C_{1ca}	gls	10 YR 5/3	stage I
15-36	C_{2ca}	kgsl	10 YR 5/3	stage I
36-63	IIC_{3ca}	kls	10 YR 5/3	stage II
63-98	$IIIC_{4ca}$	kls	10 YR 6/4	stage II
98-115	IVC_{5ca}	ks	10 YR 6/4	stage II
115-143	IVC_{6ca}	kls	10 YR 6/4	stage II
143-173	VB_{tb}	gsl	7.5 YR 5/6	---
173-230+	VC_{cab}	---	---	stage IV

Table 6. Soil and site descriptions for debris flows in Wood Canyon—Continued

Lower Wood Canyon debris flows

Debris flow A

Estimated Age: latest Pleistocene or early Holocene
Source Material: metasedimentary rocks of the Kingston Peak (?) Formation
Exposure and elevation: 5° N., 1,650 m
Number of descriptions: 1

Depth (cm)	Horizon	Texture	Dry color	Carbonate
0-2*	A_{11}	kg	---	---
2-10	A_{12}	kgsl	10 YR 7/4	---
10-45	B_{2tca}	kgscl	7.5 YR 6/6	stage I
45-100+	C_{ca}	kgsl	10 YR 6/4	stage I-II

*desert pavement, well varnished

Debris flow B

Estimated Age: middle Holocene
Source Material: metasedimentary rocks of the Kingston Peak (?) Formation
Exposure and elevation: 6° NNW., 1,700 m
Number of descriptions: 1

Depth (cm)	Horizon	Texture	Dry color	Carbonate
0-2*	A_{11}	kg	10 YR 6/4	---
2-10	A_{12}	gsl	10 YR 6/4	---
10-40	C_1	kgsl	10 YR 6/4	stage I
40-70	IIC_{2ca}	gls	10 YR 6/3	stage I
70-100	IIC_{3ca}	gls	10 YR 6/3	stage I

*desert pavement, lightly varnished

Debris flow C

Estimated Age: latest Pleistocene or early Holocene
Source Material: metasedimentary rocks of the Kingston Peak (?) Formation
Exposure and elevation: 10° NNW., 1,710 m
Number of descriptions: 1

Depth (cm)	Horizon	Texture	Dry color	Carbonate
0-2*	A_{11}	kg	---	---
2-10	A_{12}	gsl	10 YR 5/3	___
10-30	B_{21}	kgscl	7.5 YR 5/6	stage I
30-55	B_{22ca}	kgsl	7.5 YR 5/4	stage II
55-100+	C_{ca}	kgsl	10 YR 5/4	stage I-II

*desert pavement, well varnished

Table 7. Density and cover of perennial vegetation on four debris flows originating in granite in eastern Wood Canyon

[Density values, in number per hectare, were determined from four 3 X 50-m belt transects on debris flow 1 and two 3 X 50-m belt transects on the other flows. Individuals of certain species, particularly *Ephedra* on older flows, were difficult to define. Cover, in percent, was determined from eight 50-m line intercepts per debris flow, and the term reflects the standard error of the mean of these eight measurements]

Species	Density				Cover			
	1	2	3	4	1	2	3	4
Shrubs:								
Coleogyne ramosissima	0	2,600	12,500	14,500	0.2 ± 0.2	2.9 ± 0.5	17.6 ± 1.0	20.6 ± 1.0
Ephedra nevadensis	0	4,500	3,100	8,300	0.0	11.0 ± 1.1	7.8 ± 1.0	5.5 ± 0.8
Lycium andersonii	100	2,400	1,300	300	0.3 ± 0.1	4.9 ± 0.8	3.1 ± 0.7	0.4 ± 0.2
Grayia spinosa	300	1,300	400	100	0.2 ± 0.2	3.5 ± 0.5	0.8 ± 0.2	0.0
Acamptopappus shockleyi	100	3,800	200	0	0.0	2.0 ± 0.2	0.6 ± 0.2	0.0
Thamnosma montana	0	1,000	200	100	0.0	2.0 ± 0.6	0.0	0.3 ± 0.2
Haplopappus cooperi	0	900	100	0	0.0	0.8 ± 0.5	0.0	0.0
Artemisia tridentata	100	100	100	100	0.1 ± 0.1	0.0	0.1 ± 0.1	0.0
Erigonum fasciculatum	100	200	300	200	0.3 ± 0.3	0.0	0.1 ± 0.1	0.0
Chrysothamnus teretifolius	0	0	0	700	0.0	0.0	0.0	1.0 ± 0.4
Chrysothamnus nauseosus	300	0	0	100	0.0	0.0	0.0	0.0
Salazaria mexicana	0	200	0	0	0.0	1.1 ± 0.5	0.0	0.0
Gutierrezia microcephala	200	0	0	0	0.1 ± 0.5	0.0	0.0	0.0
Hymenoclea salsola	0	100	0	0	0.0	0.1 ± 0.1	0.0	0.0
Lupinus excubitus	100	0	0	0	2.3 ± 1.0	0.0	0.0	0.0
Subtotal	1,300	17,100	18,200	24,400	3.5 ± 1.0	28.3 ± 1.8	30.1 ± 1.6	27.8 ± 1.4
Herbaceous perennials:								
Sphaeralcea rusbyi	200	4,200	1,000	400	0.1 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.0
Astragalus lentiginosus	600	0	0	0	0.1 ± 0.1	0.0	0.0	0.0
Subtotal	800	4,200	1,000	400	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.0
Grasses[1]	300	1,600	11,400	800	0.0	0.1 ± 0.1	0.9 ± 0.2	0.2 ± 0.1
Others[2]	100	100	1,100	100	0.0	0.0	0.0	0.0
Total live	2,500	23,000	31,700	25,700	3.7 ± 1.3	28.6 ± 1.5	31.1 ± 1.4	28.0 ± 1.4
Dead	300	500	600	300	0.2 ± 0.2	4.6 ± 0.8	2.9 ± 0.4	2.4 ± 0.2
Total	2,800	23,500	32,300	26,000	3.9 ± 1.3	33.2 ± 1.2	34.0 ± 1.3	30.4 ± 1.4

[1] Grasses include *Stipa speciosa*, *Oryzopsis hymenoides* *Oryzopsis webberi*, *Hilaria jamesii*, and *Sitanian hystrix*. Heavy grazing by burros precluded differentiation to species.

[2] Includes *Machaeranthera tortifolia*, *Echinocereus engelmanii*, *Eurotia lanata*, *Tetradymia axillaris* and *Stanleya elata*.

Table 8. Density and cover of perennial vegetation on three debris flows originating in the Kingston Peak(?) Formation in western Wood Canyon

[Density in number per hectare; cover in percent. All values are ±1 standard error of the mean]

Species	Density			Cover		
	A	B	C	A	B	C
Shrubs:						
Coleogyne ramosissima	4,700	1,300	7,900	8.2 ± 1.4	2.2 ± 0.6	13.6 ± 2.9
Lycium andersonii	2,600	2,000	1,400	7.3 ± 1.8	6.1 ± 1.2	2.3 ± 0.8
Ephedra nevadensis	1,500	600	2,000	5.7 ± 0.9	1.1 ± 0.3	6.6 ± 1.8
Grayia spinosa	1,900	5,100	1,000	3.2 ± 0.8	7.6 ± 1.3	1.6 ± 0.4
Acamptopappus shockleyi	700	8,500	100	0.8 ± 0.6	7.8 ± 0.9	0.2 ± 0.2
Tetradymia axillaris	200	300	400	0.7 ± 0.5	0.6 ± 0.3	2.0 ± 0.5
Haplopappus cooperi	1,500	100	100	1.0 ± 0.4	0.1 ± 0.1	0.0
Artemisia spinescens	2,100	300	1,900	0.5 ± 0.2	0.2 ± 0.1	0.4 ± 0.2
Artemisia tridentata	0	0	100	0.0	0.0	0.0
Dalea fremontii	0	0	100	0.3 ± 0.2	0.0	0.0
Chrysothamnus viscidiflorus	100	0	0	0.0	0.1 ± 0.1	0.0
Eurotia Lanata	100	800	0	0.0	0.3 ± 0.2	0.0
Hymenoclea salsola	100	0	200	0.0	0.0	0.3 ± 0.2
Thamnosma montana	100	0	0	0.0	0.0	0.0
Subtotal	15,600	19,000	15,200	27.7 ± 2.7	26.1 ± 2.1	27.0 ± 3.6
Herbaceous perennials:						
Machaeranthera tortifolia	2,300	1,900	1,300	0.6 ± 0.2	0.2 ± 0.1	0.4 ± 0.2
Sphaeralcea rusbyi	700	2,200	300	0.0	0.1 ± 0.1	0.0
Castilleja chromosa	400	0	100	0.0	0.0	0.0
Subtotal	3,400	4,100	1,700	0.6 ± 0.2	0.3 ± 0.1	0.4 ± 0.2
Grasses[1]	19,900	5,000	9,000	2.6 ± 0.3	1.7 ± 0.2	1.6 ± 0.3
Total live	38,900	28,100	25,900	30.9 ± 2.7	28.1 ± 2.1	29.0 ± 3.6
Dead	1,400	600	1,000	6.9 ± 0.7	9.1 ± 0.9	6.5 ± 0.6
Total	40,300	28,700	26,900	37.8 ± 2.8	37.2 ± 2.3	35.6 ± 3.6

---

[1] Grasses include *Stipa speciosa*, *Oryzopsis hymenoides*, *Oryzopsis webberi*, *Hilaria jamesii*, and *Sitanian hystrix*. Heavy grazing by burros precluded differentiation to species.

Table 9. Carbonate morphologies of soils on debris flows in Wood Canyon

[See table 6 for soil descriptions. Weight percent carbonate measured by Chittick method (M.N. Machette, written commun., 1983). Value in parentheses is detrital dolomite]

Flow	Horizon	Maximum carbonate stage	Description of carbonate	Carbonate (in weight percent)
1	C	none	No apparent redeposition of pebbles with carbonate coatings.	2.6 (1.1)
2	IIC_{3ca}	stage I	Coatings on bottoms and some coatings on sides of pebbles. Possibly underlain by Stage II carbonate horizon (50 cm below?).	0.8 (0.6)
3	C_{2ca}	stage I	Coatings on bottoms and sides of pebbles. Weak coatings on tops of some pebbles.	2.3 (1.1)
4	IIB_{tca}	stage I	Coatings on sides and bottoms of pebbles.	0.7 (0.6)
	IIC_{ca}	stage III	Continuous pebble coatings and filling of soil matrix with carbonate.	8.4 (1.0)
A	C_{ca}	stage II	Full pebble coatings with some carbonate disseminated in the soil matrix.	0.5 (1.1)
B	IIC_{2ca}	stage I	Coatings on bottoms and sides of pebbles with some carbonate disseminated in the soil matrix.	8.4 (1.9)
C	B_{22ca}	stage II	Full pebble coatings with some carbonate disseminated in the soil matrix.	1.2 (0.7)
Wash	IIC_{3ca}	stage II	Full pebble coatings.	--
	VC_{cab}	stage IV	Plugged carbonate horizon with overlying laminar zone.	

Table 10. Description of soil near the intersection of 4th and Skidoo Streets (fig. 9, site B), Skidoo townsite

[Source material: alluvium consisting of fragmental dolomite, porphyritic granite, and minor schist and vein quartz. See table 6 for abbreviations used]

Depth (cm)	Horizon	Texture	Dry color	Carbonate
0-9	A	sl[1]	10 YR 6/3	---
9-17	C_1	gsl[2]	10 YR 6/3	---
17-33	II C_2	gs	10 YR 6/3	stage I
33-60	III C_3	gsl	10 YR 6/3	stage I
$60\text{-}100^+$	IV C_4	sl	10 YR 6/3	stage I

Hydrometer analysis of textures:

[1] 8 percent gravel; 73 percent sand - 23 percent silt - 4 percent clay.

[2] 28 percent gravel; 72 percent sand - 24 percent silt - 4 percent clay.

Table 11. Physical properties of soils in disturbed and undisturbed areas of Skidoo townsite

[All values are ±1 standard error of the mean. The moisture content at the time of measurement was between 1.5 and 4.0 percent by volume. u, undisturbed]

Site	Number of years since abandonment	Bulk density (g/cm^3)	Penetration depth (cm)
Active Road	0	1.81 ± 0.03	4.4 ± 0.1
1st Street	63	1.63 ± 0.02	8.1 ± 0.1
2nd Street	63	1.62 ± 0.01	8.7 ± 0.2
Montgomery Street	74	1.50 ± 0.02	9.3 ± 0.2
Montgomery Control	u	1.53 ± 0.03	9.9 ± 0.2
Abandoned East Road	64?	1.65 ± 0.02	6.7 ± 0.2
East Road Control	u	1.55 ± 0.02	9.4 ± 0.2

Table 12. Density and cover of perennial vegetation at Skidoo townsite

[Density in number per hectare; cover in percent. All values are ±1 standard error of the mean]

Species	Montgomery Street				1st and 2nd Streets			
	Disturbed		Control		Disturbed		Control	
	Density	Cover	Density	Cover	Density	Cover	Density	Cover
Shrubs:								
Grayia spinosa	5,900 ± 500	9.8 ± 0.9	7,400 ± 800	14.6 ± 1.2	5,500 ± 1,500	5.5 ± 0.8	5,000 ± 400	14.0 ± 1.1
Artemisia spinescens	28,400 ± 1,400	10.1 ± 1.0	12,400 ± 1,700	4.8 ± 0.5	7,700 ± 1,700	2.1 ± 0.4	6,400 ± 700	1.6 ± 0.8
Ephedra nevadensis	1,500 ± 200	4.1 ± 0.9	800 ± 100	3.2 ± 0.8	700 ± 200	3.3 ± 1.2	2,100 ± 300	7.2 ± 0.7
Lycium andersonii	1,200 ± 300	1.1 ± 0.3	900 ± 100	0.8 ± 0.2	400 ± 0	0.3 ± 0.1	1,100 ± 200	1.2 ± 0.8
Chrysothamnus viscidiflorus	700 ± 200	0.5 ± 0.2	200 ± 100	0.2 ± 0.1	2,900 ± 500	4.2 ± 0.5	300 ± 200	0.6 ± 0.4
Artemisia tridentata	0	0.0	0	0.0	0	0.0	100 ± 100	0.2 ± 0.2
Hymenoclea salsola	0	0.1 ± 0.1	0	0.1 ± 0.1	900 ± 500	0.6 ± 0.2	300 ± 100	0.1 ± 0.1
Atriplex canescens	0	0.0	0	0.0	100 ± 100	0.6 ± 0.1	0	0.0
Chrysothamnus nauseosus	0	0.0	0	0.0	100 ± 100	0.1 ± 0.1	0	0.0
Acamptopappus shockleyi	0	0.0	0	0.0	0	0.0	100 ± 100	0.0
Tetradymia spinosa	0	0.0	100 ± 100	0.0	0	0.0	0	0.0
Eurotia lanata	100 ± 100	0.0	0	0.0	100 ± 100	0.2 ± 0.0	0	0.0
Subtotal	37,800 ± 1,600	25.7 ± 1.6	21,800 ± 1,900	23.7 ± 1.5	18,400 ± 2,500	16.9 ± 1.3	15,400 ± 1,000	24.9 ± 1.8
Herbaceous perennials:								
Stanleya elata	100 ± 100	0.0	500 ± 200	0.1 ± 0.0	0	0.0	400 ± 100	0.0
Sphaeralcea ambigua	1,000 ± 300	0.1 ± 0.0	400 ± 100	0.0	3,400 ± 1,300	0.1 ± 0.0	1,200 ± 400	0.0
Mirabilis froebelii	0	0.0	0	0.0	0	0.0	100 ± 100	0.0
Subtotal	1,100 ± 300	0.1 ± 0.0	900 ± 200	0.1 ± 0.0	3,400 ± 1,300	0.1 ± 0.0	1,700 ± 400	0.0
Grasses[1]	2,700 ± 600	0.5 ± 0.2	2,400 ± 400	0.6 ± 0.1	9,100 ± 3,600	0.3 ± 0.1	18,700 ± 7,900	0.4 ± 0.2
Total live	41,600 ± 1,600	26.3 ± 1.6	25,100 ± 2,000	24.4 ± 1.5	30,800 ± 4,600	17.3 ± 1.3	35,800 ± 7,900	25.3 ± 1.8
Dead	1,800 ± 300	---	1,700 ± 300	---	1,400 ± 300	4.3 ± 0.8	1,100 ± 300	4.0 ± 0.8
Total	43,400 ± 1,700	---	26,800 ± 2,100	---	32,200 ± 4,600	21.6 ± 1.5	36,900 ± 8,000	29.3 ± 2.0

[1] Grasses include *Hilaria jamesii*, *Stipa speciosa*, and *Sitanian hystrix*. Heavy grazing by burros precluded differentiation to species.

Table 13. Calculated dry-weight biomass of abundant woody perennials at Skidoo townsite

[All values are in kilograms per hectare and are ±1 standard error of the mean, as defined in the section "Methods"]

Species	Montgomery Street	Montgomery control	1st and 2nd Streets	1st and 2nd Streets control
Grayia spinosa	3,900 ± 800	5,300 ± 1,100	1,300 ± 400	1,700 ± 300
Artemisia spinescens	1,200 ± 200	300 ± 100	200 ± 100	100 ± 0
Ephedra nevadensis	600 ± 100	300 ± 100	500 ± 200	800 ± 300
Lycium andersonii	500 ± 100	100 ± 0	[1]500 ± 500	[1]100 ± 100
Chrysothamnus viscidiflorus	200 ± 0	0 ± 0	700 ± 200	100 ± 0

[1] Volume amounts taken from those in Montgomery Street and control.

Table 14. Cover of cryptogamic crusts in disturbed and undisturbed areas and estimated recovery time at Skidoo townsite

[Cover in percent. All values are ±1 standard error of the mean, based on 40 plots of 0.10 m^2 (4.0 m^2) total area. Estimated recovery time, in years, assumes 0-percent cover at initial abandonment]

Site	Cover (percent)	Estimated recovery time
1st and 2nd Streets	16.3 ± 2.7	110
1st and 2nd Streets control	28.1 ± 2.7	
Montgomery Street	22.0 ± 3.1	110
Montgomery Street control	32.1 ± 3.1	

Table 15. Cover of perennial vegetation along three segments of the Skidoo pipeline corridor at Harrisburg Flats

[Cover in percent. All values are ±1 standard error of the mean]

Location -------------------	Harrisburg Flats		Sand Dune		Rocky Slope	
Length of intercept --------	665 m		190 m		445 m	
Species	Pipeline	Control	Pipeline	Control	Pipeline	Control
Shrubs:						
Grayia spinosa	4.8 ± 0.8	8.8 ± 1.0	1.7 ± 1.0	0.0	0.2 ± 0.2	1.8 ± 0.5
Chrysothamnus viscidiflorus	12.1 ± 1.1	7.6 ± 0.8	1.3 ± 0.9	0.2 ± 0	3.3 ± 0.8	6.1 ± 1.1
Lycium andersonii	0.6 ± 0.2	2.2 ± 0.3	0.0	0.1 ± 0	0.9 ± 0.4	4.9 ± 0.9
Ephedra nevadensis	2.4 ± 0.6	1.8 ± 0.5	8.3 ± 2.2	8.0 ± 2.2	3.6 ± 0.7	7.0 ± 0.9
Artemisia spinescens	1.4 ± 0.3	1.2 ± 0.2	0.0	0.0	0.0	0.0
Tetradymia spinosa	0.5 ± 0.2	0.2 ± 0.1	0.0	0.6 ± 0.6	0.2 ± 0.1	0.8 ± 0.4
Haplopappus cooperi	0.0	0.0	0.0	0.0	7.6 ± 1.1	4.5 ± 0.7
Hymenoclea salsola	0.1 ± 0.1	0.1 ± 0.1	10.9 ± 2.3	9.3 ± 2.1	1.9 ± 0.5	0.6 ± 0.2
Acamptopappus shockleyi	0.1 ± 0.1	0.0	0.0	0.0	1.1 ± 0.4	2.5 ± 0.6
Atriplex canescens	1.4 ± 0.3	0.3 ± 0.1	1.2 ± 0.8	0.3 ± 0.3	0.0	0.0
Salazaria mexicana	0.0	0.0	0.0	0.0	0.0	0.6 ± 0.4
Eurotia lanata	0.0	0.3 ± 0.1	0.0	0.0	0.0	0.0
Dalea fremontii	0.7 ± 0.3	0.0	0.0	0.0	0.7 ± 0.3	0.2 ± 0.1
Subtotal	24.1 ± 1.6	22.5 ± 1.4	23.4 ± 3.5	18.5 ± 3.1	19.5 ± 1.7	29.0 ± 2.1
Herbaceous perennials:						
Sphaeralcea rusbyi	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.0	0.0	0.0
Grasses[1]	0.3 ± 0.1	0.6 ± 0.1	0.1 ± 0.1	0.1 ± 0	1.1 ± 0.3	0.3 ± 0.1
Total live	24.6 ± 1.6	23.3 ± 1.2	23.6 ± 3.0	18.6 ± 2.9	20.6 ± 1.5	29.3 ± 1.5
Dead	5.1 ± 0.5	6.2 ± 0.5	3.3 ± 0.7	5.6 ± 0.9	2.7 ± 0.4	3.3 ± 0.4
Total cover	29.7 ± 1.7	29.5 ± 1.4	26.9 ± 3.1	24.2 ± 3.4	23.3 ± 1.6	32.6 ± 1.6

[1] Grasses are *Stipa speciosa*, *Oryzopsis hymenoides*, and *Sitanian hystrix*. Heavy grazing by burros precluded differentiation to species.

Table 16. Density and cover of perennial vegetation along the Skidoo pipeline corridor in Wood Canyon

[Data for the controls are repeated from table 8. Density in number per hectare; cover in percent, All values are ±1 standard error of the mean]

Species	Pipeline		Control	
	Density	Cover	Density	Cover
Debris flow A, *Coleogyne ramosissima* assemblage				
Shrubs:				
Coleogyne ramosissima	1,500 ± 700	1.3 ± 0.4	4,700 ± 500	8.2 ± 1.4
Lycium andersonii	700 ± 300	2.9 ± 1.6	2,600 ± 400	7.3 ± 1.8
Grayia spinosa	400 ± 300	0.1 ± 0.1	1,900 ± 100	3.2 ± 0.8
Ephedra nevadensis	900 ± 300	2.6 ± 1.5	1,500 ± 200	5.7 ± 0.9
Acamptopappus shockleyi	7,700 ± 2,500	4.5 ± 1.5	700 ± 200	0.8 ± 0.6
Tetradymia axillaris	200 ± 200	1.1 ± 1.1	200 ± 100	0.7 ± 0.5
Haplopappus cooperi	3,000 ± 2,300	2.2 ± 1.0	1,500 ± 500	1.0 ± 0.4
Artemisia spinescens	500 ± 300	0.0	2,100 ± 1,200	0.5 ± 0.2
Dalea fremontii	100 ± 100	0.2 ± 0.2	0	0.3 ± 0.2
Chrysothamnus viscidiflorus	5,000 ± 2,900	4.2 ± 2.4	100 ± 100	0.0
Eurotia lanata	200 ± 100	0.0	100 ± 100	0.0
Hymenoclea salsola	900 ± 800	0.5 ± 0.4	100 ± 100	0.0
Chrysothamnus nauseosus	100 ± 100	0.1 ± 0.1	0	0.0
Thamnosma montana	0	0.0	100 ± 100	0.0
Subtotal	21,200 ± 4,600	19.7 ± 3.9	15,600 ± 1,500	27.7 ± 2.7
Herbacious perennials:				
Machaeranthera tortifolia	7,100 ± 3,500	0.6 ± 0.3	2,300 ± 600	0.6 ± 0.2
Sphaeralcea rusbyi	2,400 ± 1,400	0.0	700 ± 200	0.0
Castilleja chromosa	200 ± 100	0.0	400 ± 200	0.0
Subtotal	9,700 ± 3,800	0.6 ± 0.3	3,400 ± 700	0.6 ± 0.2
Grasses[1]	20,700 ± 6,800	2.2 ± 0.7	19,900 ± 1,700	2.6 ± 0.3
Total live	51,600 ± 9,000	22.5 ± 4.0	38,900 ± 2,400	30.9 ± 2.7
Dead	1,000 ± 600	3.8 ± 1.1	1,400 ± 200	6.9 ± 0.7
Total	52,600 ± 9,100	26.3 ± 4.1	40,300 ± 2,400	37.8 ± 2.8
Debris flow B, *Acamptopappus-Grayia-Lycium* assemblage				
Shrubs:				
Acamptopappus shockleyi	16,300 ± 1,400	16.6 ± 1.8	8,500 ± 400	7.8 ± 0.9
Grayia spinosa	900 ± 400	1.0 ± 0.4	5,100 ± 600	7.6 ± 1.3
Lycium andersonii	1,200 ± 500	1.9 ± 0.4	2,000 ± 100	6.1 ± 1.2
Coleogyne ramosissima	900 ± 300	1.0 ± 0.3	1,300 ± 500	2.2 ± 0.6
Ephedra nevadensis	700 ± 200	2.9 ± 0.6	600 ± 100	1.1 ± 0.3
Tetradymia axillaris	500 ± 200	1.1 ± 0.3	300 ± 100	0.6 ± 0.3
Eurotia lanata	300 ± 100	0.1 ± 0.0	800 ± 400	0.3 ± 0.2
Chrysothamnus viscidiflorus	100 ± 100	0.1 ± 0.1	0	0.1 ± 0.1
Artemisia spinescens	0	0.0	300 ± 200	0.2 ± 0.1
Hymenoclea salsola	200 ± 100	0.3 ± 0.3	0	0.0
Haplopappus cooperi	100 ± 100	0.0	100 ± 100	0.1 ± 0.1
Chrysothamnus nauseosus	100 ± 100	0.1 ± 0.1	0	0.0
Artemisia tridentata	100 ± 100	0.3 ± 0.3	0	0.0
Subtotal	21,400 ± 1,600	25.4 ± 2.1	19,000 ± 1,000	26.1 ± 2.1
Herbaceous perennials:				
Machaeranthera tortifolia	3,600 ± 1,300	0.5 ± 0.1	1,900 ± 600	0.2 ± 0.1
Sphaeralcea rusbyi	2,000 ± 500	0.1 ± 0.1	2,200 ± 500	0.1 ± 0.1
Castilleja chromosa	100 ± 100	0.0	0	0.0
Mirabilis froebelii	100 ± 100	0.0	0	0.0
Subtotal	5,800 ± 1,400	0.6 ± 0.1	4,100 ± 800	0.3 ± 0.1
Grasses[1]	21,500 ± 3,400	3.3 ± 0.4	5,000 ± 700	1.7 ± 0.2
Total live	48,700 ± 4,000	29.3 ± 2.1	28,100 ± 1,500	28.1 ± 2.1
Dead	900 ± 200	4.3 ± 0.6	600 ± 200	9.1 ± 0.9
Total	49,600 ± 4,000	33.6 ± 2.2	28,700 ± 1,500	37.2 ± 2.3

Table 16. Density and cover of perennial vegetation along the Skidoo pipeline corridor in Wood Canyon—Continued

Species	Pipeline		Control	
	Density	Cover	Density	Cover
	Debris flow C, *Coleogyne* assemblage			
Shrubs:				
Coleogyne ramosissima	11,700 ± 1,400	12.0 ± 1.6	7,900 ± 500	13.6 ± 2.9
Ephedra nevadensis	700 ± 200	1.0 ± 0.4	2,000 ± 800	6.6 ± 1.8
Lycium andersonii	300 ± 100	0.2 ± 0.1	1,400 ± 300	2.3 ± 0.8
Tetradymia spinosa	200 ± 100	0.2 ± 0.2	400 ± 200	2.0 ± 0.5
Grayia spinosa	100 ± 100	0.3 ± 0.2	1,000 ± 100	1.6 ± 0.4
Artemisia axillaris	1,000 ± 300	0.1 ± 0.1	1,900 ± 100	0.4 ± 0.2
Hymenoclea salsola	1,000 ± 500	0.8 ± 0.5	200 ± 200	0.3 ± 0.2
Haplopappus cooperi	3,200 ± 1,900	3.2 ± 1.5	100 ± 100	0.0
Acamptopappus shockleyi	1,100 ± 700	1.1 ± 0.7	100 ± 100	0.2 ± 0.2
Chrysothamnus nauseosus	600 ± 400	2.0 ± 1.2	0	0.0
Chrysothamnus teretifolius	1,100 ± 1,000	0.9 ± 0.4	0	0.0
Chrysothamnus viscidiflorus	500 ± 400	0.6 ± 0.4	0	0.0
Artemisia tridentata	100 ± 100	0.4 ± 0.3	100 ± 100	0.0
Dalea fremontii	100 ± 100	0.2 ± 0.2	100 ± 100	0.0
Subtotal	21,700 ± 2,800	23.0 ± 2.8	15,200 ± 1,100	27.0 ± 3.6
Herbaceous perennials:				
Machaeranthera tortifolia	4,300 ± 600	0.4 ± 0.2	1,300 ± 900	0.4 ± 0.2
Sphaeralcea rusbyi	400 ± 200	0.0	300 ± 100	0.0
Castilleja chromosa	300 ± 200	0.0	100 ± 100	0.0
Subtotal	5,000 ± 700	0.4 ± 0.2	1,700 ± 1,100	0.4 ± 0.2
Grasses[1]	14,900 ± 3,700	1.7 ± 0.4	9,000 ± 1,400	1.6 ± 0.3
Total live	41,600 ± 4,700	25.1 ± 3.0	25,900 ± 2,000	29.0 ± 3.6
Dead	1,900 ± 800	4.4 ± 0.6	1,000 ± 500	6.5 ± 0.6
Total	43,500 ± 4,800	29.5 ± 2.9	26,900 ± 2,100	35.5 ± 3.6

[1] Grasses include *Stipa speciosa*, *Hilaria jamesii*, *Sitanian hystrix*, and *Oryzopsis* sp. Heavy grazing by burros precluded differentiation to species.

Table 17. Calculated dry-weight biomass for abundant woody perennials along three segments of the Skidoo pipeline corridor in Wood Canyon

[All values are ±1 standard error of the mean]

Species	Flow A		Flow B		Flow C	
	Pipeline	Control	Pipeline	Control	Pipeline	Control
Coleogyne ramosissima	400 ± 200	2,000 ± 500	200 ± 100	500 ± 200	3,000 ± 800	3,300 ± 700
Lycium andersonii	300 ± 200	1,300 ± 300	500 ± 300	1,000 ± 200	100 ± 100	700 ± 200
Grayia spinosa	100 ± 100	600 ± 100	300 ± 100	1,600 ± 300	100	300 ± 100
Ephedra nevadensis	400 ± 200	200 ± 0	300 ± 100	100 ± 100	300 ± 100	300 ± 0
Acamptopappus shockleyi	700 ± 300	100 ± 100	1,500 ± 300	800 ± 200	100 ± 100	100
Haplopappus cooperi	600 ± 500	300 ± 100	100	100	600 ± 400	100
Artemisia spinescens	100	100 ± 100	0	100	100	100 ± 100
Chrysothamnus viscidiflorus	1,300 ± 800	100	100	0	100 ± 100	0

Table 18. Cover of perennial vegetation along the Skidoo pipeline corridor and control areas at Nemo Crest, including a nearby road

[Cover in percent. All values are ±1 standard error of the mean]

Species	Downslope control	Pipeline	Road	Upslope control
Shrubs:				
Coleogyne ramosissima	11.7 ± 1.5	1.6 ± 0.5	0.6 ± 0.3	10.2 ± 1.5
Grayia spinosa	4.1 ± 1.2	1.5 ± 0.5	0.0	5.2 ± 1.0
Ephedra nevadensis	2.7 ± 1.0	0.9 ± 0.5	0.2 ± 0.2	4.5 ± 1.2
Lycium andersonii	3.0 ± 0.9	1.2 ± 0.8	0.0	2.6 ± 0.9
Eurotia lanata	1.0 ± 0.9	0.8 ± 0.4	0.6 ± 0.2	0.4 ± 0.2
Artemisia tridentata	0.5 ± 0.5	0.7 ± 0.4	1.9 ± 0.9	1.1 ± 0.8
Tetradymia spinosa	0.0	0.0	0.0	0.5 ± 0.5
Artemisia spinescens	0.1 ± 0.1	0.3 ± 0.2	0.0	0.1 ± 0.1
Atriplex canescens	0.0	0.0	0.0	0.1 ± 0.1
Acamptopappus shockleyi	0.0	0.2 ± 0.2	0.4 ± 0.2	0.1 ± 0.1
Eriogonum fasciculatum	0.1 ± 0.1	0.0	0.0	0.0
Chrysothamnus viscidiflorus	0.0	1.2 ± 0.6	1.8 ± 1.1	0.0
Chrysothamnus nauseosus	0.0	0.3 ± 0.3	1.1 ± 0.7	0.0
Haplopappus cooperi	0.0	0.0	0.1 ± 0.1	0.0
Hymenoclea salsola	0.0	0.2 ± 0.2	0.0	0.0
Subtotal	23.2 ± 2.6	8.9 ± 0.8	6.7 ± 1.7	24.8 ± 2.5
Herbaceous perennials:				
Sphaeralcea rusbyi	0.0	0.0	0.2 ± 0.1	0.4 ± 0.4
Brickellia oblongifolia	0.0	0.2 ± 0.2	0.0	0.1 ± 0.1
Subtotal	0.0	0.2 ± 0.2	0.2 ± 0.1	0.5 ± 0.5
Grasses[1]	9.6 ± 1.0	10.1 ± 1.0	8.6 ± 1.1	7.4 ± 0.8
Total live	32.8 ± 2.8	19.2 ± 1.7	15.5 ± 2.0	32.7 ± 2.7
Dead	3.0 ± 0.5	0.3 ± 0.1	0.5 ± 0.2	3.3 ± 0.6
Total	35.8 ± 2.8	19.5 ± 1.7	16.0 ± 2.0	36.0 ± 2.8

[1] Grasses include *Oryzopsis hymenoides*, *Stipa speciosa*, *Hilaria jamesii*, and *Sitanian hystrix*. Heavy grazing by burros precluded differentiation to species.

Table 19. Cover of perennial vegetation along the Skidoo pipeline corridor and control area on a sloping segment north of Nemo Crest

[Cover in percent. All values are ±1 standard error of the mean. Transect length was 100 m]

Species	Pipeline	Control
Shrubs:		
Artemisia tridentata	4.3 ± 2.5	17.4 ± 3.6
Ephedra nevadensis	0.2 ± 0.2	4.4 ± 3.6
Grayia spinosa	0.0	3.1 ± 1.2
Coleogyne ramosissima	0.0	2.8 ± 2.0
Subtotal	4.5 ± 2.5	27.7 ± 4.4
Herbaceous perennial:		
Mirabilis froebelii	0.2 ± 0.2	0.0
Grasses[1]	3.6 ± 1.3	2.1 ± 1.4
Total live	8.3 ± 2.5	29.8 ± 4.6
Dead	0.3 ± 0.2	3.1 ± 1.1
Total	8.6 ± 2.5	32.9 ± 4.7

[1] Grasses include *Stipa speciosa*, *Oryzopsis hymenoides*, and *Hilaria jamesii*. Heavy grazing by burros precluded differentiation to species.

Table 20. Cover of perennial vegetation along the Skidoo pipeline corridor and control areas at Wildrose Canyon

[Cover in percent. All values are ±1 standard error of the mean]

Location--------------------- Length-----------------------	Segment A 200 m		Segment B 200 m		Segment C 500 m		Segment D 400 m	
Species	Pipeline	Control	Pipeline	Control	Pipeline	Control	Pipeline	Control
Trees:								
Pinus monophylla	0.0	0.0	0.0	0.0	0.0	0.1 ± 0.1	2.3 ± 1.1	2.9 ± 1.6
Juniperus osteosperma	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0 ± 0.7
Shrubs:								
Artemisia tridentata	0.0	0.0	7.8 ± 2.2	17.4 ± 3.8	9.2 ± 1.3	20.4 ± 1.5	17.7 ± 1.8	11.4 ± 1.5
Coleogyne ramosissima	10.4 ± 1.2	28.7 ± 4.9	1.3 ± 1.2	8.7 ± 2.8	0.0	3.3 ± 0.8	1.4 ± 0.5	7.2 ± 1.1
Ephedra viridis	0.0	0.0	0.0	0.0	0.3 ± 0.2	1.3 ± 0.5	0.0	0.9 ± 0.5
Ephedra nevadensis	2.1 ± 1.3	12.9 ± 5.0	0.2 ± 0.1	3.0 ± 1.4	0.0	0.7 ± 0.4	0.0	0.0
Grayia spinosa	0.0	2.2 ± 1.4	0.0	0.2 ± 0.2	0.0	0.0	0.0	0.0
Chrysothamnus viscidiflorus	0.0	0.0	1.1 ± 0.6	0.3 ± 0.2	0.3 ± 0.2	1.0 ± 0.3	0.7 ± 0.3	0.6 ± 0.3
Chrysothamnus teretifolius	0.0	0.0	0.0	0.0	0.3 ± 0.2	0.0	0.1 ± 0.1	0.1 ± 0.1
Tetradymia spinosa	5.3 ± 2.2	2.1 ± 1.6	0.0	0.0	0.0	0.0	0.0	0.0
Dalea fremontii	0.5 ± 0.3	1.7 ± 1.0	0.0	0.0	0.0	0.0	0.0	0.0
Eriogonum fasciculatum	0.0	0.0	0.0	0.0	0.9 ± 0.3	0.8 ± 0.3	1.1 ± 0.4	0.5 ± 0.3
Lycium andersonii	0.7 ± 0.4	0.7 ± 0.5	0.0	0.0	0.0	0.0	0.0	0.0
Haplopappus cooperi	0.4 ± 0.4	0.5 ± 0.5	0.0	0.0	0.0	0.0	0.0	0.0
Salvia dorii	0.0	0.0	0.0	0.0	0.2 ± 0.2	0.7 ± 0.3	1.0 ± 0.4	0.6 ± 0.4
Eriogonum saxatile	0.0	0.0	0.0	0.0	0.0	0.0	0.1 ± 0.1	0.1 ± 0.1
Viguieria multiflora	0.0	0.0	0.1 ± 0.1	0.1 ± 0.1	0.0	0.0	0.0	0.0
Lupinus excubitus	0.0	0.0	0.0	0.0	0.0	0.0	0.3 ± 0.2	0.2 ± 0.2
Encelia virginensis	0.4 ± 0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Subtotal	19.8 ± 2.9	48.8 ± 7.4	10.5 ± 2.6	29.7 ± 4.9	11.2 ± 1.4	28.3 ± 1.6	24.7 ± 2.1	25.5 ± 2.7
Herbaceous perennials:								
Astragalus sp.	0.0	0.0	1.9 ± 0.3	2.0 ± 0.7	0.3 ± 0.1	0.3 ± 0.1	0.0	0.1 ± 0.1
Sphaeralcea rusbyi	0.0	0.2 ± 0.1	0.0	0.0	0.0	0.0	0.0	0.0
Subtotal	0.0	0.2 ± 0.1	1.9 ± 0.3	2.0 ± 0.7	0.3 ± 0.1	0.3 ± 0.1	0.0	0.1 ± 0.1
Grasses[1]	0.0	0.2 ± 0.2	2.3 ± 0.2	1.1 ± 0.2	0.8 ± 0.1	1.4 ± 0.2	0.7 ± 0.2	0.8 ± 0.2
Total live	19.8 ± 2.9	49.2 ± 7.4	14.7 ± 2.6	32.8 ± 5.0	12.3 ± 1.4	30.0 ± 1.6	25.4 ± 2.1	26.4 ± 2.7
Dead	--	--	--	--	1.1 ± 0.2	5.6 ± 0.6	1.0 ± 0.3	4.7 ± 2.0
Total	--	--	--	--	13.4 ± 1.4	35.6 ± 1.7	26.4 ± 2.1	31.1 ± 2.8

[1] Grasses include *Stipa speciosa*, *Oryzopsis* sp., and *Hilaria jamesii*. Heavy grazing by burros precluded differentiation to species.

Table 21. Description of soils for terrace sequences A and B in Gold Valley

[Refer to cross sections in fig. 19 for locations. See table 6 for abbreviations]

Depth (cm)	Horizon	Texture	Dry color	Carbonate
TERRACE SEQUENCE A TA_0 -- active wash				
0-2	A	gls	10 YR 6/4	---
2-30	C_1	gls	10 YR 6/4	---
30-55	C_2	gs	10 YR 6/4	---
55+	IIC_{3camb}	---	---	stage IV
TA_1				
0-6	A	gls	10 YR 6/3	---
6-26	C_1	gls	10 YR 6/4	---
26-50	C_{2ca}	gls	10 YR 6/4	stage I
50-80	C_{3ca}	gls	10 YR 6/4	stage I
80+	C_{4ca}	gs	10 YR 6/4	stage I
TA_2				
0-6	A	gsl	10 YR 6/4	---
6-33	B_2	gsl	10 YR 5/3	---
33-60	B_{3ca}	gsl	10 YR 5/3	stage I
60-80+	C_{ca}	gs	10 YR 6/3	stage I-II
TA_3				
0-7	A	cl	10 YR 7/3	---
7-25	B_{2t}	sl-scl	7.5 YR 4/4	---
25-42	B_{31tca}	gsl	7.5 YR 4/4	stage I
42-52	B_{32tca}	gsl	7.5 YR 4/4	stage I
52-95+	C_{ca}	gsl	7.5 YR 5/4	stage II-III
TERRACE SEQUENCE B TB_0				
0-7	A	gs	10 YR 6/3	---
7-18	C_{1ca}	gs	10 YR 6/3	---
18-70+	C_{2ca}	gs	10 YR 6/3	stage I
TB_1				
0-5	A	gls	10 YR 6/3	---
5-12	C_1	gsl	10 YR 6/3	---
12-29	C_{2ca}	gls	10 YR 6/3	stage I
29-71	C_{3ca}	gs	10 YR 6/3	stage I
71-72	IIC_{4ca}	gc	5 YR 4/4	stage I
72-100	IIC_{5ca}	gs	10 YR 6/3	stage I

Table 22. Density and cover of perennial vegetation on terrace sequence A in Gold Valley

[Density in number per hectare; cover in percent. All values are ±1 standard error of the mean]

Species	TA_0		TA_1		TA_2		TA_3	
	Density	Cover	Density	Cover	Density	Cover	Density	Cover
Shrubs:								
Ambrosia dumosa	300 ± 100	0.1 ± 0.1	3,200 ± 400	2.6 ± 0.4	6,300 ± 700	5.8 ± 0.9	15,000 ± 400	8.9 ± 0.5
Larrea tridentata	0	0.0	700 ± 100	9.3 ± 1.6	400 ± 200	3.5 ± 0.9	2,200 ± 100	8.4 ± 1.3
Lycium andersonii	100 ± 100	0.1 ± 0.1	700 ± 100	2.5 ± 0.7	600 ± 200	3.9 ± 1.3	700 ± 100	3.0 ± 1.0
Grayia spinosa	0	0.0	500 ± 200	2.2 ± 0.7	700 ± 100	3.0 ± 0.8	1,100 ± 300	1.6 ± 0.6
Ephedra nevadensis	500 ± 100	1.7 ± 0.4	400 ± 200	3.5 ± 0.7	700 ± 200	2.0 ± 0.7	200 ± 100	0.7 ± 0.3
Thamnosma montana	100 ± 100	0.1 ± 0.1	300 ± 200	1.1 ± 0.4	100 ± 100	0.0	0	0.2 ± 0.2
Hymenoclea salsola	7,400 ± 200	12.8 ± 1.8	700 ± 100	0.9 ± 0.4	300 ± 200	0.7 ± 0.3	300 ± 100	0.0
Acamptopappus sphaerocephalus	0	0.0	0	0.0	0	0.0	100 ± 100	0.0
Dalea fremontii	200 ± 100	1.5 ± 0.9	0	0.0	0	0.0	0	0.0
Haplopappus linearifolius	700 ± 300	0.3 ± 0.2	0	0.0	0	0.0	0	0.0
Salazaria mexicana	0	0.0	0	0.0	100 ± 100	0.1 ± 0.1	0	0.1 ± 0.1
Eriogonum fasciculatum	0	0.0	0	0.0	300 ± 200	0.1 ± 0.1	0	0.0
Coleogyne ramosissima	0	0.0	100	0.2 ± 0.2	0	0.0	0	0.0
Subtotal	9,300 ± 400	16.6 ± 2.2	6,500 ± 600	22.3 ± 1.9	9,500 ± 800	19.1 ± 0.6	19,600 ± 500	22.9 ± 1.1
Herbaceous perennials:								
Machaeranthera tortifolia	0	0.1 ± 0.1	100 ± 100	0.1 ± 0.1	100 ± 100	0.0	100 ± 100	0.2 ± 0.2
Eriogonum inflatum	2,800 ± 600	0.3 ± 0.1	600 ± 200	0.1 ± 0.1	100 ± 100	0.1 ± 0.1	3,300 ± 700	0.1 ± 0.1
Mirabilis bigelovii	200 ± 100	0.0	0	0.0	300 ± 100	0.1 ± 0.1	100 ± 100	0.0
Dyssodia cooperi	400 ± 200	0.1 ± 0.1	0	0.0	0	0.0	0	0.0
Stephanomeria pauciflora	400 ± 100	0.0	0	0.0	0	0.0	0	0.0
Subtotal	3,800 ± 600	0.5 ± 0.2	700 ± 200	0.2 ± 0.1	500 ± 200	0.2 ± 0.1	3,500 ± 700	0.3 ± 0.2
Grass:								
Stipa speciosa	500 ± 400	0.1 ± 0.1	100 ± 100	0.1 ± 0.1	300 ± 100	0.2 ± 0.2	0	0.0
Total live	13,600 ± 1,000	17.2 ± 2.3	7,300 ± 600	22.6 ± 2.0	10,300 ± 900	19.5 ± 0.8	23,100 ± 700	23.2 ± 1.2
Dead	1,300 ± 400	1.4 ± 0.5	700 ± 100	1.7 ± 0.3	1,000 ± 100	2.0 ± 0.2	2,500 ± 400	1.1 ± 0.2
Total	14,900 ± 1,400	18.6 ± 2.3	8,000 ± 600	24.3 ± 2.0	11,300 ± 900	21.5 ± 0.8	25,600 ± 900	24.3 ± 1.2

Table 23. Density and cover of perennial vegetation on terrace sequence B in Gold Valley

[Density in number per hectare; cover in percent. All values are ±1 standard error of the mean]

Species	TB_0		TB_1	
	Density	Cover	Density	Cover
Shrubs:				
Grayia spinosa	800 ± 200	2.9 ± 0.7	1,500 ± 100	5.6 ± 1.0
Larrea tridentata	0	0.1 ± 0.1	300 ± 100	5.3 ± 1.0
Thamnosma montana	500 ± 100	2.1 ± 0.5	500 ± 200	2.5 ± 1.0
Ephedra nevadensis	2,900 ± 500	5.4 ± 1.0	1,200 ± 300	2.4 ± 0.7
Lycium andersonii	300 ± 100	2.4 ± 0.8	500 ± 0	1.8 ± 0.4
Salazaria mexicana	100 ± 100	0.2 ± 0.2	700 ± 200	1.5 ± 0.5
Acamptopappus shockleyi	0	0.0	1,300 ± 500	1.3 ± 0.5
Hymenoclea salsola	6,000 ± 600	10.4 ± 1.6	400 ± 200	0.2 ± 0.1
Ambrosia dumosa	300 ± 200	0.5 ± 0.2	200 ± 100	0.2 ± 0.1
Haplopappus cooperi	0	0.1 ± 0.1	100 ± 0	0.1 ± 0.1
Tetradymia stenolepsis	100 ± 0	0.6 ± 0.4	0	0.1 ± 0.1
Eriogonum fasciculatum	600 ± 200	1.8 ± 0.6	0	0.0
Dalea fremontii	100 ± 0	0.3 ± 0.2	0	0.0
Subtotal	11,700 ± 900	26.8 ± 2.6	6,700 ± 700	21.0 ± 2.0
Herbaceous perennials:				
Castilleja chromosa	100 ± 100	0.0	0	0.0
Dyssodia cooperi	300 ± 200	0.0	100 ± 0	0.0
Eriogonum inflatum	2,900 ± 700	0.2 ± 0.1	200 ± 200	0.0
Machaeranthera tortifolia	100 ± 100	0.0	0	0.0
Mirabilis bigelovii	100 ± 100	0.1 ± 0.1	300 ± 100	0.1 ± 0.1
Sphaeralcea ambigua	400 ± 200	0.2 ± 0.2	0	0.0
Subtotal	3,900 ± 800	0.5 ± 0.3	600 ± 300	0.1 ± 0.1
Grass:				
Stipa speciosa	600 ± 300	0.2 ± 0.2	2,100 ± 600	1.8 ± 0.4
Total live	16,200 ± 1,200	27.5 ± 2.6	9,400 ± 1,000	22.9 ± 2.1
Dead	2,400 ± 300	5.1 ± 0.4	400 ± 200	2.9 ± 0.6
Total	18,600 ± 1,200	32.6 ± 2.6	9,800 ± 1,100	25.8 ± 2.3

Table 24. Description of soils for terrace sequence C and the Gold Valley townsite

[For an explanation of abbreviations, see table 6]

Depth (cm)	Horizon	Texture	Moist color	Carbonate
		Terrace TC_0		
0-7	A	gls	10 YR 4/4	---
0-32	C_1	gs	7.5 YR 5/4	stage I
32-48	IIC_{2ca}	gls	7.5 YR 4/4	stage I
48-54	IIC_{3ca}	gs	10 YR 7/2	stage II-III[1]
54-65+	IIC_{4ca}	gls	7.5 YR 4/4	stage I-III[2]

1. plugged zone preferentially in gravel lenses.
2. plugged in gravel lenses; pebble coatings where sand is present.

Depth (cm)	Horizon	Texture	Moist color	Carbonate
		Terrace TC_1		
0-8	A	gls	7.5 YR 6/4	---
8-30	C_1	gsl	7.5 YR 6/4	---
30-43	C_{2ca}	gkls	7.5 YR 5/4	stage I
43-100+	C_{3ca}	gls	5 YR 5/4	stage I
		Terrace TC_2 (Gold Valley townsite)		
0-7	A	gsl	7.5 YR 5/4	---
7-22	C_1	gsl	7.5 YR 5/4	---
22-60	C_{2ca}	gsl	7.5 YR 5/4	stage I
60-100+	IIC_{3ca}	gksl	7.5 YR 5/4	stage I
		Terrace TC_3		
0-2	A	gls	10 YR 5/3	---
2-14	C_1	gls	10 YR 5/3	---
14-52	C_{2ca}	gs	10 YR 5/3	stage I
52-62	IIB_{31cab}	gscl	7.5 YR 5/4	stage I
62-72	IIB_{32cab}	gscl	5 YR 5/6	stage II
72 +	IIC_{cab}	---	---	stage IV
		Terrace TC_4		
0-3	A	sl	10 YR 5/3	---
3-9	B_1	gcl	10 YR 5/3	---
9-32	B_{21t}	gcl	7.5 YR 4/4	---
32-45	B_{22tca}	gcl	7.5 YR 4/4	stage I
45-53	B_{31ca}	gl	7.5 YR 5/4	stage II
53-57+	B_{32ca}	gcl	7.5 YR 5/4	stage II-III
ca. 100	C_{ca}	---	----	stage IV

Table 25. Density and cover of perennial vegetation on terrace sequence C in Gold Valley

[Density in number per hectare; cover in percent. All values are ±1 standard error of the mean. Tr: species was encountered in the transect]

Species	TC_0		TC_1		TC_2		TC_3	
	Density	Cover	Density	Cover	Density	Cover	Density	Cover
Shrubs:								
Coleogyne ramosissima	1,600 ± 800	7.0 ± 1.6	2,000 ± 100	6.2 ± 0.6	1,300 ± 300	6.3 ± 1.0	3,400 ± 1,000	11.9 ± 1.7
Larrea tridentata	0	0.0	0	0.0	100 ± 100	2.2 ± 0.9	300 ± 200	6.1 ± 1.9
Lycium andersonii	400 ± 200	0.7 ± 0.4	1,300 ± 200	4.6 ± 1.1	1,300 ± 100	5.7 ± 1.1	800 ± 100	2.9 ± 0.8
Ephedra nevadensis	1,100 ± 400	2.1 ± 0.9	600 ± 300	2.1 ± 0.6	1,400 ± 300	6.8 ± 1.1	900 ± 100	2.0 ± 0.5
Grayia spinosa	100 ± 100	0.2 ± 0.2	1,900 ± 400	7.2 ± 0.6	1,200 ± 300	5.1 ± 1.0	700 ± 200	1.5 ± 0.4
Hymenoclea salsola	7,500 ± 3,200	7.1 ± 1.3	1,400 ± 600	2.8 ± 0.6	200 ± 100	0.2 ± 0.1	500 ± 300	0.9 ± 0.6
Thamnosma montana	200 ± 100	0.0	300 ± 200	0.3 ± 0.3	900 ± 500	1.1 ± 0.5	100 ± 0	0.2 ± 0.2
Tetradymia spinosa	0	0.0	200 ± 100	0.8 ± 0.4	Tr	0.1 ± 0.1	100 ± 100	0.2 ± 0.2
Haplopappus cooperi	Tr	0.0	0	0.0	0	0.0	Tr	0.2 ± 0.2
Ambrosia dumosa	0	0.0	Tr	0	100 ± 100	0.1 ± 0.1	100 ± 100	0.1 ± 0.1
Eriogonum fasciculatum	1,200 ± 200	3.4 ± 1.0	200 ± 100	0.3 ± 0.2	0	0.0	0	0.0
Acamptopappus shockleyi	0	0.0	0	0.0	100 ± 100	0.0	0	0.0
Salazaria mexicana	0	0.0	100 ± 100	0.3 ± 0.3	0	0.0	0	0.0
Dalea fremontii	500 ± 200	1.7 ± 0.7	0	Tr	0	0.0	0	0.0
Encelia virginensis	1,100 ± 400	0.2 ± 0.2	0	0.0	0	0.0	0	0.0
Gutierrezia microcephala	100 ± 100	0.1 ± 0.1	0	0.0	0	0.0	0	0.0
Subtotal	13,800 ± 3,700	22.5 ± 2.6	8,000 ± 900	24.6 ± 1.7	6,600 ± 800	27.6 ± 2.3	6,900 ± 1,100	26.0 ± 2.8
Herbaceous perennials:								
Machaeranthera tortifolia	200 ± 100	0.1 ± 0.1	700 ± 100	0.2 ± 0.1	300 ± 200	0.1 ± 0.1	300 ± 100	0.3 ± 0.2
Sphaeralcea ambigua	500 ± 200	0.0	100 ± 100	0.0	0	0.0	100 ± 100	0.0
Eriogonum inflatum	2,000 ± 600	0.1 ± 0.1	4,400 ± 2,100	0.1 ± 0.1	2,800 ± 1,000	0.1 ± 0.1	0	0.0
Arabis pulchra	Tr	0.0	100 ± 100	0.0	0	0.0	0	0.0
Stephanomeria pauciflora	100 ± 100	0.0	0	0.0	0	0.0	0	0.0
Dyssodia cooperi	0	0.0	0	0.0	200 ± 200	0.0	0	0.0
Subtotal	2,800 ± 600	0.2 ± 0.1	5,300 ± 2,100	0.3 ± 0.1	3,300 ± 1,000	0.2 ± 0.1	400 ± 100	0.3 ± 0.2
Grasses:								
Stipa speciosa	400 ± 200	0.1 ± 0.1	300 ± 100	Tr	300 ± 200	0.2 ± 0.1	0	0.0
Oryzopsis hymenoides	100 ± 100	Tr	0	0.0	100 ± 100	0.1 ± 0.1	0	0.0
Subtotal	500 ± 200	0.1 ± 0.1	300 ± 100	0.0	400 ± 200	0.3 ± 0.2	0	0.0
Total live	17,100 ± 3,800	22.8 ± 2.6	13,600 ± 2,300	24.9 ± 1.7	10,300 ± 1,300	28.1 ± 2.4	7,300 ± 1,100	26.3 ± 2.8
Dead	1,800 ± 400	3.5 ± 0.7	4,900 ± 1,400	6.8 ± 0.8	2,400 ± 600	4.2 ± 0.4	1,200 ± 200	3.1 ± 0.4
Total	18,900 ± 3,800	26.3 ± 2.7	18,500 ± 2,700	31.7 ± 1.9	12,700 ± 1,400	32.3 ± 2.4	8,500 ± 1,100	29.4 ± 2.0

Table 26. Physical properties of soils in disturbed and undisturbed areas of Gold Valley townsite

[All values are ±1 standard deviation. u: undisturbed]

Site	Number of years since abandonment	Bulk density (g/cm^3)	Penetration depth (cm)	Peak shear strength (kN/m^2)	Volume moisture content (percent)
Active road	0	1.56 ± 0.09	4.0 ± 0.6	60.0 ± 2.1	9.0 ± 1.6
Western townsite	73	1.43 ± 0.07	10.1 ± 1.0	37.9 ± 1.5	8.4 ± 3.5
Control TC_2	u	1.35 ± 0.04	13.5 ± 1.8	31.7 ± 1.1	8.1 ± 0.6
Estimated recovery time (years)		120	120	90	
Active road	0		1.6 ± 0.6		
Eastern townsite	73?		9.2 ± 2.4		4.6 ± 1.0
Control TC_3	u		10.5 ± 2.4		
Estimated recovery time (years)			90		

Table 27. Density and cover of perennial vegetation at Gold Valley townsite

[The data from the lower and upper controls (TC_2 and TC_3) are repeated from table 25. Density in number per hectare; cover in percent. All values are ±1 standard error of the mean. Tr: species was encountered in the transects]

Species	Lower control (TC_2)		Western townsite		Eastern townsite		Upper control (TC_3)	
	Density	Cover	Density	Cover	Density	Cover	Density	Cover
Shrubs:								
Coleogyne ramosissima	1,300 ± 300	6.3 ± 1.0	1,000 ± 300	4.0 ± 1.0	1,100 ± 200	3.1 ± 0.6	3,400 ± 1,000	11.9 ± 1.7
Larrea tridentata	100 ± 100	2.2 ± 0.9	0	0.0	0	0.0	300 ± 200	6.1 ± 1.9
Lycium andersonii	1,300 ± 100	5.7 ± 1.1	700 ± 200	3.8 ± 1.4	1,100 ± 100	4.4 ± 1.0	800 ± 100	2.9 ± 0.8
Ephedra nevadensis	1,400 ± 300	6.8 ± 1.1	1,300 ± 400	6.5 ± 1.4	2,400 ± 300	9.5 ± 0.9	900 ± 100	2.0 ± 0.5
Grayia spinosa	1,200 ± 300	5.1 ± 1.0	200 ± 100	1.5 ± 0.5	900 ± 200	6.3 ± 1.2	700 ± 200	1.5 ± 0.4
Hymenoclea salsola	200 ± 100	0.2 ± 0.1	11,400 ± 2,500	5.6 ± 0.5	1,500 ± 300	1.7 ± 0.6	500 ± 300	0.9 ± 0.6
Thamnosma montana	900 ± 500	1.1 ± 0.5	200 ± 100	0.7 ± 0.3	400 ± 200	1.1 ± 0.5	100 ± 0	0.2 ± 0.2
Tetradymia spinosa	Tr	0.1 ± 0.1	100 ± 0	1.4 ± 0.8	100 ± 100	2.2 ± 0.6	100 ± 100	0.2 ± 0.2
Haplopappus cooperi	0	0.0	900 ± 500	1.1 ± 0.4	900 ± 300	2.5 ± 1.1	Tr	0.2 ± 0.2
Haplopappus larisifolius	0	0.0	100 ± 100	0.1 ± 0.1	0	0.0	0	0.0
Ambrosia dumosa	100 ± 100	0.1 ± 0.1	0	0.0	0	0.0	100 ± 100	0.1 ± 0.1
Eriogonum fasciculatum	0	0.0	Tr	0.1 ± 0.1	0	0.0	0	0.0
Acamptopappus shockleyi	100 ± 100	0.0	400 ± 400	0.3 ± 0.2	600 ± 300	1.0 ± 0.4	0	0.0
Subtotal	6,600 ± 800	27.6 ± 2.3	16,300 ± 2,600	25.1 ± 2.5	9,000 ± 700	31.8 ± 2.4	6,900 ± 1,100	26.0 ± 2.8
Herbaceous perennials:								
Machaeranthera tortifolia	300 ± 200	0.1 ± 0.1	400 ± 100	0.0	400 ± 200	0.1 ± 0.1	300 ± 200	0.3 ± 0.2
Sphaeralcea ambigua	0	0.0	200 ± 200	0.1 ± 0.1	0	0.0	100 ± 100	0.0
Eriogonum inflatum	2,800 ± 1,000	0.1 ± 0.1	2,500 ± 500	0.2 ± 0.1	2,800 ± 700	0.1 ± 0.1	0	0.0
Dyssodia cooperi	200 ± 200	0.0	0	0.0	100 ± 100	0.0	0	0.0
Subtotal	3,300 ± 1,000	0.2 ± 0.1	3,100 ± 500	0.3 ± 0.1	3,300 ± 800	0.2 ± 0.1	400 ± 100	0.3 ± 0.2
Grasses:								
Stipa speciosa	300 ± 200	0.2 ± 0.1	300 ± 200	Tr	800 ± 200	0.4 ± 0.1	0	0.0
Oryzopsis hymenoides	100 ± 100	0.1 ± 0.1	0	0.0	0	0.0	0	0.0
Subtotal	400 ± 200	0.3 ± 0.1	300 ± 200	Tr	800 ± 200	0.4 ± 0.1	0	0.0
Total live	10,300 ± 1,300	28.1 ± 2.4	19,700 ± 2,700	25.4 ± 2.5	13,100 ± 1,000	32.4 ± 2.4	7,300 ± 1,100	26.3 ± 2.8
Dead	2,400 ± 600	4.2 ± 0.4	2,100 ± 800	2.6 ± 0.4	2,400 ± 700	3.5 ± 0.4	1,200 ± 200	3.1 ± 0.4
Total	12,700 ± 1,400	32.3 ± 2.4	21,800 ± 2,800	28.0 ± 2.6	15,500 ± 1,300	35.9 ± 2.5	8,500 ± 1,100	29.4 ± 2.9

Table 28. Carbonate morphologies for soils on terrace sequences in Gold Valley

[See tables 21 and 24 for soil descriptions]

Terrace	Horizon	Maximum carbonate stage	Description	Carbonate percentage[1]
TA_0	C_2	--		--
TA_1	C_{3ca}	stage I	Weak pebble coatings on bottoms and sides	--
TA_2	C_{ca}	stage I-II	Continuous with some interpebble fillings	--
TA_3	C_{ca}	stage II-III	Plugged horizon with laminar horizons at depth	--
TB_0	C_{2ca}	stage I	Faint coatings on bottoms of pebbles	--
TB_1	C_{3ca}	stage I	Coatings on bottoms and sides of pebbles	--
TC_0	IIC_{3ca}	stage II-III	Not pedogenic; probably gully-bed cementation	10.4(7.3)
TC_1	C_{3ca}	stage I	Discontinuous coatings on bottoms of pebbles	6.1(8.1)
TC_2	C_{2ca}	stage I	Continuous coatings on sides and bottoms of pebbles	6.2(7.3)
TC_3	IIB_{32cab}	stage II	Continuous pebble coatings with interped filling; this carbonate horizon is associated with overlying younger material	--
TC_4	C_{ca}	stage IV	Laminar horizon over plugged horizon	--

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[1] Measured by Chittick method (M. N. Machette, written commun., 1983). Dolomite percentages are in parentheses.

Table 29. Description of soils for Greenwater, Furnace, and Kunze townsites and Greenwater controls C and D

[For abbreviations and nomenclature, see table 6]

Depth (cm)	Horizon	Texture	Dry color	Carbonate
		GREENWATER		
		Townsite		
0-7	A	gsl	10 YR 6/4	---
7-15	B_1	gscl	7.5 YR 6/6	---
15-35	B_{2t}	gscl	5 YR 4/6	---
35-75+	C_{ca}	--	----	stage III-IV
		Control C		
0-11	A	gls	10 YR 4/3	---
11-20	B_1	gsl	7.5 YR 6/4	---
20-38	B_{2t}	gscl	7.5 YR 5/4	---
38-65+	C_{ca}	---	----	stage II-III
		Control D		
0-6	A	gls	10 YR 7/3	---
6-17	C_1	gsl	7.5 YR 7/4	---
17-65+	C_{2ca}	gsl	7.5 YR 7/4	stage I
		FURNACE		
		Townsite		
0-9	A	gls	7.5 YR 6/4	---
9-25	B_1	gsl	7.5 YR 6/4	---
25-37	B_{2tca}	gsl	5 YR 6/4	stage I
37-48	B_{3ca}	gs	5 YR 6/4	stage I
48-65+	C_{ca}	gs	---	stage I
		KUNZE		
		Townsite		
0-7	A	gsl	7.5 YR 5/4	---
7-35	C_1	gsl	7.5 YR 6/5	---
35-65+	C_{2ca}	gsl	7.5 YR 6/5	stage I

Table 30. Penetration depths of disturbed and undisturbed soils in Greenwater and Furnace townsites

[All values are ±1 standard error of the mean. All pairs marked with an asterisk are significantly different at the $P < 0.05$ level, using a t-test]

Area measured	Years since disturbance	Penetration depth (cm)
	Greenwater	
Active road	0	1.5 ± 0.1
Abandoned road	73	6.7 ± 0.2*
Control C	---	9.2 ± 0.3*
Townsite A	73	7.5 ± 0.2*
Townsite B	73	9.9 ± 0.2
Control D	---	9.4 ± 0.2
Cleared area E	73	10.7 ± 0.2
Control F	---	11.4 ± 0.3
	Furnace	
Active road	0	4.6 ± 0.1*
Townsite A	73	9.4 ± 0.2*
Control B	---	11.2 ± 0.3

Table 31. Density and cover of perennial vegetation in disturbed sites A and B and control sites C and D at lower Greenwater townsite

[Density in number per hectare; cover in percent. All values are ±1 standard error of the mean. Tr: species was encountered in the transects]

Species	Townsite A		Townsite B		Control C		Control D	
	Density	Cover	Density	Cover	Density	Cover	Density	Cover
Shrubs:								
Lycium andersonii	300 ± 100	1.1 ± 0.4	300 ± 100	1.3 ± 0.5	1,200 ± 100	6.4 ± 0.8	800 ± 200	3.8 ± 1.1
Ephedra nevadensis	600 ± 100	1.8 ± 0.4	700 ± 200	3.4 ± 0.5	1,300 ± 200	4.6 ± 0.6	1,500 ± 200	4.0 ± 0.5
Menodora spinescens	400 ± 100	1.8 ± 0.4	300 ± 100	0.4 ± 0.2	2,300 ± 300	4.0 ± 0.4	2,500 ± 300	4.6 ± 1.2
Larrea tridentata	0	0.0	0	0.0	200 ± 100	4.0 ± 1.7	200 ± 100	3.7 ± 0.9
Grayia spinosa	400 ± 100	2.1 ± 0.8	200 ± 200	0.7 ± 0.5	1,100 ± 300	2.9 ± 0.9	700 ± 100	1.8 ± 0.2
Haplopappus sp.[1]	7,200 ± 1,500	7.5 ± 1.4	3,100 ± 200	3.9 ± 0.7	3,100 ± 900	2.9 ± 0.9	3,900 ± 700	5.1 ± 1.3
Tetradymia stenolepsis	Tr	0.0	100 ± 100	0.2 ± 0.2	100 ± 100	0.7 ± 0.3	400 ± 100	1.1 ± 0.7
Hymenoclea salsola	8,300 ± 600	10.0 ± 0.6	6,100 ± 400	9.5 ± 0.3	400 ± 200	0.5 ± 0.3	400 ± 200	0.7 ± 0.2
Thamnosma montana	700 ± 300	1.5 ± 0.8	300 ± 200	1.5 ± 0.6	500 ± 200	0.5 ± 0.3	400 ± 200	0.7 ± 0.3
Salazaria mexicana	0	0.0	200 ± 100	0.7 ± 0.4	0	0.0	100 ± 100	0.9 ± 0.6
Ambrosia dumosa	100 ± 100	0.2 ± 0.1	100 ± 100	0.0	Tr	0.0	0	0.0
Subtotal	18,000 ± 1,600	26.0 ± 2.0	11,400 ± 600	21.6 ± 1.4	10,200 ± 1,100	26.5 ± 2.3	10,900 ± 800	26.4 ± 2.5
Herbaceous perennials:								
Sphaeralcea ambigua	1,300 ± 200	0.2 ± 0.1	100 ± 100	0.1 ± 0.1	800 ± 100	0.1 ± 0.1	300 ± 200	Tr
Mirabilis bigelovii	600 ± 200	0.2 ± 0.1	Tr	0.0	100 ± 100	0.1 ± 0.1	100 ± 100	Tr
Dyssodia cooperi	1,000 ± 600	0.3 ± 0.1	500 ± 300	0.1 ± 0.1	Tr	0.0	900 ± 200	0.3 ± 0.2
Subtotal	2,900 ± 600	0.7 ± 0.2	600 ± 300	0.2 ± 0.1	900 ± 200	0.2 ± 0.1	1,300 ± 200	0.3 ± 0.2
Grass:								
Stipa speciosa	5,700 ± 400	3.7 ± 0.6	11,400 ± 800	6.1 ± 0.3	2,900 ± 700	1.4 ± 0.4	7,100 ± 500	3.0 ± 0.6
Total live	26,600 ± 1,900	30.4 ± 1.3	23,400 ± 1,300	27.9 ± 0.7	14,000 ± 1,200	28.1 ± 2.1	19,200 ± 1,400	29.7 ± 1.7
Dead	1,200 ± 400	3.7 ± 1.1	700 ± 200	1.5 ± 0.5	1,000 ± 200	3.5 ± 1.0	1,100 ± 200	2.9 ± 1.0
Total	27,800 ± 1,900	34.1 ± 1.7	24,100 ± 1,400	29.4 ± 0.9	15,000 ± 1,200	31.6 ± 2.3	20,300 ± 1,500	32.6 ± 2.0

[1] *Haplopappus* sp. includes *H. cooperi* with minor amounts of *H. laricifolius*.

Table 32. Density and cover of perennial vegetation in cleared area E and control site F at upper Greenwater townsite

[Density in number per hectare; cover in percent. All values are ±1 standard error of the mean. Tr: species was encountered in the transects; nd: no data]

Species	Cleared area E		Control F	
	Density	Cover	Density	Cover
Shrubs:				
Menodora spinescens	1,200 ± 500	2.4 ± 0.9	4,000 ± 700	7.4 ± 1.5
Lycium andersonii	300 ± 100	1.5 ± 0.8	1,500 ± 300	7.3 ± 1.3
Grayia spinosa	400 ± 200	0.5 ± 0.3	2,000 ± 200	4.6 ± 0.5
Haplopappus sp.[1]	5,200 ± 1,200	6.8 ± 0.9	5,300 ± 1,300	4.6 ± 0.8
Ephedra nevadensis	800 ± 100	4.2 ± 0.6	1,300 ± 300	4.3 ± 0.6
Thamnosma montana	600 ± 400	1.4 ± 0.6	700 ± 200	1.5 ± 0.8
Coleogyne ramosissima	0	0.0	300 ± 100	1.1 ± 0.7
Hymenoclea salsola	3,500 ± 600	7.2 ± 0.8	1,800 ± 400	0.6 ± 0.4
Tetradymia stenolepsis	Tr	0.1 ± 0.1	Tr	0.0
Eurotia lanata	0	0.0	100 ± 100	0.0
Salazaria mexicana	Tr	0.1 ± 0.1	0	0.0
Subtotal	12,000 ± 1,500	24.2 ± 1.9	17,000 ± 1,600	31.4 ± 2.6
Herbaceous perennials:				
Sphaeralcea ambigua	1,500 ± 300	0.1 ± 0.1	800 ± 300	0.1 ± 0.1
Machaeranthera tortifolia	100 ± 100	Tr	0	Tr
Subtotal	1,600 ± 300	0.1 ± 0.1	800 ± 300	0.1 ± 0.1
Grass:				
Stipa speciosa	14,300 ± 900	6.1 ± 0.9	4,900 ± 900	1.3 ± 0.4
Total live	27,900 ± 1,000	30.4 ± 1.2	22,700 ± 2,000	32.8 ± 1.6
Dead	1,500 ± 400	nd	1,100 ± 200	nd
Total	29,400 ± 1,100	--	23,800 ± 2,000	--

[1] *Haplopappus* sp. includes *H. cooperi* with minor amounts of *H. laricifolius*.

Table 33. Calculated dry-weight biomass for abundant woody perennials and the perennial grass *Stipa* in lower Greenwater townsite

[Biomass in kilograms per hectare. All values are ±1 standard error of the mean]

Species	Townsite A	Townsite B	Control C	Control D
Menodora spinescens	400 ± 200	200 ± 100	1,600 ± 400	1,000 ± 300
Larrea tridentata	0	0	1,100 ± 300	1,100 ± 600
Lycium andersonii	500 ± 200	500 ± 200	800 ± 100	1,000 ± 300
Haplopappus sp.[1]	3,300 ± 1,100	600 ± 200	700 ± 300	2,100 ± 500
Ephedra nevadensis	200 ± 100	400 ± 100	400 ± 100	400 ± 100
Grayia spinosa	300 ± 300	200 ± 200	500 ± 100	400 ± 100
Hymenoclea salsola	5,300 ± 1,200	2,500 ± 600	100 ± 100	100 ± 100
Thamnosma montana	200 ± 100	100 ± 0	100 ± 0	100 ± 0
Stipa speciosa	100	100 ± 100	100	100

[1] *Haplopappus* sp. includes *H. cooperi* with minor amounts of *H. laricifolius*.

Table 34. Calculated dry-weight biomass for abundant woody perennials and the perennial grass *Stipa* in upper Greenwater townsite

[Biomass in kilograms per hectare. All values are ±1 standard error of the mean]

Species	Cleared Area E	Control F
Mendora spinescens	1,000 ± 500	6,600 ± 2,100
Lycium andersonii	500 ± 200	2,600 ± 700
Haplopappus sp.[1]	1,500 ± 700	1,900 ± 900
Grayia spinosa	300 ± 200	1,000 ± 200
Hymenoclea salsola	2,100 ± 600	900 ± 300
Ephedra nevadensis	600 ± 200	600 ± 200
Thamnosma montana	100 ± 100	200 ± 100
Stipa speciosa	100 ± 100	100

[1] *Haplopappus* sp. includes *H. cooperi* with minor amounts of *H. laricifolius*.

Table 35. Density and biomass of perennial vegetation on 16 house pads of varying size at Greenwater townsite

[Area per house pad = 50 m^2 ± 6.5 m^2; all values are ±1 standard error of the mean. Biomass data obtained from measurements in other disturbed areas of the townsite]

Species	Density (number/ha)	Biomass (kg/ha)
Shrubs:		
Hymenoclea salsola	12,600 ± 1,400	8,100 ± 1,900
Haplopappus sp.[1]	900 ± 300	400 ± 200
Lycium andersonii	500 ± 100	800 ± 200
Ephedra nevadensis	300 ± 100	100 ± 0
Grayia spinosa	200 ± 100	200 ± 100
Larrea tridentata	100 ± 100	600 ± 600
Subtotal	14,600 ± 1,700	
Herbaceous perennials:		
Sphaeralcea ambigua	3,000 ± 300	
Eriogonum inflatum	900 ± 500	
Dyssodia cooperi	200 ± 200	
Mirabilis bigelovii	100 ± 100	
Subtotal	4,200 ± 600	
Grass:		
Stipa speciosa	3,700 ± 800	100
Total live	22,500 ± 1,800	
Dead	800 ± 200	
Total	23,300 ± 1,900	

[1] *Haplopappus* sp. includes *H. cooperi* and *H. laricifolius*.

Table 36. Density and cover of perennial vegetation at Furnace and Kunze townsites and at Furnace control

[Density in number per hectare; cover in percent. All values are ±1 standard error of the mean]

Species	Furnace control		Furnace townsite		Kunze townsite	
	Density	Cover	Density	Cover	Density	Cover
Shrubs:						
Menodora spinescens	4,600 ± 500	8.1 ± 0.8	100 ± 100	0.1 ± 0.1	200 ± 200	0.3 ± 0.3
Larrea tridentata	300 ± 200	4.8 ± 1.2	100 ± 100	0.5 ± 0.4	0	0.0
Lycium andersonii	1,100 ± 300	4.4 ± 1.0	700 ± 200	5.9 ± 1.3	400 ± 100	3.5 ± 1.3
Grayia spinosa	700 ± 300	1.8 ± 0.6	300 ± 100	0.2 ± 0.1	100 ± 100	0.5 ± 0.3
Haplopappus sp.[1]	1,100 ± 500	1.1 ± 0.4	100 ± 100	0.1 ± 0.1	0	0.0
Ephedra nevadensis	300 ± 100	0.9 ± 0.3	100 ± 0	0.4 ± 0.3	100 ± 100	0.5 ± 0.3
Salazaria mexicana	200 ± 200	0.4 ± 0.3	0	0.0	100 ± 100	0.6 ± 0.4
Hymenoclea salsola	100 ± 100	0.0	2,900 ± 400	4.4 ± 0.7	7,600 ± 1,200	14.5 ± 1.4
Thamnosma montana	100 ± 100	0.2 ± 0.1	200 ± 100	0.5 ± 0.2	100 ± 100	0.1 ± 0.1
Tetradymia spinosa	100 ± 100	0.2 ± 0.2	0	0.0	Tr	0.0
Eriogonum fasciculatum	0	0.0	0	0.0	100 ± 100	0.6 ± 0.5
Acamptopappus shockleyi	100 ± 100	0.0	0	0.0	100 ± 100	0.0
Subtotal	8,700 ± 800	21.9 ± 2.0	4,100 ± 500	12.1 ± 1.6	8,800 ± 1,200	20.6 ± 0.7
Herbaceous perennials:						
Dyssodia cooperi	200 ± 200	0.0	2,400 ± 2,200	0.5 ± 0.4	7,500 ± 3,200	2.0 ± 0.7
Sphaeralcea ambigua	200 ± 200	0.0	200 ± 200	0.1 ± 0.1	700 ± 400	0.0
Mirabilis bigelovii	100 ± 100	0.0	0	0.0	0	0.0
Subtotal	500 ± 300	0.0	2,600 ± 2,200	0.6 ± 0.4	8,200 ± 3,200	2.0 ± 0.7
Grasses:						
Stipa speciosa	2,300 ± 400	0.5 ± 0.1	17,700 ± 1,700	8.9 ± 1.2	1,700 ± 700	0.8 ± 0.3
Sitanian hystrix	0	0.0	0	0.0	800 ± 100	0.1 ± 0.1
Subtotal	2,300 ± 400	0.5 ± 0.1	17,700 ± 1,700	8.9 ± 1.2	2,500 ± 800	0.9 ± 0.3
Total live	11,500 ± 500	22.4 ± 1.9	27,400 ± 1,400	21.6 ± 1.9	19,500 ± 3,500	23.5 ± 2.2
Dead	1,900 ± 200	1.6 ± 0.3	700 ± 300	1.9 ± 0.4	---	---
Total	13,400 ± 500	24.0 ± 1.9	25,100 ± 1,600	23.5 ± 1.9	---	---

[1] *Haplopappus* sp. includes *H. cooperi* and *H. laricifolius*.

Table 37. Calculated dry-weight biomass of abundant woody perennials and the perennial grass *Stipa* at Furnace and Kunze townsites and Furnace control

[Biomass in kilograms per hectare. All values are ±1 standard error of the mean]

Species	Furnace control	Furnace townsite	Kunze townsite
Menodora spinescens	9,500 ± 900	100 ± 100	100 ± 100
Lycium andersonii	1,500 ± 400	1,300 ± 300	900 ± 300
Larrea tridentata	1,200 ± 700	400 ± 400	0
Grayia spinosa	400 ± 200	200 ± 100	400 ± 100
Haplopappus sp.[1]	400 ± 200	100 ± 0	0
Ephedra nevadensis	200 ± 100	100 ± 100	100 ± 0
Hymenoclea salsola	100 ± 0	2,300 ± 500	3,600 ± 800
Thamnosma montana	100 ± 0	100 ± 0	0
Stipa speciosa	100 ± 100	100 ± 100	100

[1] *Haplopappus* sp. includes *H. cooperi* and *H. laricifolius*.

Table 38. Concentration of plant macrofossils found in packrat middens collected near Greenwater townsite

[Values given in logarithm of number of identifiable fragments per kilogram of midden matrix; --, species not present]

Midden No.-------------------	G4a	G7	G8	G15	G11a	G6b	G9d	G11b	G11c	G9b	G4b2	G4b1	G6c	Principal components scores	
USGS Dating Lab No.----------	--	--	--	--	1531	1400	1403	1530	1534	1402	1398	1397	1401		
Plant species														X-axis	Y-axis
Coleogyne ramosissima	1.10	3.52	0.90	1.03	2.00	1.13	--	--	--	--	--	--	--	-0.59	0.75
Tetradymia spinosa	1.58	--	.90	--	1.70	--	--	--	--	--	--	--	--	-.96	.46
Erodium sp.	1.51	--	--	1.34	--	1.13	--	--	--	--	--	--	--	--	--
Salazaria mexicana	--	1.40	--	--	--	1.13	--	--	--	--	--	--	--	--	--
Machaeranthera tortifolia	.80	--	1.20	--	--	--	--	1.51	--	--	--	--	--	-1.00	.09
Atriplex confertifolia	--	--	--	--	1.70	--	--	2.29	--	--	--	--	--	-.96	.86
Eriogonum fasciculatum	.80	--	--	--	2.18	--	2.74	2.90	.99	--	--	--	--	-.55	1.38
Grayia spinosa	1.58	2.55	2.54	--	2.00	1.13	2.08	1.51	--	1.04	--	--	--	-.22	.89
Hymenoclea salsola	1.10	2.91	.90	2.40	2.18	1.43	--	3.26	3.38	3.08	--	--	--	.30	.97
Salvia dorii	1.10	--	--	--	--	--	1.08	--	1.76	2.26	--	--	--	-.83	-.41
Brickellia watsonii	3.41	--	--	--	--	--	2.38	--	--	1.72	--	--	--	-.77	.05
Larrea tridentata	2.83	1.08	4.36	3.96	2.65	3.44	4.78	3.23	2.90	4.57	3.54	3.46	3.63	2.23	-1.63
Eurotia lanata	3.34	3.51	3.70	3.03	3.02	2.91	2.68	3.30	2.40	1.72	1.76	2.94	3.33	1.65	.25
Haplopappus laricifolius	3.39	4.36	1.38	3.39	3.52	3.20	4.58	4.17	3.73	4.24	2.38	3.35	3.03	2.17	.44
Lycium andersonii	2.92	3.24	2.20	1.88	2.78	2.33	3.08	2.60	2.90	2.65	1.54	3.25	2.48	1.32	.17
Ephedra sp.	3.26	2.24	--	2.03	3.08	2.03	2.76	3.54	3.53	--	2.46	2.60	2.68	1.12	1.37
Sphaeralcea ambigua	1.88	--	1.20	2.64	2.54	2.47	2.08	2.60	2.70	1.81	3.00	3.35	2.00	1.01	-.65
Thamnosma montana	2.98	1.69	--	1.03	1.70	1.43	2.08	2.30	1.29	--	1.36	--	2.11	.14	1.36
Amsinckia cf. *tessellata*	1.40	1.08	2.08	1.63	2.30	2.13	2.11	--	.99	1.79	2.11	1.89	1.11	--	--
Thysanocarpus sp.	1.10	--	--	1.03	--	1.13	1.56	2.00	--	1.51	3.20	2.91	1.11	--	--
Dithyrea californica	--	--	1.38	--	--	--	1.98	--	.99	1.04	--	1.08	--	--	--
Ambrosia dumosa	.80	--	1.38	1.03	--	--	1.86	--	--	1.51	--	2.23	--	-.65	-1.57
Atriplex canescens	3.01	--	--	--	--	1.13	--	--	--	--	--	1.89	--	-.83	-.07
Castilleja sp.	--	--	--	--	--	--	--	--	--	--	--	3.57	--	--	--
Encelia virginensis	--	--	--	1.03	--	1.43	2.59	--	--	--	--	--	1.71	-.70	-.68
cf. *Gilia* sp.	.80	--	1.20	1.63	--	--	1.38	2.66	1.59	--	--	--	--	--	--
Haplopappus cooperi	--	2.35	--	3.31	--	--	--	--	--	2.10	--	1.88	--	-.59	-1.78
Echinocactus polycephalus	1.94	--	--	--	2.00	--	--	1.51	--	--	1.54	1.08	--	-.65	.69
Lepidium cf. *fremontii*	--	1.79	--	1.34	2.30	--	2.72	--	1.89	1.79	1.61	3.72	--	.02	-1.16
Opuntia basilaris	--	--	1.20	1.94	--	--	--	--	--	--	1.91	1.89	2.04	-.53	-1.90
cf. *Stephanomeria exigua*	--	--	--	--	2.30	--	--	--	.99	--	--	--	--	--	--
cf. *Menodora spinescens*	--	1.40	--	--	--	--	--	--	--	--	--	--	--	--	--
Graminsae (cf. *Stipa speciosa*)	--	--	2.10	1.30	--	--	--	--	--	--	--	--	--	--	--
Bromus rubens	--	1.40	--	--	--	--	--	--	--	--	--	--	--	--	--
Number of species-------------	22	15	16	19	17	16	18	15	15	15	12	16	11		
Midden age[1]-------------------	M	M	M	M	M	270 ±70	290 ±50	400 ±45	740 ±120	1340 ±40	2105 ±45	2125 ±50	2235 ±35		
Midden elevation (m)----------	1350	1360	1340	1380	1410	1350	1350	1410	1410	1350	1350	1350	1350		
Aspect------------------------	NE.	E.	E.	SE.	E.	NE.	NE.	E.	E.	E.	NE.	NE.	NE.		

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[1] Units are ^{14}C yr B.P. ± standard deviation; M = modern (less than 250 yr).

Table 39. Plant assemblages occurring on surfaces differentiated by carbonate morphology in Death Valley National Monument

[See tables 7, 8, 22, 23, and 25 for quantitative data on the plant assemblages, and tables 6, 21, and 24 for descriptions of soils]

CARBONATE MORPHOLOGY	Wood Canyon		Gold Valley		AGE
	Granite	Metasedimentary	Lower terraces	Upper terraces	
Stage I	Mixed *Ephedra*-*Lycium*-*Grayia* *Coleogyne*-*Ephedra*	*Acamptopappus*-*Grayia*-*Lycium*	*Hymenoclea* (local *Larrea*) *Larrea*-*Ephedra*	*Hymenoclea*-*Ephedra* (local *Coleogyne*) *Grayia*-*Coleogyne*-*Lycium* *Ephedra*-*Coleogyne*-*Lycium*	Holocene(?)
Stage II		*Coleogyne*-*Lycium*-*Ephedra*	*Ambrosia*-*Lycium*-*Larrea*	*Coleogyne*-*Larrea*	latest Pleistocene(?)
Stage III	*Coleogyne*		*Ambrosia*-*Larrea*		late Pleistocene(?)
Stage IV				*Coleogyne*-*Larrea*	middle(?) and (or) late(?) Pleistocene

Table 40. Summary of estimated recovery times for compacted soils at four townsites

[Values based on a linear model of recovery and a comparison of soil properties in active roads, abandoned sites, and undisturbed sites]

Townsite	Recovery time (in years) based on:		
	Penetration depth	Bulk density	Peak shear strength
Greenwater (site A)	100	--	--
Greenwater (abandoned road)	110	--	--
Furnace	100	--	--
Skidoo	80	90	--
Gold Valley (western townsite)	120	120	90
Gold Valley (eastern townsite)	90	--	--

Table 41. Dominant species occurring on surfaces differentiated by degree of disturbance for all townsites

[Dominant species defined as those species contributing 3 percent or more cover, in order of decreasing contribution of cover. See tables 12, 27, 31, 32, and 36]

Townsite	Compacted sites	Noncompacted sites	Control sites
Skidoo	Grayia-Chrysothamnus-Ephedra	Artemisia-Grayia-Ephedra	Grayia-Ephedra-Artemisia
Gold Valley	Ephedra-Hymenoclea-Coleogyne-Lycium	Ephedra-Grayia-Lycium-Coleogyne	Coleogyne-Ephedra-Lycium-Grayia-Larrea[1]
Greenwater:			
Sites A, B, C, D	Hymenoclea-Haplopappus-Stipa	Hymenoclea-Stipa-Haplopappus-Ephedra	Lycium-Ephedra-Menodora-Larrea[2]
Sites E, F	--	Hymenoclea-Haplopappus-Stipa-Ephedra	Menodora-Lycium-Grayia-Haplopappus-Ephedra
Furnace and Kunze	Hymenoclea-Stipa-Lycium	--	Menodora-Larrea-Lycium

[1] Larrea contributed less than 3.0 percent cover on terrace TC_2.

[2] Haplopappus and Stipa contributed 5.1 and 3.0 percent cover, respectively, in control site D but less than 3.0 percent in control site C.

Table 42. Dominant species occurring on surfaces differentiated by degree of disturbance along segments of the Skidoo pipeline corridor

[Dominant species defined as those species contributing 3 percent or more cover, in order of decreasing contribution of cover. See tables 15, 16, 18, and 20]

Area	Pipeline segments	Control sites
Harrisburg Flats:	Chrysothamnus-Grayia	Grayia-Chrysothamnus
Sand Dune	Hymenoclea-Ephedra	Hymenoclea-Ephedra
Rocky Slope	Haplopappus-Ephedra-Chrysothamnus	Ephedra-Chrysothamnus-Lycium-Haplopappus
Wood Canyon:		
Flows A and C	Coleogyne[1]-Acamptopappus-Chrysothamnus-Haplopappus	Coleogyne-Lycium-Ephedra-Grayia
Flow B	Acamptopappus-grasses	Acamptopappus-Grayia-Lycium
Nemo Crest	Grasses	Coleogyne-Grayia-Ephedra
Wildrose Canyon:		
Segment A	Coleogyne-Tetradymia	Coleogyne[2]-Ephedra
Segments B, C, D	Artemisia	Artemisia[3]-Coleogyne

[1] Coleogyne had 1.3 and 12.0 percent cover on the pipeline segments through flows A and C, respectively.

[2] The difference in cover contributed by Coleogyne between the pipeline segment and control site was 18.3 percent.

[3] The differences in cover contributed by Artemisia between the pipeline segments and control sites were 9.6, 11.2, and -6.3 percent, respectively, for segments B, C, and D.

Table 43. Hybrid correlation matrix based on cover and density in townsites containing Larrea tridentata

Correlations based on density -- lower left; correlations based on cover -- upper right

[1]Site	1*	2	3*	4*	5	6*	7*	8	9	10*	11	12*	13*	14	15	16*	17*	18
1*		0.34	0.49	0.70	0.29	0.32	0.62	0.41	0.45	0.58	0.22	0.21	0.70	0.07	0.35	0.42	0.42	0.07
2	.90		.07	.02	.84	.00	.02	.55	.42	.00	.23	-.06	.09	.39	.51	.14	.43	.33
3*	.59	.54		.28	.04	.14	.29	.20	.28	.37	.13	-.08	.16	-.11	.22	.30	.40	-.08
4*	.97	.84	.58		.02	.53	.77	-.03	.15	.66	-.05	.45	.84	-.11	-.13	.14	-.06	-.10
5	.88	.95	.71	.85		-.09	-.05	.40	.36	-.06	-.01	-.11	.03	.38	.38	.06	.14	.59
6*	.44	.29	.22	.55	.31		.91	.21	.41	.92	.31	.72	.45	.04	-.04	.46	.22	-.10
7*	.88	.74	.49	.94	.74	.79		.18	.34	.92	.18	.76	.67	-.07	.03	.54	.25	-.09
8	.53	.57	.31	.49	.54	.56	.59		.88	.35	.85	.04	.32	.77	.60	.41	.58	.21
9	.82	.75	.49	.79	.75	.59	.81	.88		.59	.79	.00	.33	.72	.34	.26	.42	.10
10*	.91	.79	.52	.93	.79	.71	.95	.73	.92		.40	.55	.58	.10	.04	.48	.31	-.10
11	.53	.53	.28	.53	.51	.68	.66	.98	.88	.76		.05	.25	.72	.51	.38	.57	.09
12*	.12	.01	-.03	.25	.00	.51	.40	-.06	.08	.19	.06		.47	-.03	-.01	.56	.09	-.02
13*	.97	.86	.53	.98	.85	.50	.91	.50	.81	.92	.53	.28		.12	.12	.27	.09	.00
14	.35	.35	.12	.33	.31	.18	.33	.74	.64	.43	.74	-.05	.35		.22	.01	.09	.16
15	.01	.20	.01	-.06	.13	-.17	-.09	.01	-.06	-.09	-.04	-.11	-.05	-.09		.71	.84	.68
16*	.02	-.07	-.03	.18	-.07	.65	.40	-.04	-.06	.15	.11	.63	.08	-.12	.12		.78	.43
17*	.13	.22	.17	.11	.21	.25	.20	.17	.12	.13	.16	.08	.08	-.08	.80	.47		.29
18	-.09	.16	.02	-.11	.11	.03	-.08	-.01	-.15	-.15	-.04	.00	-.13	-.12	.26	.26	.46	
19*	.28	.14	.09	.44	.15	.76	.63	.13	.17	.42	.27	.68	.35	.00	-.06	.92	.28	.12
Site No.	1*	2	3*	4*	5	6*	7*	8	9	10*	11	12*	13*	14	15	16*	17*	18

*disturbed sites

[1]

Site No.	Site name
(1-5)	Wahmonie townsite (Webb and Wilshire, 1980):
1.	Streets and avenues
2.	Southwest control
3.	Old main road
4.	Townsite
5.	Northeast control

Site No.	Site name
(6-14, 19)	Greenwater district:
6.	Townsite A
7.	Townsite B
8.	Control C
9.	Control D
10.	Cleared area E
11.	Control F
19.	House pads
12.	Kunze townsite
13.	Furnace townsite
14.	Furnace control

Site No.	Site name
(15-18)	Gold Valley townsite:
15.	Lower control (TC_2)
16.	Western townsite
17.	Eastern townsite
18.	Upper control (TC_3)

Table 44. Amount of variance explained by the first three axes of the principal-components solution for sites in Larrea-dominated assemblages

[Values in percent. See table 43 for location of site numbers]

	Cumulative variance					
	Cover			Density		
Site No.	X	Y	Z	X	Y	Z
All	36	59	70	49	65	77
1	55	57	59	84	87	88
2	18	51	51	71	77	88
3	16	16	20	33	36	42
4	27	69	69	87	87	87
5	9	40	40	72	78	88
6	45	74	75	47	77	84
7	56	96	97	91	96	97
8	55	83	94	56	61	62
9	56	67	91	85	92	92
10	64	88	90	95	95	96
11	42	57	75	61	62	64
12	22	52	54	6	55	64
13	42	58	59	85	86	86
14	15	43	84	25	37	42
15	31	68	92	0	2	73
16	50	50	78	4	94	94
17	42	57	73	5	24	83
18	5	31	57	0	8	43
19	-	-	-	20	89	92

Table 45. Correlation-coefficient matrix based on cover for sites in the Panamint Range

[1]Site No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	1.00	0.88	0.74	0.76	0.31	0.58	0.16	0.09	-0.01	.18	-0.05	0.24	-0.02	0.38	-0.10	0.10	0.13	0.07	-0.08	0.24	-0.07	0.06	-0.11	-0.07	-0.10	-0.10	-0.10	-0.14
2		1.00	.79	.94	.35	.73	.16	.05	-.02	.17	-.07	.26	.00	.55	-.08	.10	.21	.11	-.06	.34	-.06	.06	-.09	-.06	-.08	-.08	-.09	-.12
3			1.00	.83	.80	.92	.35	.24	.24	.54	.27	.24	-.02	.36	-.09	.13	.13	.11	.01	.26	-.07	.10	-.06	-.07	-.10	-.09	-.11	-.16
4				1.00	.38	.73	.32	.23	.10	.36	.05	.38	.04	.54	-.06	.21	.23	.11	-.07	.40	-.02	.17	-.08	-.01	-.07	-.06	-.08	-.11
5					1.00	.86	.15	.04	.30	.58	.46	.05	-.05	.13	-.07	.00	.00	.08	.10	.06	-.09	-.01	.01	-.08	-.07	-.05	-.07	-.10
6						1.00	.14	.01	.19	.51	.33	.23	-.03	.46	-.09	.04	.15	.15	.06	.24	-.09	.00	-.03	-.09	-.08	-.08	-.09	-.13
7							1.00	.98	.33	.36	.14	.17	.01	-.02	-.03	.18	.00	-.02	-.08	.10	-.00	.17	-.09	-.02	-.09	-.08	-.10	-.13
8								1.00	.33	.35	.14	.18	.03	-.07	-.01	.21	.00	-.03	-.08	.09	.05	.20	-.09	.00	-.08	-.07	-.09	-.12
9									1.00	.74	.57	.15	.09	.00	.15	.05	-.02	.06	.07	.02	-.03	.06	-.07	-.08	-.10	-.10	-.11	-.16
10										1.00	.78	.45	.25	.34	.02	.20	.04	.04	-.01	.14	.02	.15	-.09	-.07	-.13	-.11	-.13	-.19
11											1.00	.41	.65	.50	.20	.24	.24	.29	.28	.24	.14	.17	-.01	-.04	-.12	-.09	-.13	-.10
12												1.00	.15	.53	.62	.84	.74	.28	.07	.81	.64	.76	-.00	-.24	-.12	.00	-.08	.20
13													1.00	.68	.06	.07	.10	.15	.14	.11	.01	.03	-.03	-.03	-.06	-.05	-.07	-.08
14														1.00	.12	.22	.34	.19	.03	.40	.09	.13	-.09	-.04	-.11	-.09	-.11	-.07
15															1.00	.85	.73	.18	.12	.71	.83	.87	.10	.38	-.06	.09	.01	.44
16																1.00	.78	.20	.05	.83	.89	.98	.05	.38	-.10	.06	-.03	.37
17																	1.00	.71	.56	.97	.62	.72	.19	.32	-.02	.09	.00	.34
18																		1.00	.95	.64	.05	.09	.27	.09	.07	.07	.02	.07
19																			1.00	.47	-.05	-.03	.42	.18	-.23	.21	.18	.17
20																				1.00	.64	.77	.20	.36	.01	.12	.03	.35
21																					1.00	.89	.03	.34	-.09	.06	-.02	.38
22																						1.00	.05	.40	-.09	.08	-.01	.40
23																							1.00	.90	.94	.95	.92	.83
24																								1.00	.87	.94	.89	.95
25																									1.00	.98	.98	.81
26																										1.00	.98	.89
27																											1.00	.87
28																												1.00

[1]Site No.	Site name
(1-4)	Skidoo townsite:
1.	Montgomery Street
2.	Montgomery Street control
3.	1st-2nd Streets
4.	1st-2nd Streets control
(5-10)	Skidoo pipeline on Harrisburg Flats:
5.	Harrisburg Flats pipeline
6.	Harrisburg Flats control
7.	Sand dune pipeline
8.	Sand dune control
9.	Rocky slope pipeline
10.	Rocky slope control
(11-16)	Wood Canyon segment of Skidoo pipeline:
11.	Flow A pipeline
12.	Flow A control
13.	Flow B pipeline
14.	Flow B control
15.	Flow C pipeline
16.	Flow C control

Site No.	Site name
(17-20)	Nemo Crest segment of Skidoo pipeline:
17.	Downslope control
18.	Pipeline segment
19.	Abandoned road
20.	Upslope control
(21-28)	Wildrose Canyon segment of Skidoo pipeline:
21.	Segment A pipeline
22.	Segment A control
23.	Segment B pipeline
24.	Segment B control
25.	Segment C pipeline
26.	Segment C control
27.	Segment D pipeline
28.	Segment D control

Table 46. Cumulative variance explained by the first three axes of the principal-components solution for sites in the Panamint Range

[Values in percent. See table 45 for locations of site numbers]

Site	X	Y	Z
Total	26	48	63
1	11	34	54
2	16	42	67
3	20	57	91
4	24	52	75
5	7	28	52
6	16	48	82
7	4	14	15
8	3	9	10
9	4	13	13
10	15	40	45
11	18	28	28
12	71	73	80
13	4	6	6
14	23	37	39
15	49	54	82
16	72	72	92
17	72	73	82
18	21	22	22
19	10	15	16
20	85	85	89
21	43	47	76
22	63	64	85
23	8	68	94
24	23	84	94
25	2	61	97
26	6	70	97
27	3	65	96
28	19	87	91

Table 47. Perennial vegetation found at all sites

[See text for locations, elevations, and quantitative data. All Latin names from Munz (1974) and Benson and Darrow (1981). Common names from various sources including Jaeger (1941), Munz (1974), Beatley (1976), Kay and others (1977), and Benson and Darrow (1981); Abbreviations: x, found on the site described in the text; h, found on surrounding hillslopes; hl, found on surrounding limestone hillslopes; xn, not on the site, but nearby on similar surface; -, not present]

Species	Common name	Wood Canyon debris flows						
		1	2	3	4	A	B	C
Acamptopappus shockleyi Gray	Shockley Goldenhead	x	x	x	-	x	x	x
Acamptopappus sphaerocephalus (Harv & Gray) Gray	Goldenhead	-	-	-	-	-	-	-
Ambrosia dumosa (Gray) Payne	Burrobush	-	-	-	-	-	-	-
Arabis pulchra Jones	Prince's rock-cress	-	-	-	-	-	-	-
Arenaria macradenia Wats. var. macradenia	Desert sandwort	-	-	-	-	-	-	-
Artemisia spinescens D.C. Eat	Budsage	-	-	-	-	x	x	x
Artemisia tridentata Nutt. ssp. tridentata	Great Basin sage	x	x	xn	x	xn	x	x
Astragalus lentiginosus Dougl	Dapple-pod	x	xn	xn	-	xn	xn	xn
Atriplex canescens (Pursh) Nutt ssp. canescens	Four-wing saltbush	x	xn	xn	xn	-	-	-
Atriplex confertifolia (Torr & Frem.) Wats	Shadscale	-	-	-	-	-	-	-
Brickellia arguta Rob	Spear-leaved brickellia	-	-	-	-	-	-	-
Brickellia oblongifolia Nutt. var. linfolia (D.C. Eaton) Rob	Pinon brickellia	-	-	-	-	-	-	-
Castilleja chromosa A. Nels	Desert paintbrush	x	xn	x	x	x	x	x
Chrysothamnus nauseosus var. mohavensis (Greene) Hall and Clem	Rubber rabbitbrush	x	-	-	x	x	x	x
Chrysothamnus teretifolius (Our. & Hilg.) Hall	Roundleaf rabbitbrush	x	-	-	x	xn	xn	x
Chrysothamnus viscidiflorus (Hook:) Nutt	Green rabbitbrush	x	-	-	-	x	x	x
Coleogyne ramosissima Torr	Blackbrush	x	x	x	x	x	x	x
Cowania mexicana DiDon var. stansburiana (Torr) Jeps	Cliffrose	-	-	-	-	-	-	-
Dalea fremontii Torr var. minutifolia (Parish) L. Benson	Indigo bush	-	-	-	-	x	x	x
Dyssodia cooperi Gray	Cooper dyssodia	-	-	-	-	-	-	-
Echinocactus polycephalus Engelm. S. Bigel	Barrel cactus	-	-	-	-	-	-	-
Echinocereus engelmanii (Parry) Lem	Engelman's hedgehog cactus	-	xn	x	-	-	-	-
Encelia virginensis A. Nels. ssp. actoni	Brittlebush	-	-	-	-	-	-	-
Ephedra funerea Cov. & Mort	Death Valley ephedra	-	-	-	-	-	-	-
Ephedra nevadensis Wats	Mormon tea	-	x	x	x	x	x	x
Ephedra viridis Cov. var. viridis	Green ephedra	h	h	h	x	-	xn	x
Eriogonum fasciculatum Benth	California buckwheat	x	x	x	x	-	xn	x
Eriogonum heermani. Dur. & Hilg	Heerman buckwheat	x	-	-	xn	x	x	-
Eriogonum inflatum Torr & Frem	Desert trumpet	x	x	x	-	x	xn	xn
Eriogonum saxatile Wats	Rock buckwheat	x	-	-	x	-	-	-
Eurotia lanata	Winterflat	-	xn	x	-	x	x	x
Grayia spinosa (Hook) Moq	Spiny hopsage	x	x	x	x	x	x	x
Gutierrezia microcephala (DC.) Gray	Matchweed	x	-	-	-	xn	xn	-
Haplopappus cooperi (Gray) Hall	Goldenbush	-	x	x	-	x	x	x
Haplopappus laricifolius Gray	Turpentine bush	-	-	-	-	-	-	-
Haplopappus linearifolius DC	Linear-leaf goldenbush	-	-	-	-	-	-	-
Hilaria jamesii (Torr.) Benth	Galleta grass	-	x	x	x	-	-	-
Hymenoclea salsola T & G var. salsola	Cheesebush	x	x	-	-	x	x	x
Juniperus osteosperma (Torr.) Little	Utah juniper	-	-	-	xn	-	-	-
Krameria parvifolia Benth	Range ratany	-	-	-	-	-	-	-
Larrea tridentata (Sesse & Moc. ex DC.) Cov	Creosote bush	-	-	-	-	xn	xn	xn
Lepidium fremontii Wats	Desert alyssum	-	-	-	-	-	-	-
Leptodactylon pungens (Torr.) Rydb. ssp. halli (Parish) Mason	Prickly gilia	-	-	-	-	-	-	-
Lupinus excubitus Jones var. excubitus	Adonis lupine	x	-	-	-	-	-	-
Lycium andersonii Gray	Anderson's thornbush	x	x	x	x	x	x	x
Machaeranthera tortifolia (Gray) Crong. & Keck	Mojave aster	x	xn	x	-	x	x	x
Menodora spinescens Gray	Spiny menodora	-	-	-	-	-	-	-
Mirabilis bigelovii var. retrorsa (Heller) Munz	Desert four o'clock	-	-	-	-	-	-	-
Mirabilis froebelii (Behr) Greene var. froebelii	Giant four o'clock	x	-	-	-	xn	x	xn
Opuntia acanthocarpa Engelm. and Bigel	Buckhorn cholla	-	-	-	-	-	-	-
Opuntia basilaris Engelm. and Bigel	Beavertail cactus	x	x	x	x	xn	xn	xn
Opuntia bigelovii Engelm. var bigelovii	Silver cholla	-	-	-	-	-	-	-
Oryzopsis hymenoides (R & S) Ricker	Indian ricegrass	xn	x	x	x	x	x	x
Oryzopsis webberi (Thurb.) Benth. ex Vasey	Ricegrass	-	x	x	x	-	-	-
Penstemon floridus Bdg. ssp. austinii (Eastw) Keck	Inyo beard-tongue	x	-	-	-	-	-	-
Penstemon fruticiformis Cov. ssp. fruticiformis	Death Valley penstemon	x	-	-	-	-	-	-
Petalonyx nitidus Wats	Sandpaper plant	-	-	-	-	-	-	-
Pinus monophylla Torr & Frem	One-leaf pinon pine	h	h	h	h	-	-	-
Salazaria mexicana Torr	Paperbag bush	x	x	xn	-	-	-	-
Salvia dorii (Kell.) Abram	Purple sage	x	-	-	-	-	-	-
Senecio douglasii DC. var. monoensis (Greene) Jeps	Groundsel	x	-	-	-	-	-	-
Sitanian hystrix (Nutt) J.G. Sm	Squirreltail grass	x	x	x	-	-	-	-
Sphaeralcea ambigua Gray	Globe mallow	-	-	-	-	-	-	-
Sphaeralcea rusbyi Gray ssp. eremicola	Panamint globe mallow	x	x	x	x	x	x	x
Stanleya elata Jones	Apache plume	x	-	-	-	xn	xn	xn
Stanleya pinnata (Pursh) Britton ssp. pinnata	Prince's plume	-	-	-	-	-	-	-
Stephanomeria pauciflora (Torr.) Nutt	Wire lettuce	-	-	-	-	-	-	-
Stipa speciosa Trin. and Rupr	Needlegrass	x	x	x	x	x	x	x
Tetradymia axillaris A. Nels.	Cotton thorn	-	-	-	-	x	x	x
Tetradymia spinosa var. longispina Jones	Yellow thorn	-	-	x	x	-	-	-
Tetradymia stenolepsis Greene	Cotton thorn	-	-	-	-	-	-	-
Thamnosma montana Torr. & Frem	Turpentine bush	x	x	x	x	x	xn	xn
Viguiera multiflora (Nutt) Blake var. nevadensis (A. Nels.) Blake	Nevada goldeneye	-	-	-	-	-	-	-
Yucca brevifolia Engelm	Joshua tree	-	-	-	-	-	-	-

Gold Valley sites				Ghost towns					Skidoo Pipeline corridor		
Lower (A)	Middle (B)	Upper (C)	Ghost town	Wahmonie	Greenwater	Furnace	Kunze	Skidoo	Harrisburg	Nemo Crest	Wildrose Canyon
x	x	x	x	x	-	x	x	x	x	x	-
x	-	-	-	-	x	x	-	-	-	-	-
x	x	x	x	x	x	-	-	-	-	-	-
-	-	x	x	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	x	hl	-	-	-
-	-	-	-	-	h	h	h	x	x	x	-
-	-	-	-	-	-	-	-	x	h	x	x
-	-	-	-	-	-	-	-	-	-	x	x
-	-	-	-	-	h	h	h	x	x	x	-
-	-	-	-	-	h	h	h	hl	-	-	-
-	-	-	-	-	h	h	h	-	-	-	-
-	-	-	-	-	-	-	-	x	h	x	x
-	x	-	-	-	x	x	x	x	xn	x	xn
-	-	-	-	-	x	-	-	x	xn	x	xn
-	-	-	-	-	xn	h	h	x	h	x	x
-	-	-	-	-	-	-	-	x	x	x	x
x	x	x	x	x	x	-	-	h	h	x	x
-	-	-	-	-	-	-	-	hl	-	-	xn
x	x	x	x	x	-	-	-	hl	x	x	x
x	x	x	x	-	x	x	x	-	-	-	-
-	-	-	-	-	x	x	x	h	-	x	-
-	-	-	-	-	-	-	-	-	h	x	-
-	x	x	x	-	h	h	h	h	-	-	x
-	x	x	x	-	-	-	xn	-	-	-	-
x	x	x	x	x	x	x	x	x	x	x	x
-	-	-	-	-	-	-	-	-	h	h	x
x	x	x	x	-	x	x	x	x	-	x	x
-	-	-	-	-	h	h	h	h	-	h	x
x	x	x	x	x	x	x	x	h	-	x	xn
-	-	-	-	-	-	-	-	-	-	-	x
-	xn	x	x	x	x	x	x	x	x	x	-
x	x	x	x	x	x	x	x	x	x	x	x
-	-	x	x	-	h	h	h	hl	xn	x	xn
x	x	x	x	x	x	x	x	x	x	x	-
-	xn	x	x	-	x	x	x	-	-	-	-
x	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	x	xn	x	x
x	x	x	x	x	x	x	x	x	x	x	-
-	-	-	-	-	-	-	-	-	-	-	xn
-	-	-	-	xn	-	-	-	-	-	-	-
x	x	x	x	x	x	x	x	-	-	-	-
-	x	-	-	x	x	x	x	x	-	-	-
-	-	-	-	-	h	h	h	hl	-	-	-
-	-	-	-	-	-	-	-	-	-	x	x
x	x	x	x	x	x	x	x	x	x	x	xn
x	x	x	x	-	x	-	-	x	xn	x	xn
-	-	-	-	-	x	x	x	-	-	-	-
x	x	-	-	-	x	x	x	x	xn	-	-
-	-	-	-	-	-	-	-	-	-	x	xn
-	-	-	-	xn	-	-	-	-	-	-	-
-	-	x	x	-	x	x	x	x	xn	x	xn
-	-	-	-	-	x	x	x	-	-	-	-
-	-	x	x	x	h	h	h	x	x	x	xn
-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	xn
-	-	-	-	-	-	-	-	-	-	-	xn
-	-	-	-	-	h	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	x
x	x	x	x	x	x	x	x	hl	x	x	x
-	-	-	-	-	-	-	-	-	-	-	x
-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	xn	x	x	x	xn	-	-
x	x	x	x	x	x	x	x	hl	-	-	-
-	-	-	-	-	x	x	x	x	x	x	x
-	-	-	-	-	-	h	h	x	xn	x	xn
-	-	h	-h	-	x	h	h	-	-	-	-
x	xn	x	x	x	x	x	x	-	-	-	xn
x	x	x	x	x	x	x	x	x	x	x	x
-	-	-	-	-	-	-	-	x	x	x	x
-	-	x	x	-	x	x	x	-	-	-	-
x	x	x	x	-	x	x	x	-	-	-	-
x	x	x	x	x	x	x	x	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	x
-	-	-	-	xn	-	-	-	-	-	-	-

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