Floristic analysis of the Centennial Region, Montana

by Denise R Culver

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

Abstract:
This study focuses on analysis and interpretation of biogeographic and floristic variables among the Centennial Mountains and Valley (Centennial Region) and 10 representative regional floras from western North America to test the hypotheses that: 1) the Centennial Region is a Great Basin refugium; and 2) that the Centennial Region is floristically rich. Explanations for richness generally include only ecological determinants. In contrast, historical determinants of floristic diversity may transcend ecological ones and may include how species are related, where they evolved, and what taxonomic tendencies they possess.

Phenetic analyses of the presence and absence of taxa among floras from western North America were performed to determine which province primarily influenced the Centennial Region. Utilization of regional endemics in determining biogeographic distribution is also addressed.

Historical biogeographic inferences were derived from floristic similarity indices among selected floras from western North America (Q-mode analysis). Generalized track analysis (R-mode) and vicariance biogeographic analysis were not performed due to: 1) the small size of the study areas relative to total geographical distribution of species; and 2) the lack of areas of endemism combined with a paucity of phylogenetic analyses of constituent North America taxa. Critiques of Q-mode analysis are rebutted. A data matrix consisting of 3217 taxa in 11 geographical regions was created to determine the percent similarities between the Centennial Region and the 10 western North American floras. After adjusting the data to mitigate floristic size differences (by using only the shared taxa with the Centennial Region).

Results indicate that it is the Rocky Mountain flora which dominates the flora of the Centennial Region (x=62%) and its four constituent vegetational zones. The Centennial Region is only very weakly influenced by the flora of the Great Basin (x=30%). An analysis of the sensitive plants of the Centennial Region reveals that only 3 of the 766 taxa in the Centennial Region have primary distributions in the Great Basin province.

Additionally, the richness of the Centennial flora as determined by species numbers (766 vascular plants) does not differ from other regions of similar topography in western North America. Pleistocene glaciation, geographic proximity, and latitude are discussed as factors that contribute to the strong Rocky Mountain influence observed in the Centennial Region.

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ABSTRACT

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Additionally, the richness of the Centennial flora as determined by species numbers (766 vascular plants) does not differ from other regions of similar topography in western North America. Pleistocene glaciation, geographic proximity, and latitude are discussed as factors that contribute to the strong Rocky Mountain influence observed in the Centennial Region.

INTRODUCTION

The present flora of the western United States is the result of climate, geology, soils, ecology, and evolutionary forces, and has evolved radically since the Eocene and Oligocene epochs (Wing, 1987; Wolfe, 1987). For example, the flora of the Rocky Mountain region has changed from the lowland rain and seasonally dry tropical forests and warm temperate deciduous forests during the Tertiary to the cold temperate montane vegetation of the Pleistocene. The change in vegetation from the Tertiary to the Quaternary was drastic with no ecological and very little taxonomic contiguity.

The Centennial Region lies in a biogeographically complex area at the interface of the Rocky Mountain, Great Basin, and Pacific Northwest regions. Knowledge of the historical development of the Centennial Region is important and complementary to an understanding of the ecological attributes of this region. Patterns of species distribution in the Centennial Region are undoubtedly the result of both ecological and historical processes.

In addition to detailing the flora of the Centennial Region, this study should contribute to a better understanding of floristic regions in the northern Rocky Mountain ecosystem. Additionally, the inventory of sensitive plants found in the Centennial Region should serve as a management tool for the Montana Heritage Program, Bureau of Land Management and Red Rock Lakes National Wildlife Refuge for purposes of conserving the flora of the Centennial Region.

Statement of Problem

The Centennial Region is located within the Rocky Mountain Province (Cronquist, 1982) but it has frequently been described as a refugium for Great Basin species (Kratz, 1988; Lesica et. al., 1992; Heidel et. al., 1993). This assertion has been supported by documenting the occurrences of sensitive plants and by identifying the proportion of "Great Basin" species in the Centennial Region (Heidel et. al., 1993). Does the Centennial Region belong to the Great Basin floristic province, or to what degree is the flora of the Centennial Region influenced by the flora of the Great Basin?

The southwestern region of Montana, which includes the Centennial Region, has also been described as the most floristically diverse (rich) in Montana (Lesica et. al., 1984). Similarly, Shelley (1986) described the Centennial Region as an area of high floristic and geographic diversity with a number of taxa which are either regional endemics or on the edge of their range. However, there are no taxa strictly endemic to the Centennial Region, and very few are endemic to Montana. Thus, how rich is the flora of the Centennial Region compared to other floras of comparable size in western North America?

Biogeography

Biogeography is the study of the spatial relations of animals and plants, particularly on a global scale (Polunin, 1960; Gleason & Cronquist, 1964; Daubenmire, 1978). The origins of biogeography stem from taxonomy, for only after animal and plant names were standardized could distribution information be accumulated and patterns be revealed (Daubenmire, 1978). Linnaeus (1707-1778), the founder of modern systematics first speculated that the world's biota originated from a single land mass, or "paradise" (Myers and Giller, 1988). But, it was a contemporary of Linnaeus, Buffon (1707-1788), who first alleged that the Old and New Worlds had no mammal species in common. Buffon did not discount Linnaeus's explanation of a center of origin, for he too believed that the Old World was "paradise" and the source area for all flora and fauna (Nelson and Platnick, 1981). The assumption of centers of origin has been used to explain historical distribution since the time of Darwin (1859). However, the centers of origin concept is no longer readily assumed because assumptions of vicariance have been just as useful in explaining taxonomic distributions (Croizat et. al., 1974; Nelson and Platnick, 1981). Also, such concepts do not explain patterns of Tertiary and Quaternary taxonomic distributions, which are usually very different for a given taxon (Lavin, 1994).

There are two methods, ecological and historical, to explain the biogeographical distribution of organisms. Neither method is exclusive of the other for they both have a common goal: to describe and understand how present geographical distributions evolved. However, they are essentially very different approaches. Ecological biogeography describes distribution patterns of extant species in terms of the organism's interaction with its environment. Historical biogeography explores the reasons for current distributions in terms of their history rather than exclusively in terms of their current ecology (Platnick and Nelson, 1981).

Historical Biogeography

Geographical distributions change because of the dispersal of organisms, the division of geographic regions (vicariance), adaptive radiation, and extinction (Connor, 1988). Explanations of historical biogeographical distributions have resulted in the seemingly polarized views of vicariance and dispersal.

Vicariance

Vicariance biogeography is concerned with discovering the common distribution patterns shown by unrelated taxa

(Platnick and Nelson, 1978). The relationships among areas of endemism are determined from congruent patterns of phylogenetic relationships of taxa that inhabit those areas. Primitive cosmopolitanism is assumed; that is, that the collective set of areas of endemism initially contained the same set of taxa. A certain sequence of vicariant events subsequently divided the originally cosmopolitan region into separate areas of endemism by promoting allopatric speciation. The relative ages of the sequences of these vicariant events can be inferred from the relationships between constituent taxa. Sister species should theoretically occupy the same two areas of endemism during the most recent vicariant event. Croizat et.al. (1974) state that the general features of modern biotic distribution have been determined by subdivision (vicariance) of ancestral biotas in response to changing geography.

Dispersal

Dispersal biogeography is concerned with the movement of species from a source area to a region of colonization. It follows the premise that a species expands its range either by undergoing a jump dispersal or a step by step progression (without jumps) over pre-existing barriers (Brundin, 1988). An ancestral species enlarges its range and is subsequently fragmented into two disjunct ranges. The two populations then differentiate through time forming two allopatric (geographically separated) descendant species. The appearance of a barrier which promotes the fragmentation of the ancestral species is implied. Nelson and Platnick (1981) argue that this model is the same as vicariance because the dispersal action takes place prior to the appearance of a barrier. Thus, dispersal biogeography assumes that an ancestral species crosses a pre-existing barrier (e.g. an ocean), thereby expanding and fragmenting its range simultaneously (Nelson and Platnick, 1981). Implicit in dispersal biogeography is the assumption of a center of origin.

Phenetic (Q-Mode) Analysis

The phenetic (Q-mode) method analyzes the biotic similarity among geographical sites (Conner, 1988). Site resemblance is assumed to indicate affiliation in the same biotic province (Hagemeirer and Stults, 1964), and therefore, that a historical relationship exists between sites (Nichols, 1988). The similarity of floras among regions suggests a degree of past (and present) floristic exchange due to proximity or appropriate dispersal corridors.

The main assumption of phenetics is that similarity in species ranges or floristic composition indicates historical relatedness. In biogeography, phenetic analyses of biotas have been used to assess the degree of relationship between two biotas (Connor, 1988). Initially, an extensive floristic survey is essential to pursue the question of historical influences using phenetics. Floristics provide an "objective, exhaustive and repeatable approach to vegetation analysis" (Major and Taylor, 1977). Floristics can thus become a standard by which historical biogeographic hypotheses can be tested (Hadley, 1984). Regional floristic data are essential for the recognition of phytogeographic problems and for any paleo-environmental reconstruction (Charlet, 1991). Floristic studies are repeatable and distribution data for all taxa can be collected and continually updated. Major and Taylor (1977) have emphasized that even data on the presence and absence of plants in an area contains environmental and evolutionary (historical) clues. Legendre (1986) states that the presence or absence of a species in a region can be regarded as a descriptor that does not change at random. The existence of repeated patterns in species distributions implies the operation of some general causal processes which in part explain the present day distribution of taxa (Myers and Giller, 1988). McLaughlin (1989) also found that analysis based on shared species reflects the floristic composition of an area. Investigation of floristic similarity establishes a basis from which regional floristic history can be developed and can provide additional information helpful in defining floristic provinces rather than using physical boundaries alone.

The relationship between sites can then be estimated by computation of an ad hoc or probabilistic statistic based on the number of taxa shared between sites (Simberloff and Connor, 1979).

Criticisms of Phenetic Analysis

Connor (1988) is critical of phenetic similarity indices stating that they may be poor estimates of historical relationships. One reason is that they depend on areas of different sizes, and the number of taxa are affected by the size differences. This criticism is accounted for in this study by adjusting: 1) the land areas of different-sized floras to a standard size; and 2) the floristic size by comparing only the shared taxa among the Centennial Region and the comparative floras. Additionally, Connor dismisses phenetic analysis because of the assumption that the diversity of all taxa at a particular site is controlled largely by forces operating on an ecological time scale (Hamilton and Rubinoff, 1963; Hamilton et.al., 1963; Strong et. al., 1977). However, historical influences can also be identified as determinants and would precede the ecological ones.

Species-Area Relationship

It is well known that the number of species increases systematically in samples of larger area and that the rate of increase of species number decreases with increasing area (Williamson, 1988). Species-area relationships have been discussed concerning islands (MacArthur & Wilson, 1967), but they can also be observed in the numbers of species occupying different-sized areas of the same geographical region (Begon et. al., 1990). This arithmetic plot of species number against area is described as curvilinear, with the number of species increasing more slowly at larger areas (Goodall, 1952). Species-area plots, by their nature, emphasize the continuity of natural variation (Williamson, 1988). Species richness may be positively correlated with area because larger areas constitute samples of more varied habitats, each with its respective species pool (Williams, 1964).

Another illustration of the species-area relationship is accomplished by plotting the species number against area on a log scale (Harper et. al., 1978, Begon et. al., 1990). MacArthur and Wilson (1967) give an approximation for the number of species with the equation:

$$S = CA^z \qquad (1)$$

where S is the number of species, A is the area, C is a constant and z is the slope of the line.

OPERATIONAL GEOGRAPHIC UNITS

Centennial Region, MT

The Centennial Mountains form much of the Continental Divide along the border between southwestern Montana and Idaho (Figure 1). It is one of the few ranges in North America that runs in an east-west direction, forming the south side of Centennial Valley from Monida Pass, Montana to the Henry's Fork of the Snake River in Idaho. Mount Jefferson on the east side of the range is the highest point, reaching an elevation of 3,114 meters.

The Centennial Valley is a high elevation (2,031 meters) intermontane valley centered on the headwaters of the Red Rock River and may be accessed via two passes: Monida Pass (2,061 meters) and Red Rock Pass (2,136 meters). The valley is located between 44^0 30' and 44^0 45' latitude and 111^0 30' and 112^0 40' longitude. Centennial Valley encompasses an area approximately 1,365 km^2, and is bordered on the northeast, northwest, and the south by the Gravelly Range, the Snowcrest Mountains, and the Snake River Plains respectively.

Geology

The Centennial Mountains belong to the Laramide orogeny

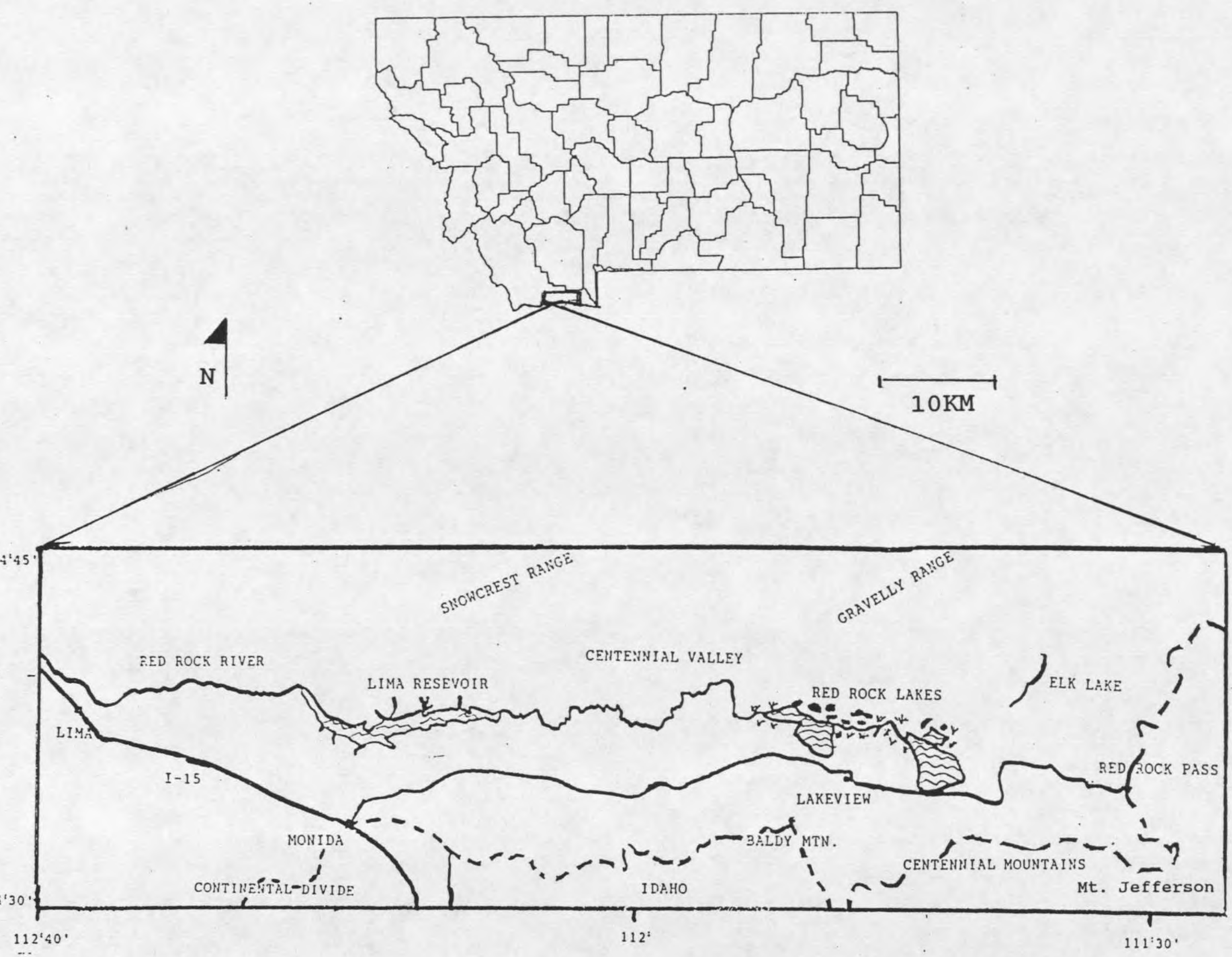


Figure 1. Location of the Centennial Region in southwestern Montana

system and are included in the broader category of the central Rockies (Eardley, 1951). The mountains are tectonic in origin, arising from the prominent Centennial fault, a fault block of east-west orientation which runs along the northern foot slope of the mountains. The Centennial Mountains to the south of the fault are the uplifted range-block and the Centennial Valley to the north is the down-thrown basin block, resulting in a 3,000 foot fault scarp. The uplift of the Centennial Range began in Lower Cretaceous time, which marked the advent of the Laramide orogeny, and continued to early Eocene time (Honkala, 1960).

The Centennial escarpment was further modified by glaciation during the Pinedale (70,000 to 15,000 y.a.) and Bull Lake (200,00 to 130,000 y.a.) stages (Taylor and Ashley, 1990). Small terminal moraines at the foot slope of the mountains are common as are small north-south trending glacial valleys and cirques. More recently, the scarp has been modified by avalanches and landslides which are evident along the mountain sides.

The rocks comprising the Centennial Mountains are: 1) Precambrian metamorphics; 2) Paleozoic, Mesozoic, and Cenozoic sediments; and 3) Cenozoic volcanics. The watershed to the east of the mountains which includes the Alaska Basin area and the Tom Creek drainage is comprised almost entirely of Precambrian metamorphosed carbonates (Taylor and Ashley, 1990).

Above these Precambrian metamorphics, at the headwaters of Red Rock Creek and Tom Creek, sedimentary rocks prevail. Represented in these high altitude rocks are Cambrian rocks progressively overlain by sedimentaries of: 1) Devonian Jefferson Limestone or Three Forks Formation; 2) Mississippian Madison Formation Limestone; 3) Permian Phosphoria Formation, Pennsylvanian Amsden and Quadrant Formation; and in some areas 4) Tertiary volcanics (Egbert, 1960; Taylor and Ashley, 1990). With the exception of the Phosphoria Formation which contains cherts, shales, and phosphorite (Cressman and Swanson, 1960), the above strata are primarily composed of limestone, dolomite, and sandstones (Mann, 1954).

The continuity of the Centennial Mountains is disrupted by a north-south trending fault through the Odell Creek drainage. Honkala (1960) theorized that this is a high-angle normal fault. The area west of the fault is composed of Tertiary volcanics. Mount Baldy dominates this area at an elevation of 3,016 meters.

The geologic composition of the Centennial Valley floor is Quaternary alluvium which resulted from the erosional breakdown of the surrounding mountains (Taylor and Ashley, 1990).

Climate

The Centennial Region is characterized by long cold winters and short cool summers. The average precipitation for 1993 was 45 cm. Average snowfall during the winter months is 385 cm (NOAA, 1993). The occurrence of snowfall in every month of the year is not uncommon.

The mean annual temperature is 1.1^{0}C. During extreme cold periods, air temperatures commonly drop to the -1^{0}C to -5^{0}C range. The maximum summer temperature rarely exceeds 32^{0}C (NOAA, 1993).

Although frost occasionally occurs during every month of the year, the average length of the frost-free season is approximately 51 days extending from mid-June to mid-August (Caprio et. al., 1990).

Soils

The soils of the eastern portion of the Centennial Mountains (east of Odell Creek) consist of rock outcrops and talus slopes at higher elevations and mollisols on the benches and terraces. The soils of the Centennial Mountains west of Odell Creek, north and south of the Red Rock River basin, are inceptisols and alfisols. The parent materials are colluvium and igneous and sedimentary rocks. The Red Rock River drainage contains characteristic mollisols from a cold, wet basin derived from the alluvium parent material. The soils surrounding the Lima Reservoir are calcareous aridisols and mollisols developed from the parent materials of alluvium and colluvium (Caprio et. al., 1990).

Soils of the Centennial Valley are currently in the process of being mapped by the Soil Conservation Service (Gomez, 1993).

Vegetation

In this study, the Centennial Region was divided into four vegetation zones: sagebrush\grassland, riparian, montane, and subalpine according to the classification presented by Pfister et. al. (1977) and Mueggler and Stewart (1980).

The sagebrush\grassland zone included three types at the lower elevations: 1) the foothills are dominated by big sagebrush (*Artemisia tridentata*), three-part sagebrush (*A. tripartita*), rabbit brush (*Chrysothamnus nauseosus* and *C. viscidiflorus*), Junegrass (*Koeleria nitida*), Sandberg bluegrass (*Poa secunda*), Idaho fescue (*Festuca idahoensis*), wheatgrasses (*Agropyron smithii, A. spicatum, A. dasystachyum*) and rye grasses (*Elymus cinerus, E. canadensis*); 2) the Centennial sandhills are dominated by thickspike wheat grass (*Agropyron dasystachyum*), silverleaf phacelia (*Phacelia hastata*), big sagebrush (*Artemisia tridentata*), threetip sagebrush (*Artemisia tripartita*), and Idaho fescue (*Festuca idahoensis*); and 3) the vegetation of roadside and disturbed areas consists mostly of smooth brome (*Bromus inermis*), Kentucky bluegrass (*Poa pratensis*) and Canada thistle (*Cirsium arvense*).

The riparian zone consists of lower, wetter meadows dominated by tufted hairgrass (*Deschampsia cespitosa*), sedges (*Carex* spp.) and rushes (*Juncus balticus*). The marshes and drainages are dominated by willows (*Salix* spp.) and small stands of aspen (*Populus tremuloides*) and spruce (*Picea engelmannii*). The aquatic areas include bullrush (*Scirpus acutus*), water milfoil (*Myriophyllum spicatum*), and water weed (*Elodea canadensis*).

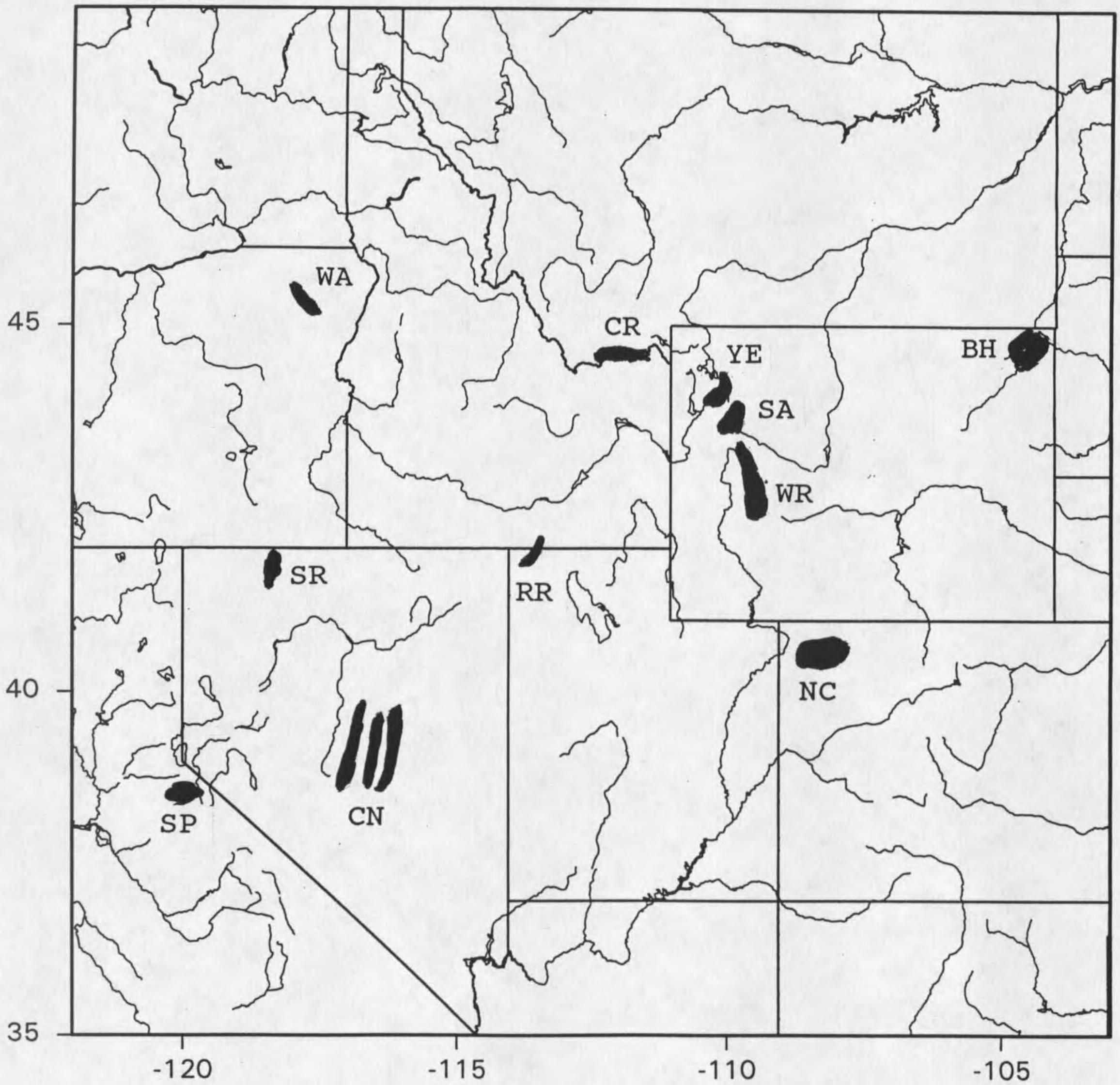
The montane zone is predominately coniferous forest dominated by Douglas fir (*Pseudotsuga menziesii*), northern reedgrass (*Calamagrostis stricta*), lodgepole pine (*Pinus contorta*), meadow rue (*Thalictrum venulosum*) and birchleaf spiraea (*Spiraea betulifolia*). The streams and cool higher slopes are characterized by spruce (*Picea engelmannii*) and false soloman's seal (*Maianthemum stellata*).

The subalpine zone consists of whitebark pine (*Pinus albicaulis*) and subalpine fir (*Abies lasiocarpa*) with occasional stands of limber pine (*Pinus flexilis*) with Idaho fescue (*Festuca idahoensis*). Rock cliffs and outcroppings included in this zone were dominated by rock mat (*Petrophytum caespitosum*), whitlow grass (*Draba oligosperma*) and mountain sorrel (*Oxyria digyna*).

Comparative Floras

The flora of the Centennial Region was compared with 10 regional floras. The comparative floras were chosen from available theses of floristic surveys of western North America in an attempt to include all geographic regions adjacent to the Centennial Region (Figure 2). In a phenetic (Q-mode) biogeographic analysis, each flora constitutes a Operational Geographic Unit (OGU) as described by Crovello (1981). The floras are drawn from 7 states and from areas ranging in size from 341 km^2 to 34,000 km^2.

Figure 2. Location of the study areas (Operational Geographical Units) according to their relative latitudinal positions.



Abbreviations:
CR-Centennial Region, MT
YE-Headwaters of the Yellowstone, WY
BH-Northwest Black Hills, WY
SA-Southeastern Absarokas, WY
NC-Flat Tops and White River Plateau, CO
WR-Western Wind River Range
WA-Wallowa Mountains, OR
SP-Sonora Pass, CA
CN-Toiyabe, Toquima, and Monitor Ranges, NV
SR-Santa Rosa Range, NV
RR-Raft River Range, UT

The author(s) of the floras, observed number of taxa (OBS), latitude and longitude, and area of the floras are given in Table 1. The floras are from the following floristic regions and provinces of North America according to Cronquist (1982):

<u>North American Prairies Province</u>
Northwest Blackhills, WY

<u>Vancouverian Province</u>
Sonora Pass, CA
Wallowa Mountains, OR

<u>Rocky Mountain Province</u>
Centennial Region, MT
Yellowstone Headwaters, WY
Western Wind River Range, WY
Southeast Absarokas, WY
Flat Tops and White River Plateau, CO

<u>Great Basin Province</u>
Raft River Range, UT
Toiyabe, Toquima, and Monitor Ranges, NV (Central NV)
Santa Rosa Range, NV

A total of 3217 native, exotic, terrestrial, and aquatic species including infraspecific taxa were recorded from the 11 western North American floras including the Centennial Region.

Table 1. Data used in the statistical analyses by Operational Geographic unit (OGU). Location of the OGUs are shown in Figure 1.

OGU	ABBV.	REFERENCE(S)	OBS	AREA (km^2)	LAT	LONG
Centennial Region, MT	CR	Culver, App.A Lowry, 1979 Dorn, 1968	766	1,347	44 35	111 50
Yellowstone WY	YE	Snow, 1989	887	3,820	44 00	110 00
Southeast Absarokas, WY	SA	Kirkpatrick, 1987	902	4,351	43 90	109 37
Western Wind Rivers, WY	WR	Fertig, 1992	1029	4,403	43 00	109 50
Flat Tops and White River Plateau, CO	NC	Vanderhorst, 1993	882	6,475	40 00	107 50
NW Black Hills, WY	BH	Marriot, 1985	976	6,475	44 50	104 50
Raft River, UT	RR	Preece, 1950	318	341	41 50	113 40
Santa Rosa Range, NV	SR	Charlet, 1991	375	1,595	41 60	117 50
Toiyabe, Toquima, & Monitor Ranges, NV	CN	Goodrich, 1981	1064	34,000	39 10	117 20
Sonora Pass, CA	SP	Lavin, 1983	824	2,500	38 40	119 80
Wallowa Mtns., OR	WA	Mason, 1975 Abrams, 1950, 1953, 1955 Abrams & Ferris, 1960	907	714	45 30	117 30

Abbreviations:

OGU-Operational geographic unit
OBS-Observed number of taxa per OGU
LAT-Latitude (estimated mid-point)
LONG-Longitude (estimated mid-point)

METHODS

Floristic Survey

The floristic survey of the Centennial Region was conducted between 10 May and 20 September 1993 and between 1 June and 20 August 1994. A total of 863 plant specimens were obtained and the primary set was deposited at the Montana State University Herbarium (MONT). Collection sites were chosen to represent the complete range of habitats and geography. These collection sites were sampled repeatedly during both field seasons and attempt was made to spend equal amounts of time in each of the four vegetation zones. However, due to constraints of access, some areas were sampled only a few times (e.g. avalanche chutes, scree slopes, rock outcrops). At each location, voucher specimens of all flowering and fruiting species were collected. Habitat information, associated species, and elevation were recorded for each specimen. The specimens were identified at the MSU Herbarium during the academic years of 1993-94 using floras of: Dorn (1984), Hitchcock and Cronquist (1961, 1964, 1973), Hitchcock et. al. (1959, 1969), Hermann (1970), Cronquist (1955, 1989), Cronquist et. al. (1984), Barkley (1978), Rollins (1993), and Barneby (1964). The more difficult determinations were verified by comparisons with specimens in the Montana State University Herbarium. Verification of many specimens was done by Dr. Jack Rumely and all *Castilleja* specimens were verified by Sarah Mathews. Following identification of the specimens, an annotated checklist was compiled. The checklist (Appendix A) was supplemented with riparian taxa from Dorn (1968) and subalpine taxa from Lowry (1979).

Sensitive Plant Survey

During the 1993 field season, populations of sensitive plants of the Centennial Region were surveyed under a contract with The Montana Natural Heritage Program (Nature Conservancy). Table 2 lists the sensitive plants that occur in the Centennial Region and their presence or absence within the 10 comparative floras. Known Centennial Region populations were relocated in addition to searching for new populations in appropriate habitats. The results are in the unpublished report, Sensitive Plant Species Inventory in the Centennial Valley, Beaverhead County, Montana (Culver, 1993).

The sensitive plant survey was continued in the summer of 1994 under a contract with the Bureau of Land Management. An addendum to the above report was submitted in September 1994 to the Billings, MT office (Culver, 1994).

Table 2. The presence or absence of the sensitive plant species (as of March 24, 1993) for the Centennial Region, MT within the 10 Operational Geographical Units (OGUs).

	CR	YE	BH	SA	NC	WR	WA	SP	CN	SR	RR
Aquilegia formosa	X	-	-	-	-	-	X	X	X	X	X
Astragalus argophyllus var. *argophyllus*	X	-	-	-	-	X	-	-	X	-	-
Astragalus ceramicus var. *apus*	X	-	-	-	-	-	-	-	-	-	-
Astragalus lentiginosus var. *salinus*	X	-	-	-	-	-	-	-	X	-	-
Astragalus leptaleus	X	-	-	-	-	-	-	-	-	-	-
Astragalus terminalis	X	-	-	-	-	-	-	-	-	-	-
Atriplex truncata	X	-	-	-	-	-	-	-	X	-	-
Balsamorhiza macrophylla	X	-	-	-	-	-	-	-	-	-	-
Carex idahoa	X	-	-	-	-	-	-	-	-	-	-
Carex multicostata	X	-	-	-	-	-	X	-	-	-	-
Carex vallicola	X	X	-	X	X	X	-	X	X	X	-
Castilleja rustica	X	-	-	-	-	-	-	-	-	-	-
Cryptantha fendleri	X	X	-	-	-	X	-	-	-	-	-
Downingia laeta	X	-	-	-	-	-	-	-	X	-	-
Elymus flavescens	X	-	-	-	-	-	-	-	-	-	-
Erigeron gracilis	X	X	-	X	-	X	-	-	-	-	-
Eriogonum ovalifolium var. *nevadense*	X	-	-	-	-	-	-	X	-	-	-
Gentiana aquatica	X	-	-	-	-	X	-	-	-	-	-
Gentianopsis simplex	X	-	-	-	-	-	X	-	-	-	-

Table 2 continued. The presence or absence of the sensitive plant species (as of March 24, 1993) for the Centennial Region, MT within the 10 Operational Geographical Units (OGUs).

	CR	YE	BH	SA	NC	WR	WA	SP	CN	SR	RR
Haplopappus nanus	X	-	-	-	-	-	-	-	X	-	-
Helenium hoopsii	X	X	-	-	X	X	-	X	-	-	X
Ipomopsis congesta var. *crebifolia*	X	-	-	-	-	X	-	-	-	-	-
Lesquerella sp. novum	X	-	-	-	-	-	-	-	-	-	-
Oenthera pallida var. *idahoensis*	X	-	-	-	-	-	-	-	-	-	-
Orobanche corymbosa	X	-	-	-	-	-	X	-	X	-	-
Potentilla plattensis	X	-	-	X	-	X	-	-	-	-	-
Primula alcalina	X	-	-	-	-	-	-	-	-	-	-
Ranunculus jovis	X	-	-	-	-	X	-	-	-	-	-
Senecio debilis	X	X	-	-	-	X	-	-	-	-	-
Sphaeralcea munroana	X	-	-	-	-	-	-	-	X	X	X
Stellaria crassifolia	X	-	-	X	-	X	-	-	-	-	-
Thalictrum alpinum	X	X	-	X	X	X	X	-	-	-	-
Thelypodium paniculatum	X	-	-	-	-	X	-	-	-	-	-
Thelypodium sagittatum var. *sagittatum*	X	-	-	-	-	-	-	-	-	-	-

Abbreviations: CR-Centennial Region, YE-Yellowstone, BH-Black Hills, SA-Southeastern Absarokas, NC-Northwestern Colorado, WR-Wind Rivers, WA-Wallowa Mtns., SP-Sonora Pass, CN-Central Nevada Ranges, SR-Santa Rosa Range, RR-Raft River Range

Quantitative Analysis

The Q-Mode site comparison method was used to analyze the flora of the Centennial Region with the 10 comparative floras. Comparisons of the individual vegetation zones within the Centennial Region and the 10 comparative floras were performed in an attempt to determine which modern day floristic region is more dominant in each elevational gradient with the Centennial Region.

The vicariance approaches were not used in this study due to: 1) the lack of areas of endemism (Centennial Region has no endemic taxa); and 2) the lack of phylogenetic studies of constituent taxa. Generalized track analysis (R-mode) or panbiogeography is a method that consists of mapping the geographic distributions (tracks) of monophyletic (descended from unique ancestry) taxa in an effort to determine if two or more tracks coincide. It is assumed that a given generalized track circumscribes regions that have a common history (Croizat et. al., 1974). Unlike the phenetic analysis where similarities using shared taxa are determined among biotas of different geographic areas, panbiogeography focuses on spatiotemporal analysis of the distribution patterns of organisms (Craw, 1983). R-mode is not amenable in this study since species distributions would extend to include most of western North America, if not much of the northern hemisphere. Therefore, little resolution could be achieved concerning the floristic relationships of the Centennial Region.

Q-mode analysis is based on the number of shared taxa among sites and is, therefore, amenable to the study of floristic relationships of the Centennial Region. Q-mode analysis will identify the relative cosmopolitanism among a set of sites. Given the very widespread nature of the species that occur in the Centennial Region (from Pacific Northwest to the Great Plains), Q-mode analysis was selected for this study. A phenetic analysis of the Centennial Region with the other floras from the contiguous geographic regions can identify the degree of cosmopolitanism.

Floristic Similarity

All similarity indices were calculated with the computer program NTSYS-pc (Rohlf, 1993). The degree of similarity between sites was determined by calculating the Jaccard's (1908) Index of Floristic Similarity (S_J). Jaccard's Index is based on the presence-absence relationship between the number of species common to two floras and the total number of species (Mueller-Dombois and Ellenberg, 1974). The assumption of shared absences is accounted for by omitting the absences or negative matches.

$$S_J = \frac{\text{species in common}}{\text{total sample size}} \qquad (2)$$

The Sorenson (1948) Index of Floristic Similarity (S_S) referred to as the Dice Similarity Index (Sokal and Sneath, 1963) in the NTSYS-pc program was calculated for each pairwise comparison. Although the results were similar to those obtained with the Jaccard Index, Dice's Index is not discussed here since it considers shared absences as an indication of relationship among geographical sites.

Jaccard's floristic similarity index was calculated for all pair-wise comparisons of plant associations and geographical regions. A rectangular data matrix consisting of 3217 taxa as rows and 11 geographical regions as columns was constructed in order to generate distance measures. When infraspecific identifications were not available for a given species, the nominate variety was assumed and entered for that species. The nomenclature of each flora was cross-checked for synonymy using Hitchcock and Cronquist (1961, 1964, 1973), Hitchcock et. al. (1959, 1969), Hermann (1970), Cronquist (1955, 1989), Cronquist et. al. (1984), Rumely and Lavin (1992) for Poaceae, and Hermann (1970) for Cyperaceae.

Distance (Similarity) Measures and Cluster Analysis

The distance data obtained from the similarity matrices were subjected to cluster analysis via the unweighted pair group method using arithmetic average (UPGMA) in the NTSYS-pc program. Relative similarities can thus be readily visualized on a dendrogram. The size of the floras should be kept in mind when determining results of cluster analysis since this type of distance measures is strongly biased by large differences in the sizes of floras forcing the small floras to cluster together and apart from the larger one. In an effort to diminish clustering artifacts due to size differences, distance matrices were generated by eliminating from the original matrix all those species that did not have an occurrence in the Centennial Region. The structure of the resulting dendrograms from such a modified distance matrix reflects primarily the number of taxa in each area, and secondarily shared similarity among the sites not including Centennial Region. Also, a distance matrix was derived from a data matrix of only shared genera among the geographical sites.

Species Richness

Connor (1988) stated that phenetic similarity indices may be poor estimates of historical relationships, because of the sensitivity of taxa numbers (richness) to area size. To account for this criticism, species richness of the Centennial Region was compared to the other floras by standardizing each flora's area. The data were adjusted to a standard area of 100 km^2 to compensate for the effect of different-sized areas of the OGUs, following Whitaker (1975):

$$\frac{\text{observed number of taxa}}{\log\ (\text{OGU area})} = \frac{\text{adjusted number of taxa}}{\log\ (100\ \text{km}^2)} \quad (3)$$

Additionally, the adjusted numbers of taxa allowed for a more accurate comparison of floristic richness of the Centennial Region with other regions of similar topography.

Species-Area Relationship

The asymptotic relationship between species and area was tested by plotting the observed number of species against the actual area. The number of observed taxa for each OGU was then plotted against actual area on a log graph. The equation from MacArthur and Wilson (1967) was used to obtain an approximation for the number of predicted species (Equation 1). The values for C and z were calculated using an optimizer function in Quattro Pro v5.0 (Borland International, Inc.), minimizing the sum of squared error. Finally, a linear regression was executed on the log-log plot. The analysis of the species-area relationship was performed to illustrate the parameter values that a regression yields, permitting a comparison of the bivariate distribution of species number and area (Connor and McCoy, 1979). The species-area relationship of the Centennial Region and the adjacent regional floras are examined here as a secondary component of biogeographical patterns.