Pioneer plant communities five years after the 1988 Yellowstone fires

by Robert J Ament

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences
Montana State University

Abstract:
The Yellowstone fires of 1988 burned many different types of vegetation. This initiated secondary succession in environments from valley bottoms to alpine tundra. Five years after fire, plant communities were measured. Species presence was recorded in 100 m^2 macroplots and cover was sampled in twenty 1000 cm^2 quadrats. Pioneer community composition after severe fire in late-seral vegetation was compared across the elevational gradient in nine environmental types with three replications in each. In two of the subalpine fir environments, communities arising from four different pre-fire serai stages were sampled to test the hypothesis that pioneer community compostion differs when early-seral versus late-seral forests burn in one environmental type.

Plant cover tends to decrease with increasing elevation. Along the elevational gradient, the wet grasslands had the strongest recovery from fire (plant cover averaged 97%), while the lowest cover was in the subalpine zone near treeline (39% average cover). Species richness was between 32 and 42 species per 0.01 hectare in the seven lowest environmental types. Diversity in the two highest elevational environmental types was distinctly low (19 and 20 species/0.01 hectare, respectively). Forty-two of the 262 species identified occurred in nearly all environments. Many of the others were concentrated in various portions of the gradient (i.e. grasslands, montane forests, subalpine fir forests). Each species and its distribution was tabulated.

To test the hypothesis that pioneer communties were influenced by previous vegetation, ordinations (principal component analysis and principal coordinate analysis) were conducted on postfire communities representing four pre-fire serai stages. Neither method indicated communities arising from any pre-fire serai stages were distinct from any others. Chi-square goodness-of-fit to random distribution and Monte Carlo randomizations of individual species in these environmental types identified only three species that were significantly non-randomly distributed among postfire communities from pre-fire serai stages. All three were more strongly represented in pioneer communities from early prefire serai stages. Eighteen species in each environmental type possibly had non-random distributions (P=0.06 to 0.15) indicating they may deserve further study.

PIONEER PLANT COMMUNITIES FIVE YEARS AFTER THE 1988 YELLOWSTONE FIRES

by

Robert J. Ament

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, MT

May 1995

APPROVAL

of a thesis submitted by

Robert John Ament

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

23 May 1995 — T. Weaver

Date — Chairperson, Graduate Committee

Approved for the Major Department

25 May 1995 — Robert S Moore

Date — Head, Major Department

Approved for the College of Graduate Studies

7/20/95 — R L Brown

Date — Graduate Dean

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a master's degree at Montana State University, I agree that the Library shall make it available to borrowers under rules of the Library.

If I have indicated my intention to copyright this thesis by including a copyright notice page, copyright is allowable only for scholarly purposes, consistent with "fair use" as prescribed by U.S. Copyright Law. Requests for permission for extended quotation from or reproduction of this thesis in whole or in parts may be granted only by the copyright holder.

Signature Robert J. Arnott

Date May 25, 1995

ACKNOWLEDGEMENTS

I would like to express gratitude to those who helped and guided me during this study. The encouragement, advice, and talks of all things ecological with my major professor, Dr. Tad Weaver, was appreciated. Dr. Don Despain, adjunct professor, and employee of the newly christened National Biological Service, illuminated various aspects of fire ecology and other facets of the Greater Yellowstone Ecosystem for me. A special thank you to Dave Clark, with the support of his family, in helping me relocate most of the study sites in the Yellowstone area. Dr. Jack Rumely helped in verifying identifications of difficult taxa in the MSU herbarium. Dr. Mark Taper gave me needed support for programming in MATHCAD and understanding the multivariate analyses. Dr. Dan Gustafson wrote a program to present the multivariate analyses in three dimensional figures. Few endeavors are as complete without the help of others and this was no exception. I thank them all. This study was funded by USDA-Forest Service, Intermountain Research Station Grant No. INT-93837-RJVA. I also was supported by a seasonal Yellowstone National Park research position.

TABLE OF CONTENTS

TABLE OF CONTENTS--Continued

TABLE OF CONTENTS--Continued

LIST OF TABLES

LIST OF TABLES--Continued

LIST OF TABLES--Continued

LIST OF TABLES--Continued

LIST OF FIGURES

ABSTRACT

The Yellowstone fires of 1988 burned many different types of vegetation. This initiated secondary succession in environments from valley bottoms to alpine tundra. Five years after fire, plant communities were measured. Species presence was recorded in 100 m^2 macroplots and cover was sampled in twenty 1000 cm^2 quadrats. Pioneer community composition after severe fire in late-seral vegetation was compared across the elevational gradient in nine environmental types with three replications in each. In two of the subalpine fir environments, communities arising from four different pre-fire seral stages were sampled to test the hypothesis that pioneer community compostion differs when early-seral versus late-seral forests burn in one environmental type.

Plant cover tends to decrease with increasing elevation. Along the elevational gradient, the wet grasslands had the strongest recovery from fire (plant cover averaged 97%), while the lowest cover was in the subalpine zone near treeline (39% average cover). Species richness was between 32 and 42 species per 0.01 hectare in the seven lowest environmental types. Diversity in the two highest elevational environmental types was distinctly low (19 and 20 species/0.01 hectare, respectively). Forty-two of the 262 species identified occurred in nearly all environments. Many of the others were concentrated in various portions of the gradient (i.e. grasslands, montane forests, subalpine fir forests). Each species and its distribution was tabulated.

To test the hypothesis that pioneer communties were influenced by previous vegetation, ordinations (principal component analysis and principal coordinate analysis) were conducted on postfire communities representing four pre-fire seral stages. Neither method indicated communities arising from any pre-fire seral stages were distinct from any others. Chi-square goodness-of-fit to random distribution and Monte Carlo randomizations of individual species in these environmental types identified only three species that were significantly non-randomly distributed among postfire communities from pre-fire seral stages. All three were more strongly represented in pioneer communities from early pre-fire seral stages. Eighteen species in each environmental type possibly had non-random distributions (P=0.06 to 0.15) indicating they may deserve further study.

GENERAL INTRODUCTION

The Yellowstone fires of 1988 burned all types of vegetation. Thus, secondary succession was initiated in numerous environments.

Five years after the fires, in the summer of 1993, this study was conducted to describe early pioneer communities appearing after severe fire in climax vegetation of nine environmental types. Seed banks of most of the study sites had been examined by Clark (1991). These sites and nine more were visited to acquire three replicate pioneer communities in each of nine major environmental types of the northern Rocky Mountains.

The pioneer communities of the nine environmental types have never been described and compared. These environments represent relative positions along the elevational gradient so that direct gradient analyses of pioneer communities can be performed. This approach also allows examination of species distribution patterns on the elevational gradient.

In comparing pioneer communities following severe fire in late-seral vegetation of different environments, it was also possible to test whether pioneer communities would differ if early-seral vegetation in these environments had burned. Thus, in Part II, in two environmental types, the effects of the pre-fire vegetation (different seral stages) on postfire community composition appearing five years after severe fire was examined. This hypothesis was tested on both integrated communities (via ordination) and on individual species. The distribution of individual species in pioneer communities on a gradient of pre-fire seral stage was assessed with three different statistical tests.

PART I

PIONEER COMMUNITIES FIVE YEARS AFTER FIRE IN NINE ENVIRONMENTAL TYPES ALONG THE ELEVATIONAL GRADIENT

INTRODUCTION

Yellowstone Fires.

In the summer and fall of 1988 Yellowstone National Park and adjoining lands, both public and private, experienced the most extensive wildfires of the century. In three months, a series of fires burned 276,533 hectares (683,305 acres) of forests and grasslands (Rothermal and others 1994). The fires were started by both lightning and human ignitions. The northern Rocky Mountains (NRM) had not experienced a combination of fires of this size and extent since 1910 when over 1,200,000 hectares (3,000,000 acres) of the forests in Montana and Idaho burned (Pyne 1982).

The burning in Yellowstone was the most significant ecological event that a National Park has experienced (Scullery 1989). The fires also burned large parts of the surrounding National Forests [Bridger-Teton, Gallatin, Shoshone and Targhee], as well as lands under other ownership.

The fires left a landscape comprising grasslands, shrublands, forests and alpine tundra effected to varying degrees by fire. The result was a mosaic of burn intensities and patch sizes reaching from valley bottoms to the alpine ridges. The heterogeneity of the burn was superimposed over a pre-fire landscape that contained vegetation of different environmental zones each occupied by vegetation of different ages (Knight and Wallace 1989).

The scope of the fires should not have been an unexpected occurrence in the temporal scale of centuries (Whitlock and others 1994). In the late 1600s and early 1700s several equally large fire events had burned extensive areas in Yellowstone National Park's high volcanic plateaus (Romme 1982). Intervals between stand-replacing fires are often three hundred years in these subalpine fir forests. At lower elevations, where the shrub-steppe is interspersed with coniferous forest, eight to ten large fires burned previous to the twentieth century (Houston 1973). The average fire interval for the lower elevation northern range is twenty to twenty-five years. Thus, studies of the two different environments in YNP, subalpine forests and shrub-steppe, indicates that although they have different fire regimes, the Greater Yellowstone Ecosystem (GYE) has a history of extensive fires that predates settlement, fire management strategies and suppression.

Fire size events are described logarithmically with time (Pyne 1982). That is, large events are infrequent, medium-sized ones more common, and smaller fires are much more numerous. Thus, while the 1988 fires' size was a rare ecological occurrence in recent time, burns of a smaller dimension are a common component of the disturbance regime in plant communities of the Greater Yellowstone Ecosystem and the NRM. The many fires of 1988, were of varying intensities, in all types of plant communities on the environmental gradient, and established a landscape-level disturbance pattern typical of the northern Rocky Mountains.

Objectives

The Yellowstone fires of 1988 created an unusual opportunity to describe and compare postfire pioneer communities that established themselves concurrently in many different environments. Vegetation dominated by sagebrush, Douglas fir forests, aspen groves, mountain meadows, subalpine fir forests, and alpine tundra were burned.

The objective was to locate stands (with three replications) burned at maturity (near-climax) in major environments (nine habitat types) representing the altitudinal gradient. Resultant information will be useful in predicting early postfire succession after future fires on sites in these environments.

To make the study finite, sites were selected from those where the pre-fire vegetation was near-climax and all were severely burned.

Since this study is to describe pioneer communities of major elevational zones an environmental classification system was used to characterize the study sites. The only ecological classification widely employed in the NRM (Daubenmire 1952, Steele and others 1983, Mueggler and Stewart 1980) was used for this study. The units of this classification are environmental types (habitat types) and they are descriptors of the environment--not of the vegetation. This report will use the term -- "environmental type" -- synonymously with habitat type (HT).

Environmental Classification

The environmental type (habitat type) is the basic unit for classifying and identifying land potential (Daubenmire 1966). Thus, it can be used both to distinguish sites with different environmental conditions and to extrapolate observations from such sites to a larger geographic setting. It would be expected that the composition of a pioneer community appearing after stand-replacing fire, in any specified NRM habitat type, will approximate corresponding units of the environmental type observed in Yellowstone after the 1988 fires. This expectation is based on the assumption that similar environmental and historical constraints are operative on all units of a habitat type.

In the United States, the habitat type system of environmental classification was developed in eastern Washington and northern Idaho (Daubenmire 1952). It was extended to the forests of Montana (Pfister and others 1977), the forests of eastern Idaho and western Wyoming

(Steele and others 1983) and the grasslands/shrublands of Montana (Mueggler and Stewart 1980). Most of the riparian areas of Montana have been added to this system (Hansen and others 1995). The vegetation of Yellowstone National Park has been described with this environmental classification (Despain 1990).

While acknowledging some variability between sites this system of classification nonetheless regards all units of an environmental type to be comparable across the landscape. Thus, units with a similar environment, regardless of the present successional status, are all categorized as the same habitat type.

The environmental type of a land unit is identified by recording the climax vegetation that occupies the site. If the vegetation is not at climax, then the vegetation that would occur at climax is deduced and recorded. On the burned sites of this study, potential was identified by examination of adjacent unburned vegetation, unburned material left within the sample stand, and vegetation maps of Yellowstone National Park (Despain and others, unpubl.)

This classification of vegetation appears to conflict with the continuum theory (Curtis and MacIntosh 1951, Gleason 1962, Whittaker 1960, Goodall 1963) of plant community change across the landscape. Observation that vegetation sometimes varies continuously over the landscape has prompted many to doubt that plant communities comprise distinct, coevolved plant populations. Classification is useful for studies like this and for explanations of the results whether or not there is a belief in discontinuites in vegetation composition.

This study uses the environmental type of classification with the knowledge that the scheme may divide a continuum into arbitrary, somewhat variable units. This choice was to maximize the extrapolation of our observations. In defense of the habitat type classification method, it was stated, "while this debate may be of interest academically, it need not preoccupy the natural resource managers and field biologists who need a logical, ecologically-based classification with which to work" (Pfister and others 1977). It is due to the efficacy of the habitat type that this study utilizes this classification system as the basis of describing early postfire pioneer communties in various environments in the Greater Yellowstone Ecosystem.

In defense of discontinuities that would sometimes support discrete typal communities, Daubenmire demonstrated the use of his data could also support a continuum theory. He showed that the methodology and interpretation of continuum theory adherents are biased against observation of coevolved units (Daubenmire 1966). Further contrasts of continuum and classification theory are summarized by continuum adherents (MacIntosh 1967, Whittaker 1967), a proponent (Dansereau 1968), and an integrator (Allen and Hoekstra 1992). The latter note that viewpoints affect the conclusions drawn; while continuum advocates use the individual species as their point of departure, advocates of distinct units consider the ecosystem from the spatial scale of the landscape.

Pioneer Communities of NRM Habitat Types

Most vegetation classifications are based on undisturbed, mature plant communities. Early seral communities appearing in major environmental types (habitat types) have rarely been described. The few environments that have been investigated in the northern Rocky Mountains are pioneer communities of forested types in western Montana and northern Idaho. Most of these studies have been on lands disturbed by management activities either directly or on adjacent sites. A compilation by habitat type of postfire pioneer communities in coniferous forests that have been described in the NRM is listed in Table 1.

In another forest type, after a prescribed fire south of Yellowstone NP, on the Bridger-Teton National Forest, a three year study of aspen community response to moderate and high intensity burning was conducted (Bartos and Mueggler 1981). This was described before aspen communities had been classified (Mueggler 1988) for the intermountain western United States.

Table 1. Northern Rocky Mountain coniferous forest postfire pioneer community studies by habitat type.

Habitat type	Primary[1] Investigator	
Abies lasiocarpa/Xerophyllum tenax	Lyon	1976
" " " "	Lyon	1984
" " " "	Arno*	1985
Abies lasiocarpa/Menziesia ferruginea	Arno*	1985
Abies lasiocarpa/Linnaea borealis	Crane*	1983
Pseudotsuga menziesii/Vaccinium globulare	Arno*	1985
Pseudotsuga menziesii/Physocarpus malvaceus	Arno*	1985
" " " "	Crane*	1983
Pseudotsuga menziesii/Vaccinium globulare	Crane*	1983
Tsuga heterophylla/Pachistima myrsinites	Stickney	1986

[1] Other authors contributed to studies marked with an asterisk(*) (Arno and others 1985, Crane and others 1983).

There have been several reports of grassland and shrubland pioneer communities after fire; but, these studies did not use habitat types to characterize study site environments. An ungrazed grassland dominated by Rough fescue, *Festuca scabrella* was found to quickly return to pre-burn composition within three years in western Montana (Antos and others 1980). Three sagebrush studies west and south of the GYE were in sagebrush, *Artemisia tridentata*, dominated stands (Harniss and Murray 1973, Humphrey 1984, and Akinsoji 1988). The long-term study in the Snake River plain (Harniss and Murray 1973) recorded vegetative transformation for thirty years.

This study describes pioneer communities in nine different habitat types of grassland, shrubland, and forest after severe fire. The habitat types considered do not overlap the environments of previous studies. All of the sites were located in a landscape unaffected by multiple-use management both before and after the fires.

METHODS

Study Area

This study was conducted in Yellowstone National Park and should reasonably represent major environmental types of the Greater Yellowstone Ecosystem (GYE) and the northern Rocky Mountains. The GYE is a mountainous area surrounding Yellowstone National Park (Figure 1). It straddles the continental divide and is mid-way between the equator and the north pole; the 45th degree northern latitude runs through it from east to west. It includes Yellowstone National Park, six adjacent National Forests, two National Wildlife Refuges as well as other public and private land holdings. Grand Teton National Park is included in the southern portion of the ecosystem. There is a complexity of land ownership and its changing environmental character make definition of exact boundries for the GYE difficult (Glick and others 1991). The land base is approximately 17 million acres (7 million hectares) and includes portions of the states of Idaho, Montana, and Wyoming.

The climate of the area is characterized by long, cold winters and short, cool summers. The temperatures are typical of a cool, dry continental climate and vary with elevation (Weaver 1980, Despain 1990). Most of the area receives between thirty and fifty inches of annual precipitation depending on the elevation (Despain 1990). Lower elevations in the northwest corner of Yellowstone National Park receive only 10 to 12 inches (25 to 31 cm.). Higher elevations receive well over 70 inches (178 cm.) of precipitation annually (Glick and others 1991). The climates along the elevation gradient have been described for the northern Rocky Mountains for each vegetation type (Weaver 1980). Elevations in the region vary from 1300 meters in the river valleys to over 4,000 meters near the summits in several of the ranges.

Despain (1990) describes the geology of the Yellowstone area. Five separate blocks of sedimentary and granitic formations were uplifted during the Laramide orogeny: the Beartooth, Targhee, Gallatin, Washakie, and Teton uplifts. During the Eocene, volcanic activity extruded andesite and basalt. Later, in the Pliocene, more faulting and uplift occurred. In the more recent Quartenary, a violent explosion generated a large caldera which contains the present Yellowstone Lake, destroyed portions of Mount Washburn and adjacent mountain ranges. It spread rhyolitic tuff and flows over most of the area. Glacial activity in the Pleistocene left kettle and kame topography, moraines, glacial till, and erratics in the valley bottoms.

Soils vary and depend on parent materials, climate, and associated vegetation. Forest soils are commonly alfisols or inceptisols with shallow, rocky profiles (Trettin 1986).

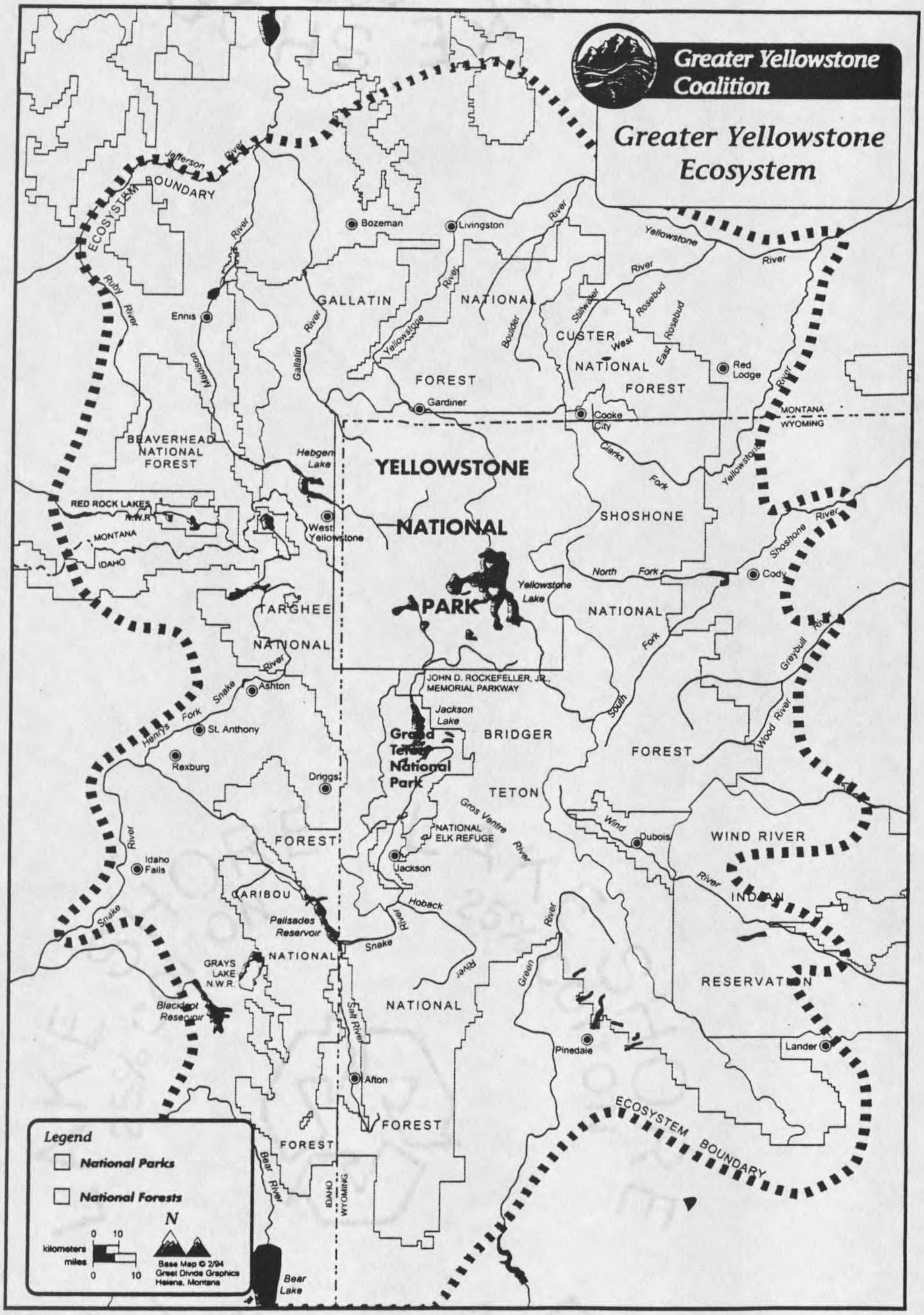

Figure 1. The Greater Yellowstone Ecosystem (courtesy of the Greater Yellowstone Coalition).

Grasslands and shrublands occur primarily on mollisols (Munn and others 1978) in the NRM. These are derived mostly from alluvium and are typically well drained. In the higher valleys and mountain meadows mollisols commonly form on fine-grained alluvium and heavy soils derived from shales and andesitic volcanics (Despain 1990). Predominant parent materials of the soils in the Yellowstone area are andesite and rhyolite (Despain 1990). These two underlying bedrocks arose from separate volcanic events in the tertiary and quartenary, respectively.

Key characteristics of soils; such as carbon/nitrogen ratios, nitrogen concentrations, pH, cation exchange capacity and phosphorous availability change in a predictable manner as one moves from dry, low elevation grasslands up through the forested zone to the alpine in the northern Rockies Mountains (Weaver 1979). Like the vegetational gradient, the soil gradient reflects changes in abiotic and biotic processes with differences in climate.

Study Site Selection

To characterize pioneer communities of each of the vegetational zones three sample stands were located in each of nine habitat types which were severely burned in 1988. The location of the sites sampled are listed in Table 2 and displayed in Figure 2. Each site's environmental type is listed in Table 3.

Table 2. Sample stand codes, names, legal descriptions (Universal Transverse Mercator - Zone 12), elevations and relative fertility.

Stand Code	Site Name	UTM Coordinates	Elevation (meters)	Soils[1]
A1	Crystal Bench	49730 N, 5532 E	1920	A
A2	Lamar	49672 N, 5619 E	2067	A
A3	Canyon West	49521 N, 5619 E	2621	A
B1	Bunsen	49765 N, 5243 E	2164	A
B2	Waterplant	49774 N, 5231 E	2042	A
B3	Blacktail	49743 N, 5416 E	2195	A
C1	Terrace	49787 N, 5213 E	2269	A
C2	Floating Island	49762 N, 5433 E	2044	A
C3	Wraith	49761 N, 5299 E	2072	R
D1	Bunsen	49746 N, 5244 E	2134	A
D2	Lamar	49673 N, 5657 E	2127	A
D3	Waterplant West	49776 N, 5230 E	2059	A
E1	Lamar	49689 N, 5618 E	2012	A
E2	Frog Rock	49780 N, 5342 E	2114	A
E3	Washburn	49660 N, 5450 E	2438	A
F1	Indian Creek	49683 N, 5174 E	2316	A
F2	Heart Junction	48966 N, 5385 E	2245	A
F3	North Indian Creek	49688 N, 5172 E	2316	A
G1	Willow Park North	49681 N, 5208 E	2246	R
G2	North Roaring Mtn.	49598 N, 5208 E	2316	R
G3	Tuff Creek	49441 N, 5132 E	2121	R
H1	Golden Gate	49756 N, 5215 E	2251	R
H2	Madison	49440 N, 5015 E	2238	R
H3	Grotto Geyser	49246 N, 5126 E	2246	R
I1	South Canyon	49495 N, 5401 E	2380	A
I2	Southeast Swan	49716 N, 5221 E	2199	A
I3	Obsidian Creek	49653 N, 5206 E	2253	A
J1	Washburn	49637 N, 5438 E	2626	A
J2	Blacktail	49764 N, 5395 E	2275	A
J3	Specimen	49720 N, 5574 E	2074	A
K1	Fan Creek	49781 N, 4967 E	2230	A
K2	Cygnet Lakes	49469 N, 5315 E	2569	R
K3	Canyon - Norris	49521 N, 5372 E	2469	R
L1	Lulu Pass	49865 N, 5866 E	2487	A
L2	Willow Park	49628 N, 5215 E	2254	R
L3	Grizzly Trailhead	49609 N, 5207 E	2322	R
M1	West Thumb	49192 N, 5335 E	2377	A
M2	Lewis Lake	49039 N, 5306 E	2412	R
M3	Lewis Canyon	48974 N, 5275 E	2359	R
N1	Little Thumb	49185 N, 5312 E	2503	R
N2	Canyon - Norris	49522 N, 5374 E	2469	R
N3	Virginia Falls	49507 N, 5282 E	2417	R
O1	Washburn High	49618 N, 5443 E	2804	A
O2	Observation	49570 N, 5363 E	2692	A
O3	Washburn Low	49641 N, 5443 E	2534	A

Table 2--Continued.

P1	Observation East	49569 N, 5370 E	2681	A
P2	Dunraven	49576 N, 5435 E	2560	A
P3	West Dunraven	49600 N, 5427 E	2659	A

[1] Soils: Substrate of soils derived from: A - Andesite, basalt, sedimentary (fertile soils); R - Rhyolite, gneiss, granite (infertile, well-drained soils)

The majority of the sites were originally located by Clark (1991) immediately after the 1988 fires for a seed bank investigation and were relocated with his help. The present study found stands used in that project by locating the metal stakes left in 1988 with the aid of a metal detector. Sites were located near an unburned portion of the plant community so that verification of vegetative composition and therefore the habitat type and seral stage could be made.

Of Clark's 45 transects, 39 were suitable for this study. Six of the original transects were unusable due to logging disturbance, mis-classification, or could not be relocated. Habitat type maps of Yellowstone National Park (Despain and others, unpubl.) were used to find new sites for replacement stands. These replacement stands are noted in Table 2.

Three new sites were established to provide additional replications for cover types originally under-sampled. The new sites were located with Despain and others' (unpubl.) habitat type map and verified by noting adjacent unburned vegetation.