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Early Plant Succession on Pinyon-Juniper Controlled Burns

Abstract

Pinyon (*Pinus monophylla*)-juniper (*Juniperus osteosperma*) woodlands are too often burned to increase understory production without sufficient information on probable postfire response. Post-burn vegetation response on six controlled pinyon-juniper burns in eastern Nevada demonstrated multiple entrance points into the standard successional model. Postfire succession was found to be partially explained by both initial and relay floristics successional theories. Species richness increased over time as species turnover rates declined and the proportion of perennial and preburn species increased. Several perennial forb species had maximum cover values during early succession. Predictability of early plant response to burning remains low because of the large species pool adapted to postburn conditions, inadequate detection of fire tolerant forb species, and unpredictable response from soil seed reserves. Once initial postburn plant response occurs, qualitative predictability of midsuccessional stages is thought to increase under the initial floristics successional model.

Introduction

Singleleaf pinyon (*Pinus monophylla* Torr. and Freem)-Utah juniper (*Juniperus osteosperma* (Torr.) Little) woodlands of the Great Basin are increasing in area and density with a concomitant loss of forage for livestock and wildlife (West *et al.* 1975). This widespread phenomenon in the western pygmy forests is generally thought to be largely the result of fire suppression and concurrent livestock grazing (Barney and Frischknecht 1974, Burkhardt and Tisdale 1969). A management response to restore the "natural state" has been controlled burning of woodland stands.

In the past, the standard postfire pinyon-juniper successional model presented succession as an ordered series of life forms from the annual forb to the tree stage (Erdman 1970, Barney and Frischknecht 1974). These models were useful in describing the general trends in succession. Recent reemphasis that succession is a species-by-species process (Drury and Nisbet 1973, Werner 1976) dependent upon a species "vital attributes" (Noble 1981) and the resurgence of Gleason's (1917) individualistic community theory in the form of "multiple successional pathway concepts" (Cattelino *et al.* 1979) has prompted a reevaluation of these standard models. If, as Noble (1981) suggests, there is no "unifying successional scheme" but only a collection of species specific trends (Pickert 1976), then a rigid adherence to the standard successional model could be disadvantageous to land managers making fire response predictions.

The dominant successional pathway may enhance or constrain the predictability of

postburn response. Succession may proceed by "relay floristics," the sequential migration to and dominance of the site by later successional species, or by "initial floristics," the sequential dominance of the site by higher successional species present on the site immediately following disturbance, or by both (Egler 1954). Early successional species may modify the site to the benefit of later-occurring species (facilitation model), or later successional species may just tolerate long periods of suppression (tolerance model) (Connell and Slatyer 1977). Predictability of response increases relative to the response potential for remnant plants and inversely with an increase in the size of the species pool that can immigrate to the site or emerge from undefined soil and seed reserves. Thus, initial floristic-tolerance model controlled systems should be more predictable in succession pattern than relay floristic-facilitation model controlled systems influenced by chance migration factors.

This paper examines plant response on six prescribed burns in the pinyon-juniper woodlands, tests results against a standard pinyon-juniper successional model (Erdman 1970), and examines the relative importance of relay and initial floristics in succession. Cover of major species is also examined to relate individual species response to the successional process.

Study Site

Controlled burns were conducted in 1975 and 1976 on alluvial terraces and drainage bottoms at an elevation of approximately 2000 m in a pinyon-juniper woodland on the east slope of the White River Mountains in eastern Nevada. Sites selected for burning appeared similar in cover of major plant species. Ellenberg's cover similarity index (Mueller-Dombois and Ellenberg 1974, p. 215) gave high similarity index values among sites, corroborating this observation. Soils of the burns are similar, having been previously described by Ward (1977) as Aridic Argixerolls. Livestock grazing was intensive in the late 1800s and early 1900s, but since the 1960s sites have been used only as summer range under moderate stocking rates. No livestock use occurred on any site after burning.

The climate is semiarid, with a mean annual precipitation of 225 mm fairly evenly distributed, peak winter snows in December, and peak summer thunderstorms in June (20 years of record, Lund, Nevada, elevation 1700 m, 41 km east of study area). On-site precipitation from 1 April to 15 September, as determined by a standard rain can, was 86 mm (1976), 203 mm (1977), and 76 mm (1978).

Methods

Six controlled burns were conducted at various times in the spring, summer, and fall. Method of burning and concurrent environmental conditions have been previously described by Bruner and Klebenow (1979). Smudge pot lighters (filled with 50 percent gasoline and 50 percent diesel oil) were used to burn scattered and dense stands of pinyon-juniper under conditions of low relative humidity (8-26%) and soil moisture (2-13%), moderate air temperatures (12-25°C), wind speeds (13-42 kph), and vegetative cover (42-56%) (Bruner and Klebenow 1979). Burning intensity varied among burns, but all burns were sufficiently intense to consume most aboveground understory vegetation less than 0.3 mm in diameter. On three sampled burns, the maximum surface soil temperatures in the interspace between trees were 305°, 200°, and 310°C; soil

surface temperatures under bitterbrush (*Purshia tridentata* (Pursh.) D. C.) plants exceeded that of the interspace by 200° to 400° (Klebenow *et al.* 1977).

Vegetative cover of understory species was recorded prior to burning and at the end of the growing season following the burn for 4 to 5 years. Detailed description of the sampling methods has been previously reported (Ward 1977). Briefly, at each potential burn site a set of two or three permanent transects, 30 m in length, were established. The line-intercept technique (Canfield 1941) was used to estimate tree and shrub cover. Grass and forb cover was estimated using Daubenmire's (1959) canopy coverage method within 15 microplots (30 × 60 cm) established at every other meter mark along the transect. Species nomenclature used followed that of Holmgren and Reveal (1966).

Preburn and postburn cover data from the transects were summed by species and plant form (annual forb, perennial forb, perennial grass, and shrub) and means derived for each burn. Annual grasses were rare on the sites and not considered further. The proportion of the preceding year's species pool lost from one year to the next (species turnover rate), percent of original preburn species present, species richness, and plant cover were used to characterize the pre- and post fire plant assemblages. Paired "t" tests of differences between means were used to evaluate selected phenomena at the 5 percent probability level following tests for skewness and kurtosis (Snedecor 1956).

Results and Discussion

Successional Pathways

Plant succession following fire has previously been presented as a series of contiguous stages with one plant form following the other (Fig. 1, Erdman (1970)). Our data suggests that succession is site specific and starts from a continuum of preburn assemblages such that there are multiple entrance points into the successional model (Fig 1B).

Annual forbs coyote tobacco (*Nicotiana attenuata* Torr.), flixweed ransymustard (*Descurainia sophia* (L.) Webb), and goosefoot (*Chenopodium album* L. var. *album*) dominated response on the 25 April burn, but this was the only burn that closely followed the successional models of either Erdman (1970) or Barney and Frischknecht (1974) (Fig. 2.) Rapid regrowth of perennials, the shrub Douglas rabbitbrush (*Chrysothamnus viscidiflorus* (Hood) Nutt. var. *viscidiflorus*), and perennial forbs tailcup lupine (*Lupinus caudatus* Kellog) and skullcap (*Scutellaria nana* A. Gray), altered the standard successional pathway in postburn vegetation of 9 May, 9 October, and 22 June burns, respectively; but regrowth was insufficient to prevent subsequent dominance or codominance by annual forbs tumbledustard (*Sisymbrium altissimum* L.), eriastrum (*Eriastrum sparsiflorum* (Eastw.) Mason), groundsmoke (*Gayophytum ramosissimum* Nutt.), stickseed (*Lappula redowskii* (Hornem.) Green), and goosefoot (Fig. 2). Germinating soil seed reserves of the perennial forb Munro globemallow (*Sphaeralcea munroana* Dougl.) provided sufficient plants to dominate the postburn vegetation on the 13 June burn, and regrowth of Douglas rabbitbrush was sufficient to almost continuously dominate plant response on the 3 May burn (Fig. 2).

Differences in plant form dominance among the six burns indicate succession starts from multiple points along the successional model (Fig. 1B). The data suggests that, given a sufficient number of burns, we would find a continuum of plant form combinations in early postfire plant assemblages.

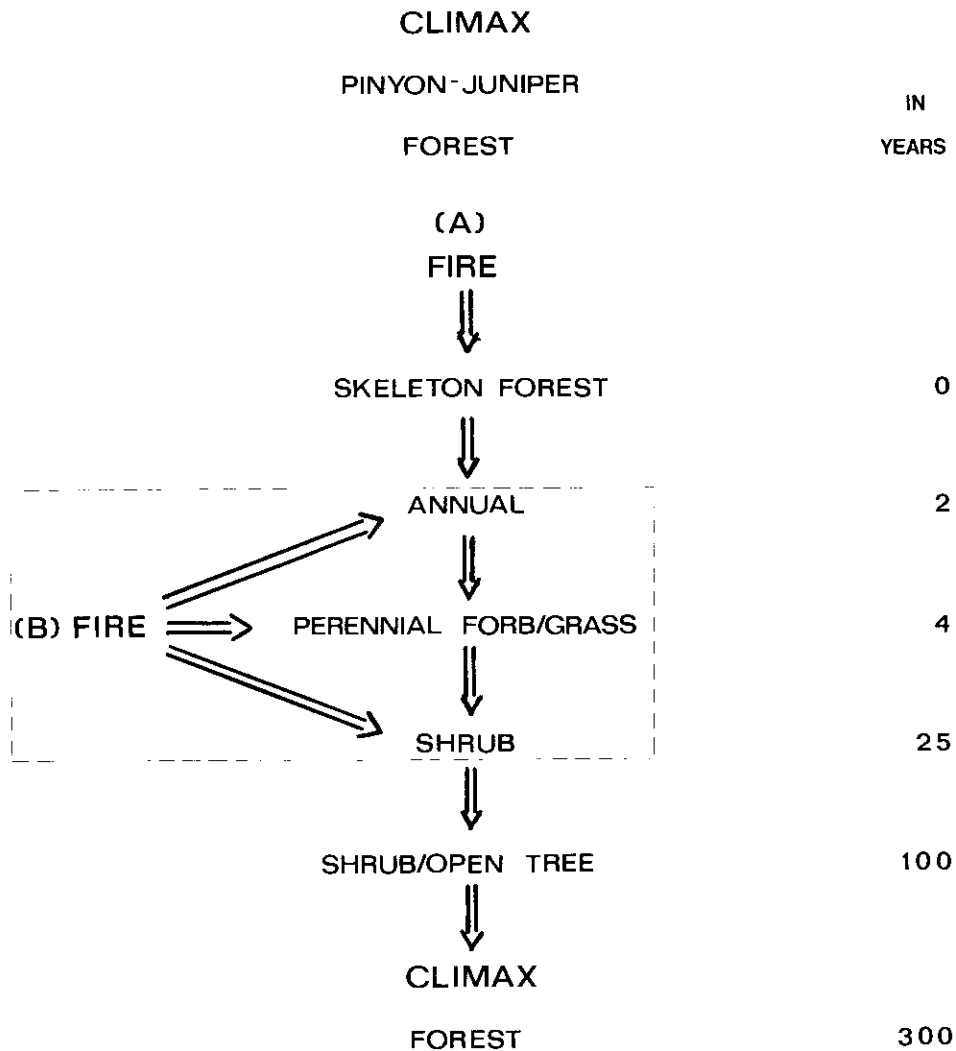


Figure 1. Successional model of pinyon-juniper woodland following fire (Erdman 1970). Multiple (A & B) entrance points into the successional model.

The ebb and flow of species were not consistent among the burns so there was no single scenario of species changes during early succession. On the 25 April burn first coyote tobacco then flixweed tansymustard and then stickseed predominated on the site. On the 9 May burn groundsmoke and goosefoot gave way to stickseed, but eriastrum was continually the dominant annual forb on the 9 October burn.

The annual forb stage may be skipped if succession has already eliminated annuals from the stand and fire responsive perennial species can rapidly reoccupy the burn. The presence and magnitude of the annual forb stage was dependent upon the creation of a regenerative niche (Noble 1981) due to the absence of perennial species regrowth or establishment from soil seed reserves. There was a "gradient of decreasing opportunities" (Pickett 1976) for annual forb dominance as the initial response of perennial forbs and shrubs increased. On the 3 May, 12 June, and 22 June burns a definite annual

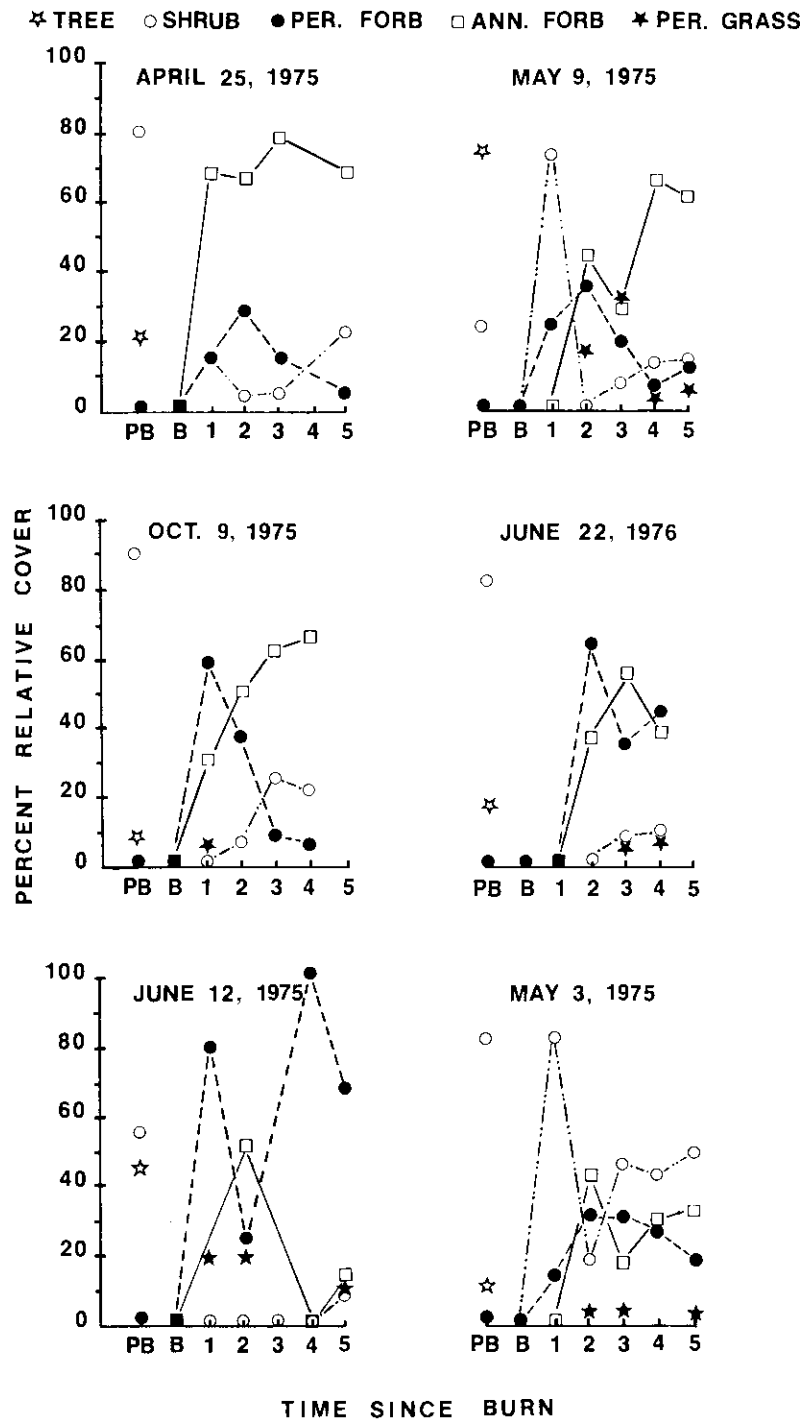


Figure 2. Percent relative cover by plant form on the six burns by number of growing seasons since burn occurred. (PB = preburn; B = burn date; 1-5 = postburn growing seasons.)

forb stage did not occur (Fig. 2), but instead skullcap, Munro globemallow, and Douglas rabbitbrush dominated the respective sites. The skipping of early successional stages (Fig. 1B) was previously suggested by Barney and Frischknecht (1974).

Successional Processes and Predicting Plant Response

The rapid return of preburn species to the burn sites and the appearance of species dominant in midsuccession (shrubs) seems to predispose the character of later successional stages. All burns had several plant forms (shrub, forb, grass) present almost immediately following fire, including many present in the preburn vegetation (Fig. 2). The data, therefore, indicate "initial floristics" (Egler 1954) or "tolerance" (Connell and Slatyer 1977) successional models are appropriate for early to midsuccessional stages. Succession proceeding on an "initial floristics" basis denotes an internally controlled system, a system with a measure of qualitative predictability (Lyon and Stickney 1976).

Preburn prediction of early plant response can be negated when fire-tolerant forbs are not obvious in preburn vegetation and/or plant response comes from soil seed reserves. Numerous forb species recorded on burn sites were apparently absent in preburn vegetation. Munro globemallow had moderate postburn cover values (14 percent, 12 June burn and 4 percent, 3 May burn) but was not recorded in preburn vegetation on either site. Plummer *et al.* (1957) reported dramatic increases in *Sphaeralcea* spp. following tree harvesting of pinyon (*Pinus edulis* Engelm.) and Utah juniper and ascribed *Sphaeralcea* spp. response to germination of soil seed reserves. Stimulation of Munro globemallow seed reserves following a fire could be expected as both alternating temperature extremes and increased nitrate levels (characteristics of burned soils) have been shown to increase *Sphaeralcea* spp. germination (Page *et al.* 1966).

Postburn succession was not observed through the tree stage. But the absence of singleleaf pinyon in early succession, its low seed viability, and its requirement for a nurse plant (Phillips 1909) indicate relay floristics (Egler 1954) must determine the rate of pinyon tree reinvasion and thus the character of later successional stages. Pinyon establishers from postburn seed caches by birds (Vander Wall and Balda 1977, Ligon 1978, Lanner and Vander Wall 1980) or rodents (our observation) are probably the principal migration processes.

Plant Assemblage Response

A relatively large species pool was adapted to postburn conditions, including many preburn species. Postburn plant assemblages contained numerous new perennial (12) and annual (14) forbs. No new shrub species and only two grass species occurred after the burns.

Species richness of both perennial and annual species increased over preburn conditions, especially the annuals (Fig. 3). This figure graphically demonstrates Pickett's (1976) "gradient of decreasing opportunity" for annual species establishment as perennial species numbers and dominance (preburn) increased. The data corroborates Nabi's (1978) report of decreasing species richness during pinyon-juniper succession.

The proportion of preburn species in postfire plant assemblages increased rapidly (>60 percent) lending credence to the use of Egler's (1954) initial floristics model on these sites (Fig. 4). The species turnover rate (proportion of species lost from the preceding year's species pool) declined over the same period (Fig. 4). The return

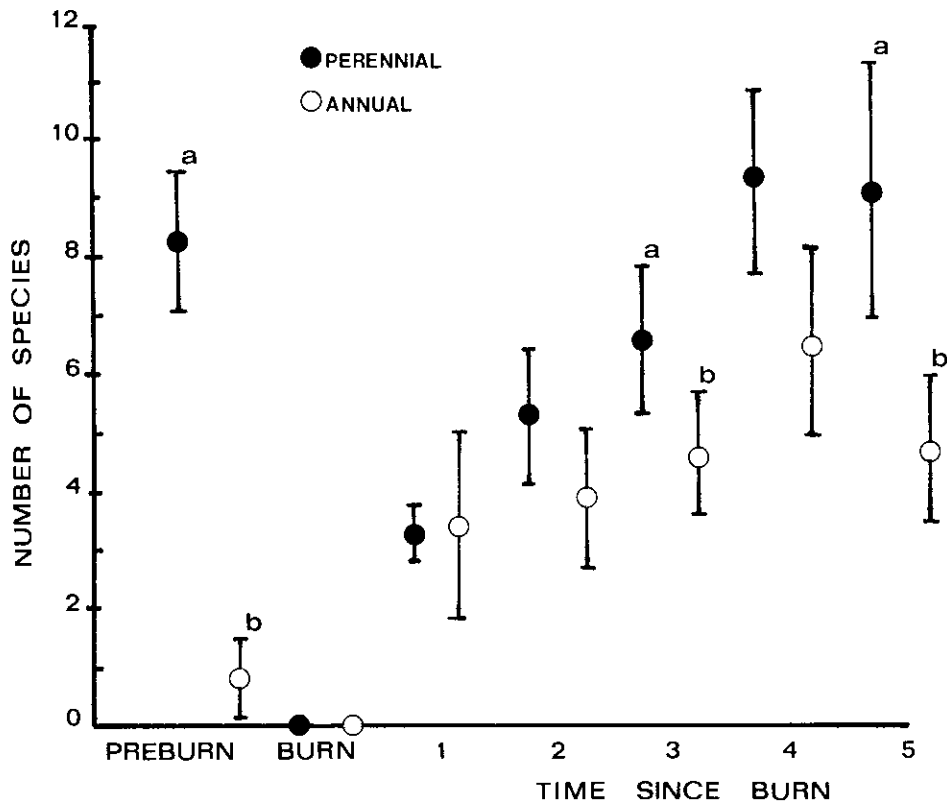


Figure 3. Mean number of perennial and annual species on the six burn sites by number of growing seasons following burning. Vertical bars reflect two standard errors of the mean and denote the range in expected mean response from a sample of six burns. Significant differences ($p = 0.05$) between annual and perennial species are denoted by superscripts and were determined from "t" test of differences on each site.

of preburn species did not precipitate this decline in species turnover; rather the number of species lost each year remained fairly constant as the total number of species and the proportion of perennials increased. Reinvading preburn species had significantly ($p = 0.05$) less cover ($\bar{x} = 7.1\%$) than new postfire species ($\bar{x} = 19.8\%$) for four to five growing seasons following burning. The decline in species turnover was interpreted as indicating the remaining species were more adapted to conditions in the developing plant assemblage than their more opportunistic predecessors.

The mean plant cover on burn sites rapidly returned to two-thirds of the original cover (Fig. 5), but this is a group mean and individual burn sites differ. Cover provided by annual species was so variable among years that total cover for a burn could decrease as well as increase over time. Vertical bars in Fig. 5 reflect two standard deviations from the mean and show the wide range in cover among sites. Preburn conditions indicate cover should increase as shrub and tree species become dominant.

Individual Species Response

Noble (1981) suggests a working knowledge of species' "vital attributes" during regeneration, establishment, and reproductive phases is required to accurately predict succes-

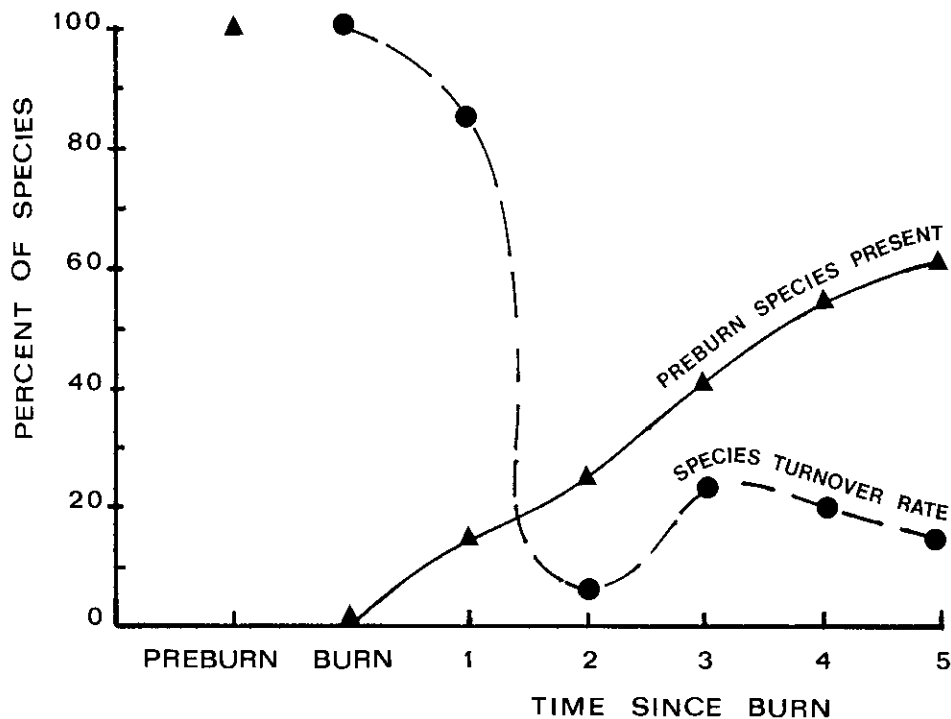


Figure 4. Percent species turnover rate and percent of preburn species present on the six burns by number of growing seasons following burning. (Turnover rate = proportion of total species lost from one year to the next.)

sion. At the time of this study there was little information available on the fire response of the observed species, and often the presence of individual species on burns was not predictable. Now we can provide information on the rapid increase and decline of major understory species and, in part, explain observed changes in plant form and species composition over time. This information is rudimentary and provides only a base for further individual species investigation.

As anticipated by earlier successional models, several annual forb species exhibited a short cycle to maximum cover on these burns. Two examples are Groundsmoke and Coyote tobacco, which had vigorous growth on a given site for only one growing season (Fig. 6A). Coyote tobacco cover peaked the second growing season following seed dispersal from scattered but extremely robust plants that occurred the previous year. Groundsmoke cover peaked four growing seasons after fire, and Stickseed (not shown) had yet to reach maximum cover at the conclusion of this study. Time and height of cover peaks in Fig. 6A represent successional phenomena and are not solely the result of climatic factors. All burns were not conducted in the same year, and not all species responded favorably to the wettest year, 1977. The first growing season following the 25 April and 3 May burns was in 1976, but for the 9 October and 22 June burns, the first growing season was in 1977.

Coyote tobacco, groundsmoke, and several other annuals had only a short period of vigorous growth in which to replenish soil seed reserves. If site conditions during the

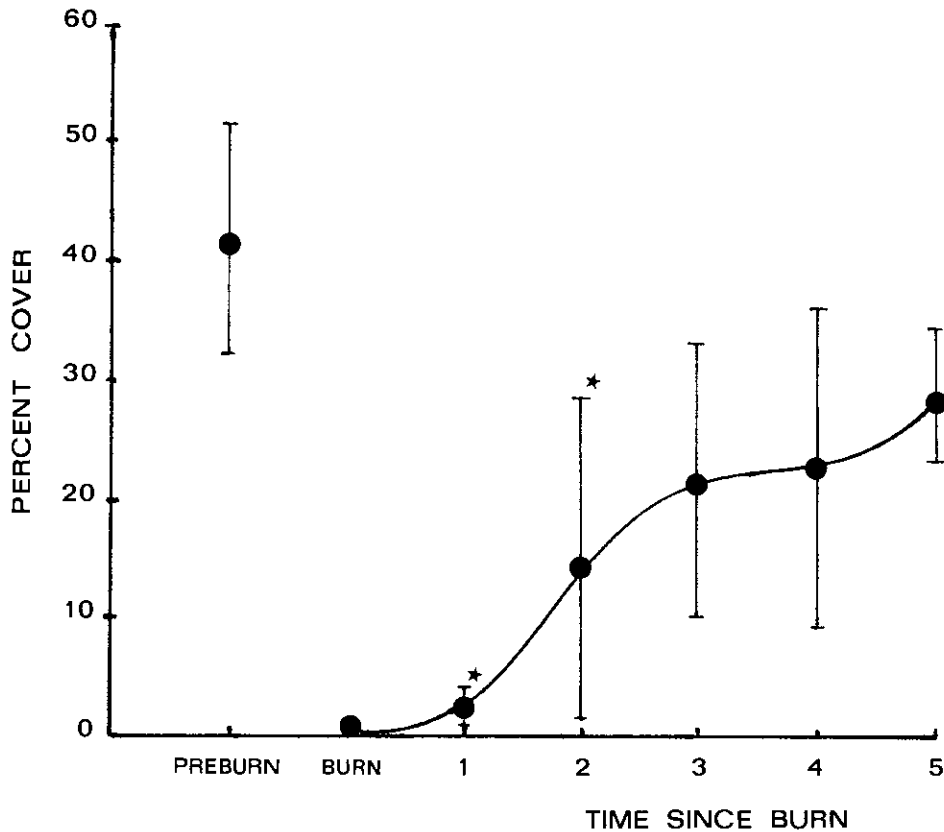


Figure 5. Mean percent herbaceous cover on the six burns by growing season following burning. Vertical bars reflect two standard deviations from the mean. The symbol * denotes significant ($p = 0.05$) difference in cover from the previous year.

last catastrophic event prohibited this annual forb expression, then the lack of annual forb response following some of the current burns appears convincing.

Several of the perennial forbs also show rapid peaks in cover. Relatively high cover values occurred only for a short time (2-3 years) and in early succession for prickly poppy (*Argemone polyanthemus* (Fredde) G. B. Owenby), skullcap, tailcup lupine, and Munro globemallow (Fig. 6B). Peaks in cover generally occurred the third or fourth growing season following fire and lasted for two growing seasons. These perennial forbs had a limited period of maximum growth and reproduction potential that occurred in early succession, although they may remain secondary components of the plant assemblage for long periods of time.

Perennial grass cover was noticeably lacking in postburn vegetation. Preburn cover values were low, and postburn remnant plants could not respond sufficiently to make a significant contribution to postburn plant cover. Postburn response by isolated plants of Breat Basin wildrye (*Elymus cinereus* Scribn. and Merr.) was dramatic, but the species did not occur in great numbers on a majority of the burn sites.

Douglas rabbitbrush increased from a preburn cover of 3 to 14 percent on the 3 May burn by rapidly resprouting from burned crowns. Harniss and Murray (1973) reported

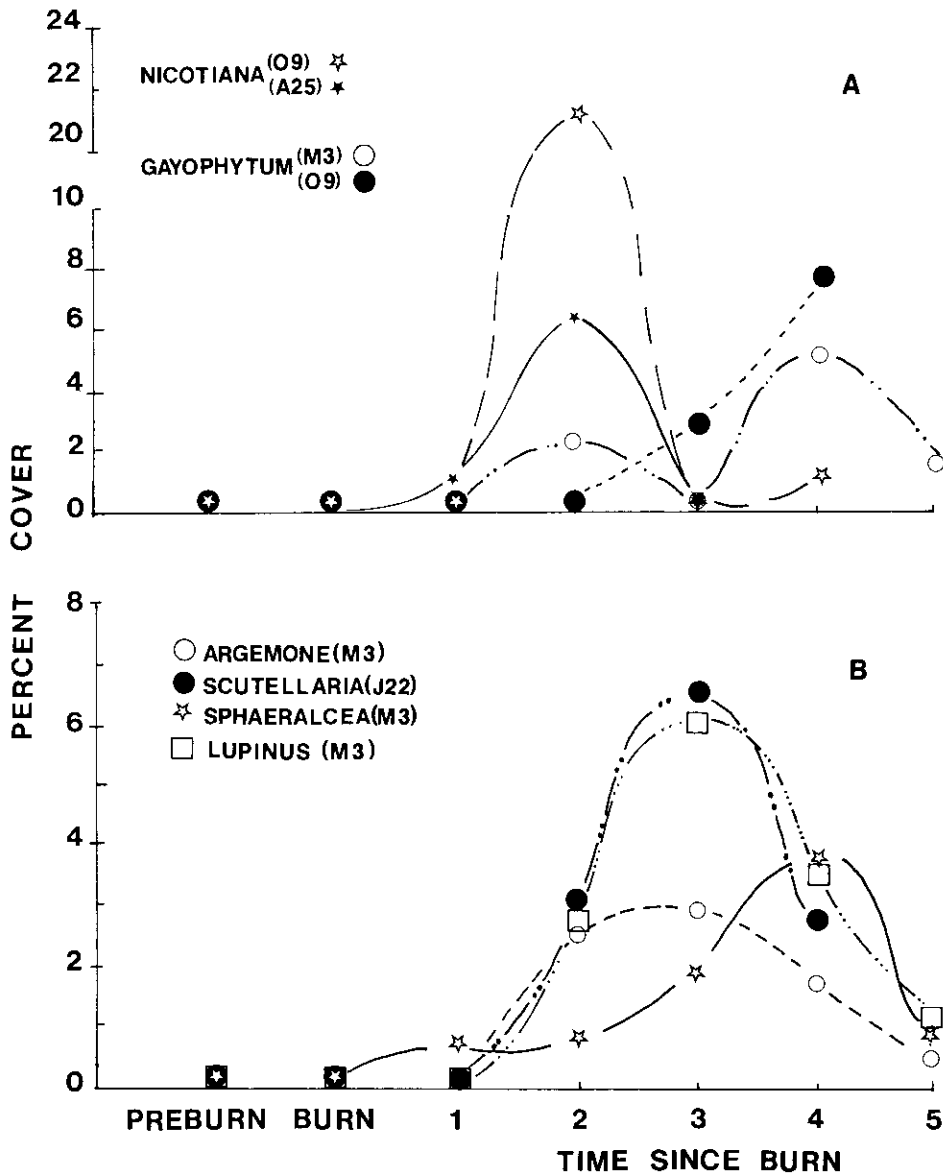


Figure 6. Cover of *Nicotiana attenuata* and *Gayophytum ramosissimum* by number of growing (A & B) seasons since burning. Cover of *Argemone polyanthemus*, *Scutellaria nana*, and *Sphaeralcea munroana* and *Lupinus* spp. by growing season following burning. Data for burns on 24 April (A25), 3 May (M3), 22 June (J22), and 9 October (O9) are presented.

a sharp increase in rabbitbrush cover following burning and a decline in cover after 10 years. Douglas rabbitbrush must decline on these sites if the species is to return to preburn cover levels. Desert bitterbrush (*Purshia glandulosa* Curran) cover declined after burning but is increasing slowly. Postfire Desert bitterbrush cover was derived solely from postburn rodent cache seedlings (Ward 1977).

Conclusions

Early plant succession on pinyon-juniper burns in the study area suggests multiple entrance points into the standard successional model. Variability in the entrance point is the rule rather than the exception, as seen in the variation in plant response observed among burns conducted at approximately the same time in a given year. If a burn is large enough, we could expect several early successional stages to occur concurrently.

Prior to burning, quantitative predictability of immediate postburn vegetation is difficult because of unobtrusive fire-tolerant herbaceous species, unpredictable response from soil seed reserves, variable postfire weather, and a large species pool of plants adapted to postburn conditions. The consistent postfire growth response from root sprouting shrubs, bunchgrass (Great Basin wildrye), and a few perennial forbs allow us to make qualitative estimates, but no more. Where remnant plant survival is more robust or the potential postburn species pool reduced, response may be more predictable because opportunism is depressed. Knowledge of species "vital attributes" (Noble 1981) may improve our predictability of plant response in the future, but a fundamental problem remains in predicting what species will be present in the postburn plant assemblage and whether postfire conditions will be favorable for the species to exhibit these "vital attributes." Once initial postburn plant response occurs, qualitative predictability of midsuccessional stages increases under the initial floristics successional model.

Initial and relay floristics successional models are both operative in pinyon-juniper succession. Original preburn species rapidly reappear on the burns, perennial species outnumber annuals, and the species turnover rate rapidly declines (initial floristics); but relay floristics (migration) determines the character of later stages, as we did not find singleleaf pinyon seedlings.

Understory cover increased rapidly to two-thirds of the original preburn total for sites taken collectively. The composition of this cover changed as numerous species were gained and lost from the plant assemblage. Many perennial and annual forb species had only a short period of maximum growth during early succession. Thus, if species expression is inhibited by climate or competition, alternate successional pathways are thought to occur following the next burn period.

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