

APPENDIX C
APPLICATION FOR USE
OWL CANYON PINON GROVE NATURAL AREA

Name of Applicant _____

Group Represented _____ Size of Group _____

Address _____
Street Town State

Phone Number _____

Period of time for which permit is requested _____ - _____
From To

Describe intended use, research or observations to be made.

A. Objectives _____

B. Methods _____

Expected number of visits _____ Size of group _____

Except by special permission, the applicant agrees to remove all evidence of human activity created by the applicant or applicants group before expiration of the permit and report any irregularities to CSFS.

Permittee Signature _____

Permit Number _____ Date _____

Permission _____
Granted Denied Permittee

Reason for denial:

Colorado State Forest Service
Administrator

Other Referrals

CSU Natural Areas Committee

STATE OF COLORADO

Division of Parks & Outdoor Recreation
Colorado Natural Areas Program

1313 Sherman Street, Rm. 618
Denver, Colorado 80203
Phone (303) 866-3437

cc: *Tom*
Ray M



October 7, 1988

Mr. Jim Hubbard, State Forester
Colorado State Forest Service
Colorado State University
Ft. Collins, Colorado 80523

Mr. Walt Gaul, Regional Supervisor
Colorado Division of Wildlife
317 West Prospect Street
Ft. Collins, Colorado 80526

Roy Romer
Governor
Ron C. Holliday
Director
David W. Kuntz
Program Administrator

Dear Walt and Jim: *Jim*

I updated the Colorado Natural Areas Council at its September meeting in Meeker on the current situation at the Owl Canyon Pinyon Grove Natural Area and the Division of Wildlife's Brackenbury property. The following summary captures the essence of the Council discussion.

o Retain Natural Areas Designation for Brackenbury Property

The Council recommended retaining the entire Brackenbury property (north and south of U.S. 287) in the designated Colorado Natural Area. The Council determined that the Brackenbury property provides a valuable buffer for the main part of the pinyon grove, in addition to the good quality grassland (north portion) and the archeological value and pinyon trees on the property. The Council supported the development of educational and interpretive uses for the Brackenbury property, although it was unwilling to specify how that development might be accomplished.

o Revise and Update Owl Canyon Management Plan

The Council supported revising and updating the Owl Canyon Management Plan to include the Brackenbury property and to address current management issues. The Council indicated that it was satisfied with Colorado State Forest Service management oversight for Owl Canyon, although it recommended improving and strengthening the efficiency of the access permit process. The Council directed Program staff to coordinate with the Division of Wildlife and State Forest Service to complete the management plan. As part of that process I will request an opinion from the State Archeologist regarding the significance and condition of the Folsom site.

o Continue to Permit Public Access by State Forest Service

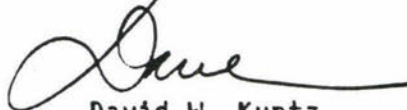
The Council determined that more information was needed before it could make a recommendation on the public access issue. The Council directed Program staff to evaluate public access during the revision of the Owl Canyon Management Plan. The Council indicated that controlled public access is desirable within the constraints of existing and future land uses on the Brackenbury property. Council recommended continuing the permit system used by the State Forest Service.

Council action did not specifically address the question of retaining the Brackenbury property in public ownership. I am assuming that the Council supports retaining the Brackenbury property in public ownership, since the Council supported retaining the Colorado Natural Area designation for the property. The Council briefly discussed the possibility of the Colorado Division of Parks assuming management responsibility for Owl Canyon. The Council decided to wait until the Owl Canyon management plan is revised before recommending a change in agency management.

All of the interested parties agree on the desirability of revising the Owl Canyon Management Plan. I will work with you on setting a meeting date to begin that process and to prepare a revised draft of the management plan for that meeting.

Thanks very much for your help and willingness to resolve the management issues at Owl Canyon. I will be in touch soon and look forward to getting together with you. Be sure to let me know if loose ends remain on this end regarding recommendations from the Natural Areas Council.

Sincerely,



David W. Kuntz
Director
Colorado Natural Areas Program

DWK:11:2730A

cc: John Wilkes, SLB
Ron Holliday, DPOR

OUTDOORS/Nature

As bird migration goes, hawks steal the show

By KEVIN COOK
For The Coloradoan

When the hawks migrate, oh what a show they can put on.

Thousands and thousands of hawks all turning flank to wind.

Little songbirds, shorebirds and some seabirds migrate in enormous flocks, too. But they make a less spectacular show of their movements.

Songbirds and shorebirds migrate at night when you can hear their stay-in-touch call notes but can't see the birds themselves. The great swarms of seabirds typically migrate far out to sea where few people ever get to see them.

Hawks migrate by day. They patiently wait until morning sun has warmed the land and set the air in motion. They work the wind until they find the right updraft then they spiral upwards until they're mere specks.

A mile or more high, the hawks depart, gliding southward, losing altitude and searching for their next updraft.

The activities of hawks which have found their updraft attracts the attention of other hawks that join them. By mid-morning a small gathering of hawks, called a "kettle," forms and they move southward as a group. Different kettles may merge as they meet.

Swainson's and broad-winged hawks are the two species most likely to form kettles. Other hawks frequently mingle in, especially northern harriers, red-taileds and sharp-shinned.

Certain localities around the country attract exceptionally high numbers of migrating hawks: Cape May, N.J., Hawk Mountain, Pa., and Duluth, Minn., among others.

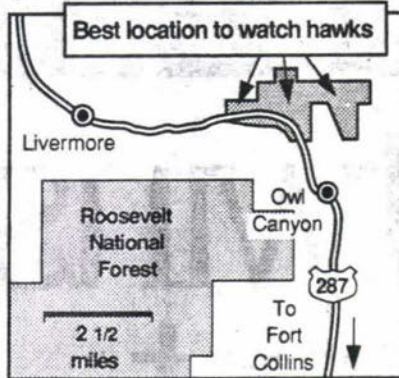
Pathfinder

Attracting as many hawk-fancying people as hawks, Hawk Mountain is undoubtedly the most famous North American hawk-watching spot. Several thousand hawks a day may pass the mountain in season.

Colorado has some hot spots, too, though nothing like Hawk Mountain. The best local area is the pinyon grove north of Fort Collins. In early September you may see a couple hundred hawks of maybe 13 species in one day.

Only the most unimaginative mind could witness all those hawks and fail to consider all the mouse dinners and grasshopper hors d'oeuvres that fuel these annual migrations.

Pack yourself a lunch, a cooler of cold drinks, some sunscreen and a notepad then go give the hawk migration a try.



DIRECTIONS: Take U.S. 287 18 miles north of Fort Collins to the Brackenbury State Wildlife Area. Climb atop the ridge and watch particularly to the north and west for incoming hawks.

MEMORANDUM

Pinyon Grove
Folder
Management Plan

TO: ALL FIELD OFFICES
FROM: TOM OSTERMANN *Tom*
DATE: APRIL 6, 1987
SUBJECT: PINYON-JUNIPER SITE QUALITY - GROWING STOCK RELATIONS
REMARKS:

Attached is a copy of a draft "SITE QUALITY AND GROWTH - GROWING STOCK RELATIONS FOR SOUTHWESTERN PINYON-JUNIPER WOODLANDS."

The manuscript was originally written in metric so the typed figures that you see above the line are the English conversion.

APR 7 1987

DRAFT

SITE QUALITY AND GROWTH - GROWING STOCK RELATIONS FOR
SOUTHWESTERN PINYON-JUNIPER WOODLANDS

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ACKNOWLEDGEMENTS

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USDA Forest Service Rocky Mountain Experiment Station and
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Affairs.

SITE QUALITY AND GROWTH - GROWING STOCK RELATIONS
FOR SOUTHWESTERN PINYON-JUNIPER WOODLANDS

ABSTRACT

Site quality and growth-growing stock relations were developed for southwestern pinyon-juniper woodlands. Anamorphic height-age site index curves were developed from a regional sample of 60 woodlands. Site index was unaffected by variation in stocking and was correlated with woodland yield when used in conjunction with density.

Pinyon and juniper PAI, when taken separately, were highly correlated with stand density and pinyon site index. Pinyon was twice as productive as juniper at similar stand densities. Pinyon and juniper yields in woodlands of average density and site index were estimated at 0.29 and $2.1 \text{ ft}^3/\text{acre}/\text{yr}$ ^{4.1} $0.15 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$. At high densities pinyon and juniper yields increased to 0.61 and $0.31 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ ^{8.7} $4.4 \text{ ft}^3/\text{acre}/\text{yr}$. Pinyon and juniper yields appeared independent of the density of the other species in an individual woodland. Maximum yield of dense mixed stands on average sites was $0.78 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ ^{11.1 ft³/acre/yr}, and occurred when pinyon accounted for 65% of woodland density. The influence of structural stage on yield and the effect of density on diameter development should be quantified to provide a complete set of density management tools for woodland managers.

growth and yield, mixed species, Pinus edulis, Juniperus monosperma, Juniperus osteosperma

INTRODUCTION

The ability to assess potential productivity and to estimate growth rates on lands covered by southwestern pinyon-juniper woodlands is a critical element for improving silvicultural practices. Indiscriminate exploitation and attempted type conversion to grasslands have been common practices in the past (Aro 1971). More recently, woodlands are seen as a manageable, renewable resource providing a unique mix of benefits over a substantial land area. Estimates of potential productivity and response to management activities are required to devise and assess treatment alternatives.

The xeric environment and complex stand structures of woodlands have discouraged development of quantitative managerial tools similar to those available for most forested lands in the United States. Growth of pines and junipers found in woodlands is often assumed to be fundamentally different from the growth of trees in more mesic environments since complete tree canopy closure rarely occurs in the xeric environment. Woodlands are complex mixtures of tree ages and species. Southwestern woodlands are commonly composed of one Pinus species and one or more Juniperus species of the three Pinus and five Juniperus species found in the region (Pieper 1977). Age class and species structures are influenced by past human use and fire history (Meeuwig and Cooper 1981). These conditions have often been taken as indications that common

site and yield estimation approaches are not applicable to woodlands.

A reasonable estimate of site quality is an essential element of many forest management activities, especially yield forecasting and silvicultural prescription. At its most basic level, a site quality classification scheme ranks land, according to relative potential to produce a given crop (Tesch 1981). More sophisticated schemes may use direct measurement of actual yields (Bradley et al. 1966) or predict site quality from site environmental variables (Meeuwig and Cooper 1981). Site quality is specifically defined as the "amount of wood produced in a given time..." (Daniel et al. 1979) and is a basic characteristic of the land itself. Since actual yields are influenced by management history direct estimators are rarely used. Rather, indirect estimators of site quality, such as site index, are much more common.

Another critical factor for developing silvicultural prescriptions is an understanding of the specific relation between yields and density for a forest type. Density management regimes define the density required to achieve a desired level of volume production. Regions of volume production can be defined in relation to density for a given site index (Long 1985). At low densities volume production may increase more or less linearly with increased density. At these densities, the stand is not fully stocked, and some volume increment is sacrificed.

However, gains may be made in diameter growth rates or understory forage production due to the low stocking of the overstory (Clary et al. 1974, Rippel et al. 1980). At some increased density, the stand is fully stocked, and most of the gross volume production of the site is realized. It is therefore important to define the relation between gross volume increment and density.

Despite the extensive coverage of the pinyon-juniper forest type in the southwestern United States, relatively little empirical growth information is available. This includes the lack of a generally applicable method for assessing site quality, and estimates of yield in relation to woodland density and species composition. Our first objective was to develop a site quality estimation system that was consistent with inventory procedures, independent of density, and useful in developing yield functions. Our second objective was to determine if whole stand yield estimation procedures could be applied to structurally complex pinyon-juniper woodlands.

METHODS

The study area was restricted to the southwestern pinyon-juniper woodland type which covers 4.29 million acres in New Mexico, 4.94 million hectares in Arizona and 1.90 million hectares in Colorado. Further, species composition was restricted to woodlands composed of pinyon pine (Pinus edulis Engelm.), and one-seed (Juniperus

monosperma (Engelm.) Sarg.), or Utah juniper (J. osteosperma (Torr.) Little). These woodlands are generally found between 1400 and 2300 m in elevation where annual precipitation is between 30 and 50 cm (Springfield 1976). The type is variable with respect to climate where seasonal, latitudinal and elevational differences in precipitation occur (Jameson 1969), and geomorphology where soil texture, parent material and depth differ throughout the region (Springfield 1976).

Temporary plots were established in 129 woodlands in rough proportion to their occurrence in the study area. Woodlands were stratified by apparent site quality, stocking, size, and species composition and were selected to represent a range of woodland types with respect to these variables (Table 1). Plots were not located in stands with insect or disease damage that would effect growth. Care was taken to avoid woodlands where black-stain root disease (Verticicladiella wagnerii) was present and where infection by pinyon dwarf mistletoe (Arceuthobium divaricatum) and juniper mistletoe (Phoradendron juniperinum) exceeded very light levels. Also, stands disturbed within the past 20 years were excluded from sampling.

Variable-size, rectangular plots were established to encompass 30 to 40 live and dead pinyon and juniper trees over 2.5 cm in diameter at stump height (DSH) where SH was taken at 15 cm above the root collar. Plot size was

Table 1. Characteristics of sampled southwestern pinyon-juniper woodlands.

VARIABLE	MEAN	S.D.	MIN.	MAX.
Average stand diameter (cm)	7.9	2.6	3.8	17.8
Stems (ha ⁻¹)	20.1	6.7	9.6	45.3
Average stand height (m)	36.7	23.3	20.2	1445.1
Stand density index	90.7	57.6	50	3571
Pinyon stand density index	12.5	3.3	6.9	26.6
Juniper stand density index	3.8	1.0	2.1	8.1
Basal area (m ² ha ⁻¹)	218.5	97.1	17.8	457.3
Volume (m ³ ha ⁻¹)	540	240	44	1130
Site Index (m)	100.4	85.4	0	351.7
Percent Pinyon (%)	248	211	0	869
Gross volume increment (m ³ ha ⁻¹ /y ⁻¹)	111.7	97.9	0	356.9
Net volume increment (m ³ ha ⁻¹ /y ⁻¹)	276	242	0	882
	108.9	53.6	10.0	250.5
	25.0	12.3	2.3	57.5
	877.5	624.5	80.0	4123.1
	61.4	43.7	5.6	288.5
	24.0	6.6	12.8	45.9
	7.3	2.0	3.9	14.0
	43	35	0	100
	5.1	2.7	1.0	16.9
	0.36	0.19	0.07	1.18
	2.3	8.7	-49.0	16.9
	0.16	0.61	-3.43	1.18

limited to approximately ^{0.25 acre} 0.1 ha. Understory cover was measured along three line transects evenly spaced within each plot. Plot dimensions, landform, elevation, slope aspect, soil parent material, and soil depth were recorded.

Age at the root collar and total height were measured for two or three vigorous pinyons on or near each plot. Selected trees were free of visible defect and were of good crown form, but were not necessarily the largest trees present. Sixty plots were used to develop height age site index for pinyon. One-third of the 60 plots were located in each of three visually determined site quality classes - good, medium and poor. Thirteen of these were "fully-stocked" plots where understory cover was 10% or less (Meeuwig and Cooper 1981) paired with nearby "less-than-fully-stocked" plots of similar apparent site quality of lower stocking where understory cover was greater than 10%.

All living and dead trees greater than ^{1.0 in} 2.5 cm DSH were numbered for reference. Species, crown class, condition, DSH, crown form, crown dimensions and total height for each tree were recorded. Additionally each tree was recorded as live, dead less than ten years or dead greater than ten years. If a fork occurred below DSH, each of the individual stems were measured at stump height and the equivalent diameter was determined. In the case of multiple stems below stump height, an equivalent quadratic mean diameter was determined for each tree as follows:

$$\text{Equivalent Diameter} = \sqrt{\sum_{i=1}^n \text{DSH}_i^2}$$

where: DSH = diameter at stump height
 n = number of stems at stump height

Equivalent diameter was used for all further calculations which depended on DSH.

Following measurement of the standing trees, a disk or two increment cores were removed from the primary stem of each tree at stump height. Disks and cores were labelled and returned to the laboratory for measurement of 10-year radial growth increment. Ten year diameter increment for each core or disk was measured on a Bannister Incremental Measuring Device and was used to determine DSH 10 years prior to sampling by subtraction from current DSH. Diameter growth of multiple stem trees was determined as a function of the ratio of equivalent stem to primary stem basal areas and the diameter growth of the primary stem. Height 10 years prior to measurement was determined by subtraction of estimated 10-year height increment from measured current height. Current height and height 10 years prior to sampling was estimated from a height - diameter regression based on a random sample of 225 pinyon and 187 juniper trees. Estimated 10-year height increment was determined as the difference between estimated current and backdated heights.

Current and backdated tree volumes to a 1.0 in 2.5 cm top were determined from volume equations developed by Clendennon

(1979). Pinyon volumes were estimated from DSH and height, and juniper volumes were estimated from equivalent DSH, height and number of stems per tree below SH. Ten-year volume increment was determined by subtraction.

RESULTS AND DISCUSSION

Site Quality Estimation

Our first objective was to develop a procedure to characterize potential productivity of southwestern woodlands. We felt that any index derived should not be influenced by density or stand history, must be compatible with commonly measured inventory data, and should be a continuous variable useful in developing growth estimators. Therefore, we examined the relation between height and total age for pinyon trees to evaluate the feasibility of height-age site index curves for woodlands.

Graphical analysis indicated that height-age data for the pinyon site index trees was similar in form to that observed for most conifers. The Chapman-Richards function was fit to these data. Guide curve development based on this function requires the estimation of parameters θ_1 , θ_2 , and θ_3 in the following equation (Clutter et al. 1983, Aguirre-Bravo and Smith 1986):

$$H = \theta_1 [1 - \exp (- \theta_2 A)]^{[(1 - \theta_3)^{-1}]}$$

θ_1 = Asymptotic height
 θ_2 = Rate " θ_1 " is approached
 θ_3 = Allometric parameter
 H = Tree height
 A = Tree age

The parameters θ_1 , θ_2 , and θ_3 of the Chapman-Richards function were estimated using a non-linear regression procedure (Dixon 1983). The non-linear procedure minimized the residual sum of squares of the predicted values while producing unconstrained final parameter estimates:

$$\begin{aligned} \theta_1 &= 7.63 \text{ m} \quad 25.03 \text{ ft} \\ \theta_2 &= .01353 \\ \theta_3 &= .0621 \end{aligned}$$

Residual sum of squares = 282

Mean square error = 2.91

When these estimates are substituted into the Chapman-Richards equation, the guide curve is:

$$H = 7.63 \left[1 - \exp \left(- \frac{25.03}{A} \right) \right]^{1.06628}$$

A height-age curve for one site index given the age of reference (A_0) and the asymptotic level (θ_1) is as follows:

$$S = \theta_1 \left[1 - \exp \left(- \frac{25.03}{A_0} \right) \right]^{1.06628}$$

Prediction of individual tree site index from height and age measurements at A_0 of 200 years is determined from the following equation:

$$S = H \left[\frac{.93305}{1 - \exp(-.01353811 A)} \right]^{1.06628}$$

The reference age of 200 years was chosen with regard to the age at which the height age curves approach an asymptotic height. These equations produce a family of anamorphic site index curves which can be used to derive an estimate of site index at base age 200 for pinyon pine from measures of total age and height (Figure 1).

We applied two tests to determine the stability and relevance of height-age based site index for these woodlands: 1.) whether estimates were repeatable and independent of density and 2.) whether site index explained variation in volume increment after an adjustment was made for density. In the first analysis, we compared estimates of site index for "fully-stocked" plots to similar estimates for paired "less-than-fully-stocked" plots. When plotted against each other, differences in estimates appeared unbiased (Figure 2) and the slope of a regression through the data was not significantly different from 1. In the second analysis, we compared the results of two regression models to predict gross stand volume increment (ln PAI) - one using an estimate of woodland density expressed as Stand Density Index (SDI) (Reineke 1933, Daniel et al. 1979, Long 1985) alone and one using SDI in

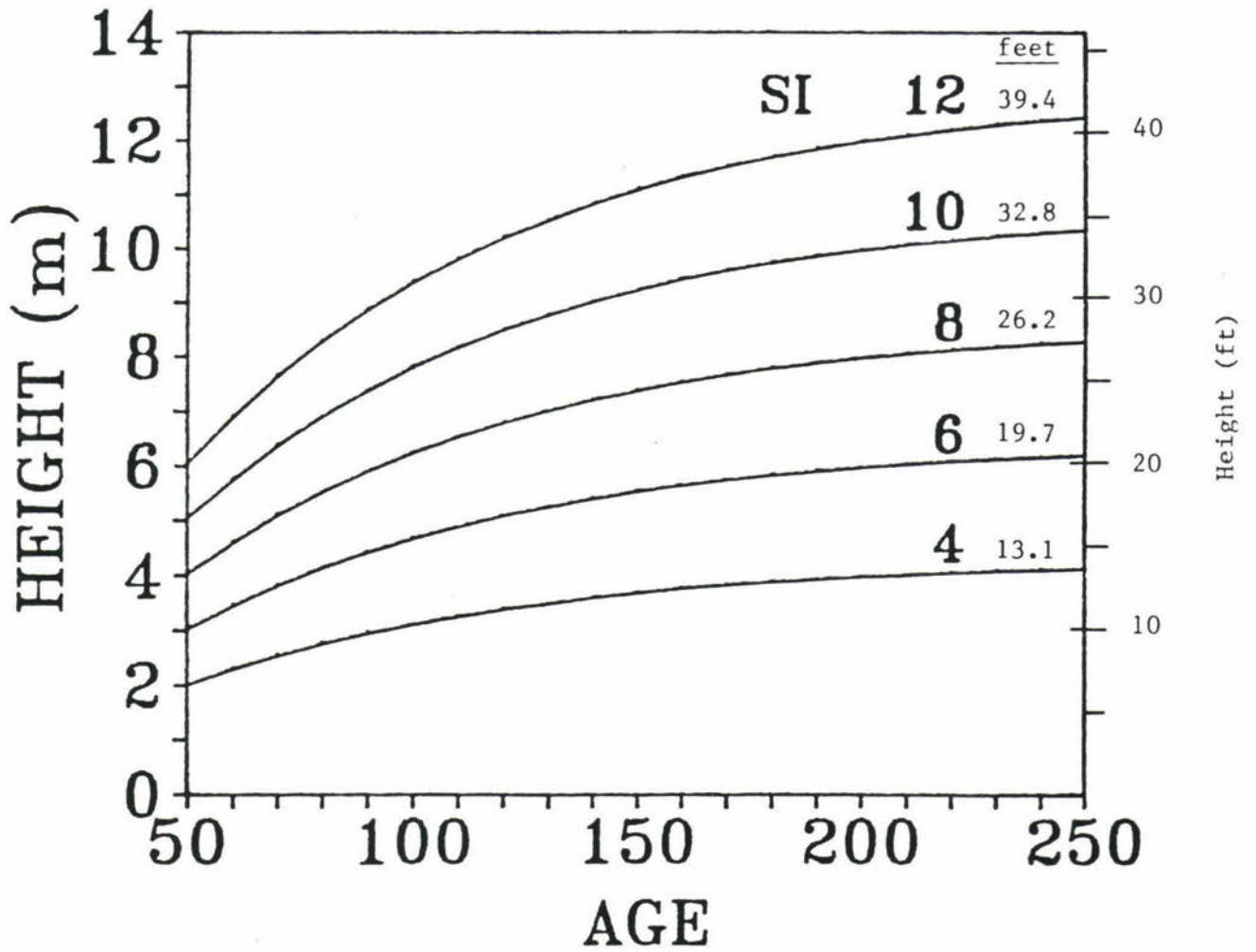


Figure 1. Total height - total age anamorphic site index curves for southwestern pinyon pine at base age 200 years (SI_{200}).

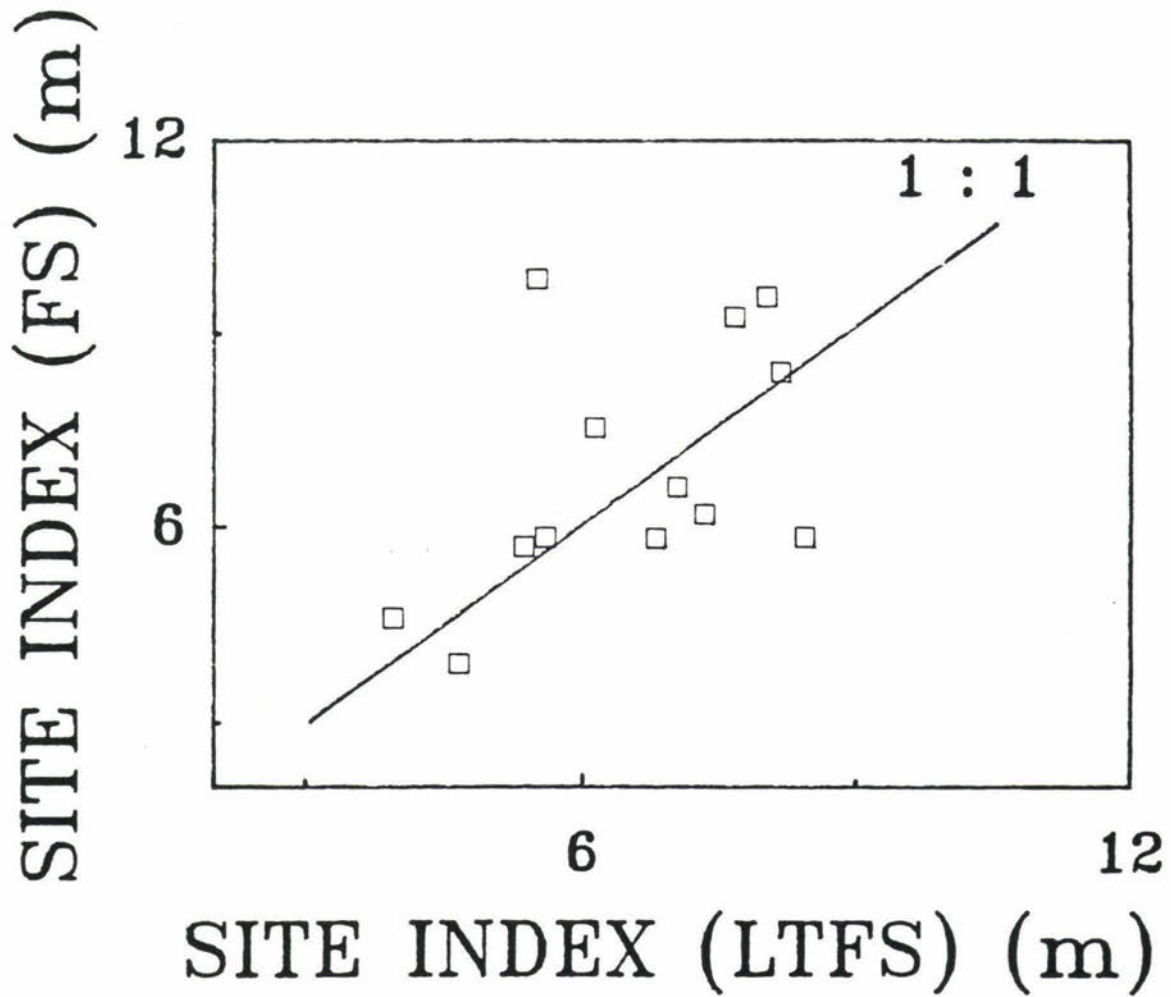


Figure 2. Site index comparison of paired plots for "fully-stocked" (FS) and "less-than-fully-stocked" (LTFS) woodlands.

conjunction with SI_{200} . The addition of SI_{200} to the model increased the coefficient of determination from 0.50 when using SDI alone to 0.70.

Height-age based site index curves meet two critical quantitative tests for use in woodlands. Estimates are repeatable and are apparently unaffected by density. Also, site index is correlated with volume increment when the model is adjusted for differences due to density. Further, site tree measurements are commonly incorporated in inventory design.

We feel that these site index curves represent an important improvement over existing site quality estimators for pinyon-juniper woodlands. Woodland basal area (Howell 1940) and basal area growth of "fully-stocked" woodlands (Meeuwig and Cooper 1981) have been proposed as measures of site quality. Basal area is itself a measure of density and is affected by management practices. Determination of "full-stocking" is based on understory cover which may be affected by grazing (Arnold et al. 1964) and even year-to-year variation in weather (Campbell and Ryan 1982). Allometric relations between height and diameter (Daniel et al. 1966) and diameter and crown volume (Tausch 1980) have also been suggested as site quality estimators for woodlands. Height and crown allometry may be influenced by stand density, potentially obscuring a relation between height at a given diameter or an allometric constant, and site quality. Height-age relations are relatively

insensitive to density effects, and provide a useful index for yield estimation.

Growth-Growing Equations

We examined the relationship between 10-year periodic annual increment (PAI) and SDI of woodlands. There is a general increase in volume increment as SDI increases, but there is considerable variability in the relation. Two factors may explain a considerable proportion of this variation - differences in species composition and differences in site quality. Volume increment at a given density would be expected to vary directly in proportion to differences in land productivity, as measured by site index, and soil type. Also, it might be expected that there are fundamental differences between the growth of pinyon and juniper. For example, in a woodland where density was evenly divided between pinyon and juniper, more than half of the volume increment may be produced by one species. Gross PAI is higher for pinyon than juniper at any given density (Figure 3). Therefore, separate relations were developed for pinyon and junipers. No differences were found in the growth relations of J. osteosperma or J. monosperma and they were treated as a group.

We described gross PAI as a function of density and site for pinyon and junipers (Table 2). All growth equations are fit with a monomolecular growth function

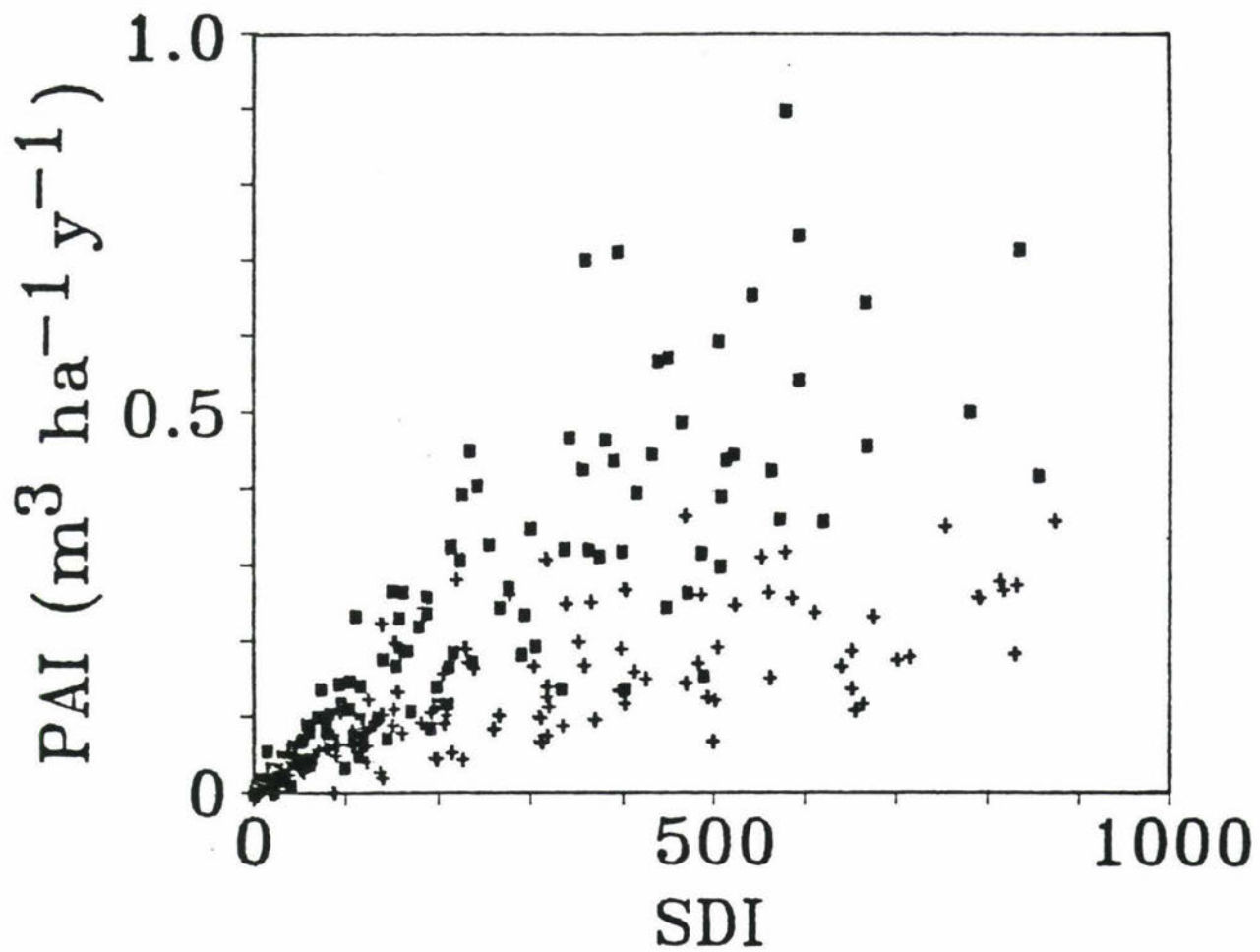


Figure 3. Gross periodic annual increment (PAI) of pinyon (squares) and juniper (crosses) components of southwestern pinyon-juniper woodlands in relation to Stand Density Index (SDI).

Table 2. Growth - growing stock equations for southwestern pinyon-juniper woodlands by species and soil parent material. All data were fit with the equation: $PAI = SI(x_1 - x_2 \exp^{-x_3 SDI})$. PAI is 10-year gross periodic annual increment ($m^3 ha^{-1} y^{-1}$), SI is pinyon site index at base age 200 (m), SDI is stand density index, and x_1 , x_2 and x_3 are parameter estimates.

Species	Soil parent material	x_1	x_2	x_3	n	R ²	Mean Square Error
Pinyon	all	9.5167×10^{-2}	9.5071×10^{-2}	1.8832×10^{-3}	118	0.70	0.009893
Juniper	all	4.6431×10^{-2}	4.5441×10^{-2}	2.0011×10^{-3}	115	0.63	0.005251
Juniper	sandstone	5.1502×10^{-2}	4.9971×10^{-2}	1.2033×10^{-3}	51	0.67	0.005676
Juniper	volcanic	4.8279×10^{-2}	4.8408×10^{-2}	2.6133×10^{-3}	33	0.71	0.007074
Juniper	other	4.8331×10^{-2}	4.6051×10^{-2}	2.2937×10^{-3}	32	0.29	0.015043

equivalent English units equations are:

$$PAI = 4.356 SI (x_1 - x_2 \exp^{-2.471x_3 SDI})$$

where PAI is $ft^3/acre/year$

SI is site index (feet)

SDI is stand density index acre basis

using a nonlinear parameter estimation procedure (Caceci and Cacheris 1984). Stand density index and pinyon SI were significantly correlated with PAI for pinyon and juniper woodland components. The coefficients of determination of the relations for pinyon and juniper were 0.70 and 0.63 and mean square errors were 0.00989 and 0.00525. Substitution of basal area for SDI resulted in slightly lower coefficients of determination for both pinyon and juniper (Table 3). We feel these equations are adequate descriptors of pinyon-juniper woodland yield relations. The correlations between SDI and SI_{200} , and PAI were relatively high considering the inherent variability in size, age and species composition of woodlands.

Growth - growing stock curves can be developed from the individual species growth equations and used to analyze the volume production capabilities of woodlands with respect to stocking and site (Figures 4 and 5). There are substantial differences between yields of pinyon and juniper components of woodlands when densities are similar.

At SI_{200} ^{26.2 ft} 8m, PAI of pinyon and juniper are estimated as ^{4.1 ft³/acre/yr} 0.29 m³ha⁻¹y⁻¹ and ^{2.1 ft³/acre/yr} 0.15 m³ha⁻¹y⁻¹, when SDIs of both are 101 (acre basis) 250, near the average for sampled woodlands. At densities near the ^{344 (acre basis)} observed maximum (SDI = 850), ³PAI's were estimated at ^{8.7 ft³/acre/yr} 0.61 m³ha⁻¹y⁻¹ for pinyon and ^{4.4 ft³/acre/yr} 0.31 m³ha⁻¹y⁻¹ for junipers. Across a wide range of densities, pinyon is about twice as productive as juniper.

Species composition and relative stocking of woodlands

Table 3. Growth - growing stock equations for southwestern pinyon-juniper woodlands by species and soil parent material. All data were fit to the equation: $PAI = SI(x_1 - x_2 \exp^{-x_3 BA})$. PAI is 10-year gross periodic annual increment ($m^3 ha^{-1} y^{-1}$), SI is pinyon site index at base age 200 (m), BA is basal area ($m^2 ha^{-1}$), and x_1 , x_2 and x_3 are parameter estimates.

Species	Soil parent material	x_1	x_2	x_3	n	R ²	Mean Square Error
Pinyon	all	6.7050×10^{-2}	6.8564×10^{-2}	9.2300×10^{-2}	118	0.68	0.010659
Juniper	all	3.9960×10^{-2}	3.9095×10^{-2}	5.6021×10^{-2}	115	0.59	0.005751
Juniper	sandstone	4.2432×10^{-2}	4.0681×10^{-2}	3.0370×10^{-2}	50	0.64	0.005960
Juniper	volcanic	4.2125×10^{-2}	4.1310×10^{-2}	6.4288×10^{-2}	33	0.82	0.007612
Juniper	other	4.0957×10^{-2}	3.9508×10^{-2}	7.8797×10^{-2}	32	0.41	0.014755

equivalent English units equations are:

$$PAI = 4.356 SI (x_1 - x_2 \exp^{-0.2296x_3 BA})$$

where PAI is $ft^3/acre/year$
 SI is site index (feet)
 BA is basal area ($ft^2/acre$)

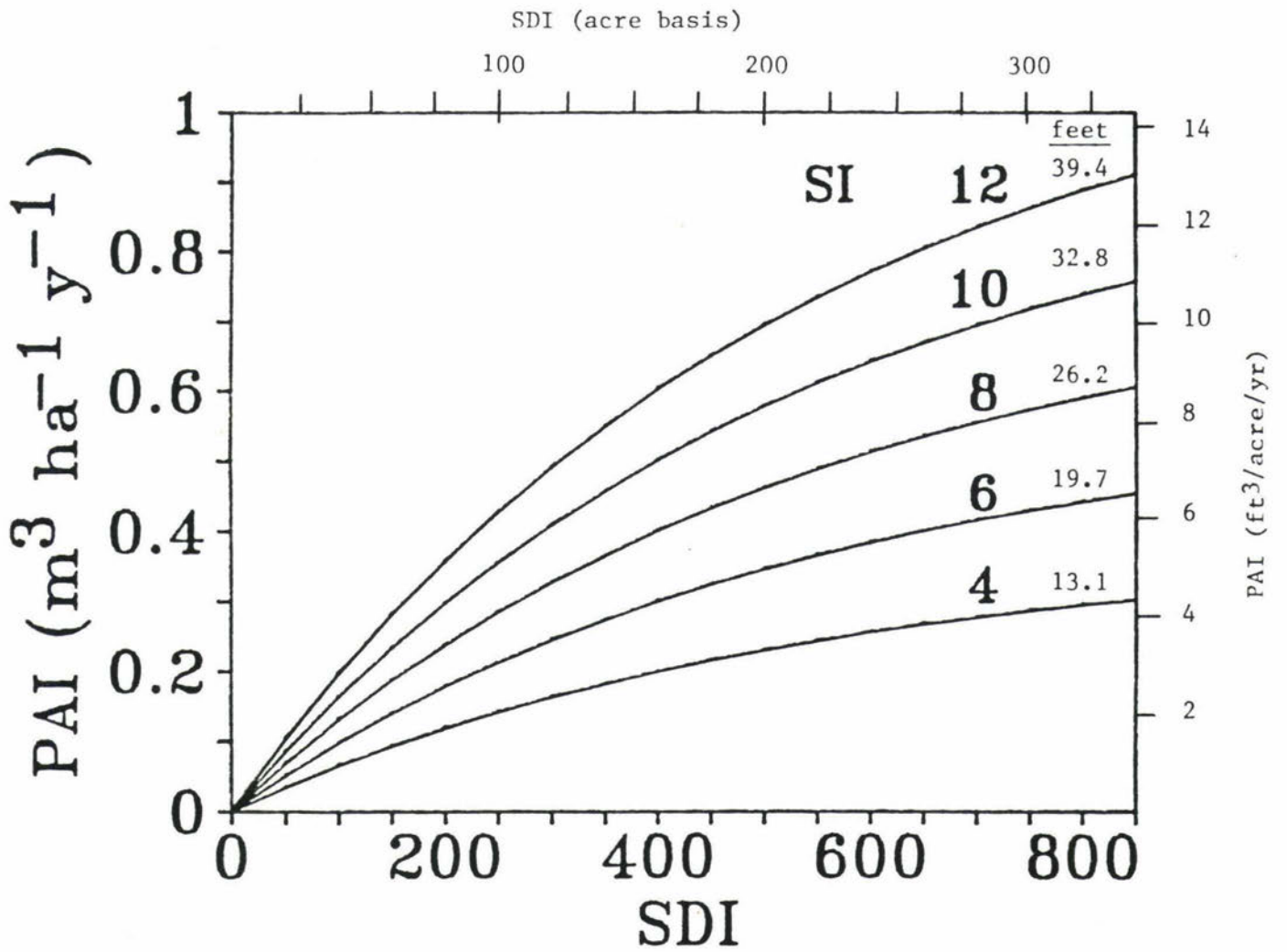


Figure 4. Estimated gross periodic annual increment (PAI) for the pinyon component of southwestern pinyon-juniper woodlands in relation to Stand Density Index (SDI) and pinyon site index (SI_{200}).

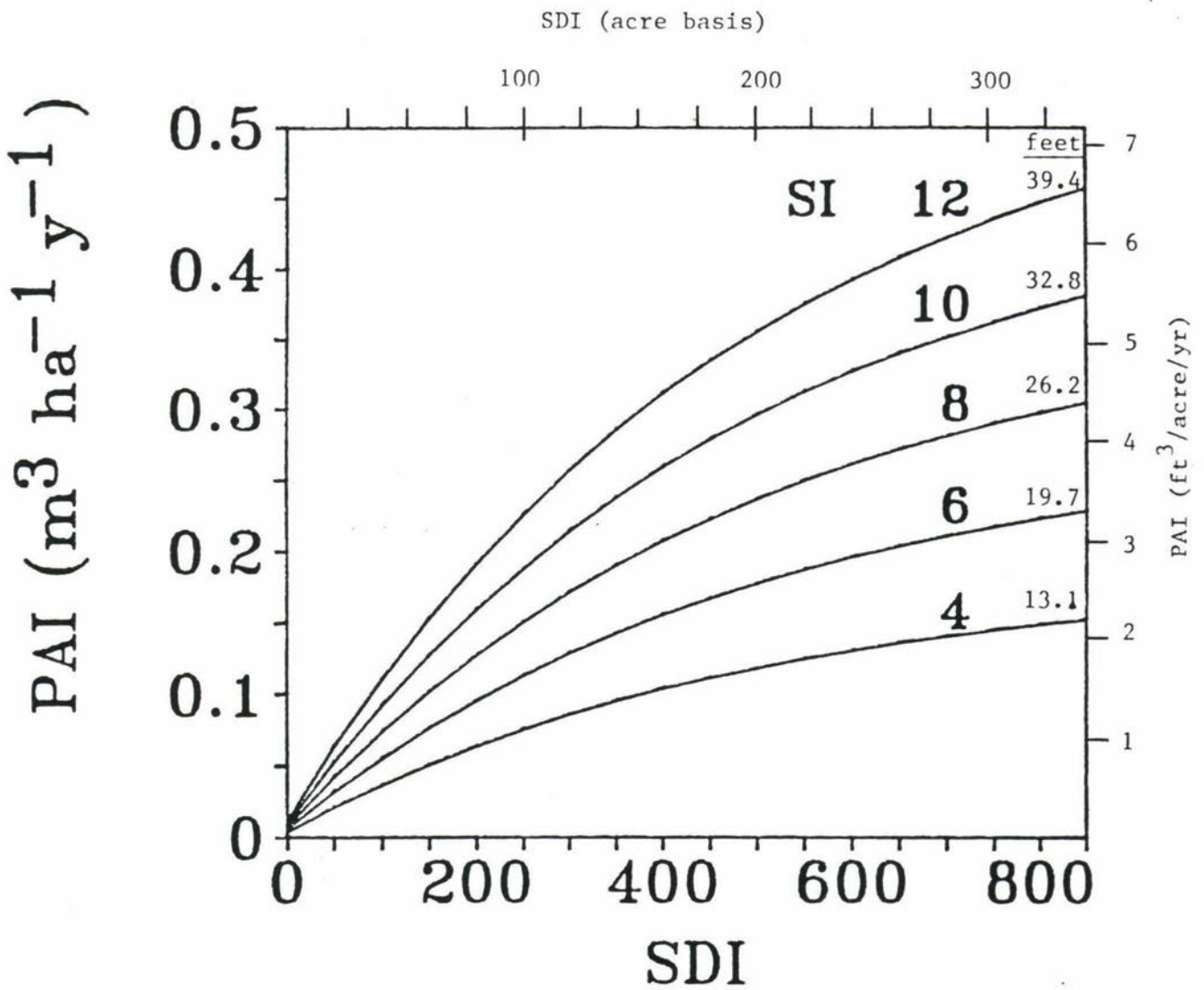


Figure 5. Estimated gross periodic annual increment (PAI) for the juniper component of southwestern pinyon-juniper woodlands in relation to Stand Density Index (SDI) and pinyon site index (SI_{200}).

would influence the expected growth rate because of the large differences in PAI between species. Gross PAI of one species must be independent of the density of the other species present to use separate equations for pinyon and juniper to describe growth of mixed species stands. We examined residuals of each species' growth equation relative to the SDI of the other species present (Figure 6). Residuals were unbiased, indicating that growth of either species is independent of the density of the other. Therefore, the effect of species mix was examined by varying species densities within the limits of the observed maximum density for woodlands (SDI = ^{465 (acre basis)} 1150) and for separate species components (SDI = ^{344 (acre basis)} 850) (Figure 7). Maximum woodland PAI at SI₂₀₀ ^{26.2 ft} 8 m of ^{11.1 ft³/acre/yr} 0.78 m³ha⁻¹y⁻¹ occurs when pinyon represents 65% of woodland SDI. Increment declines rapidly when the percentage of pinyon falls below about 60% of the total woodland density. At SI₂₀₀ ^{45.9 ft} 14 m, the highest observed site index, PAI at a woodland SDI of ^{465 (acre basis)} 1150 was ^{19.6 ft³/acre/yr} estimated at 1.37 m³ha⁻¹y⁻¹.

Besides species differences in yield, there are also differences in volume increment across soil types. For juniper, PAI was higher on soils derived from a volcanic parent material than on soils derived from a sandstone parent material. Volume growth equations were derived for junipers on three soil parent material classifications - sandstone, volcanic and other (Table 2). Pinyon SI was a significant variable for each soil parent material, but

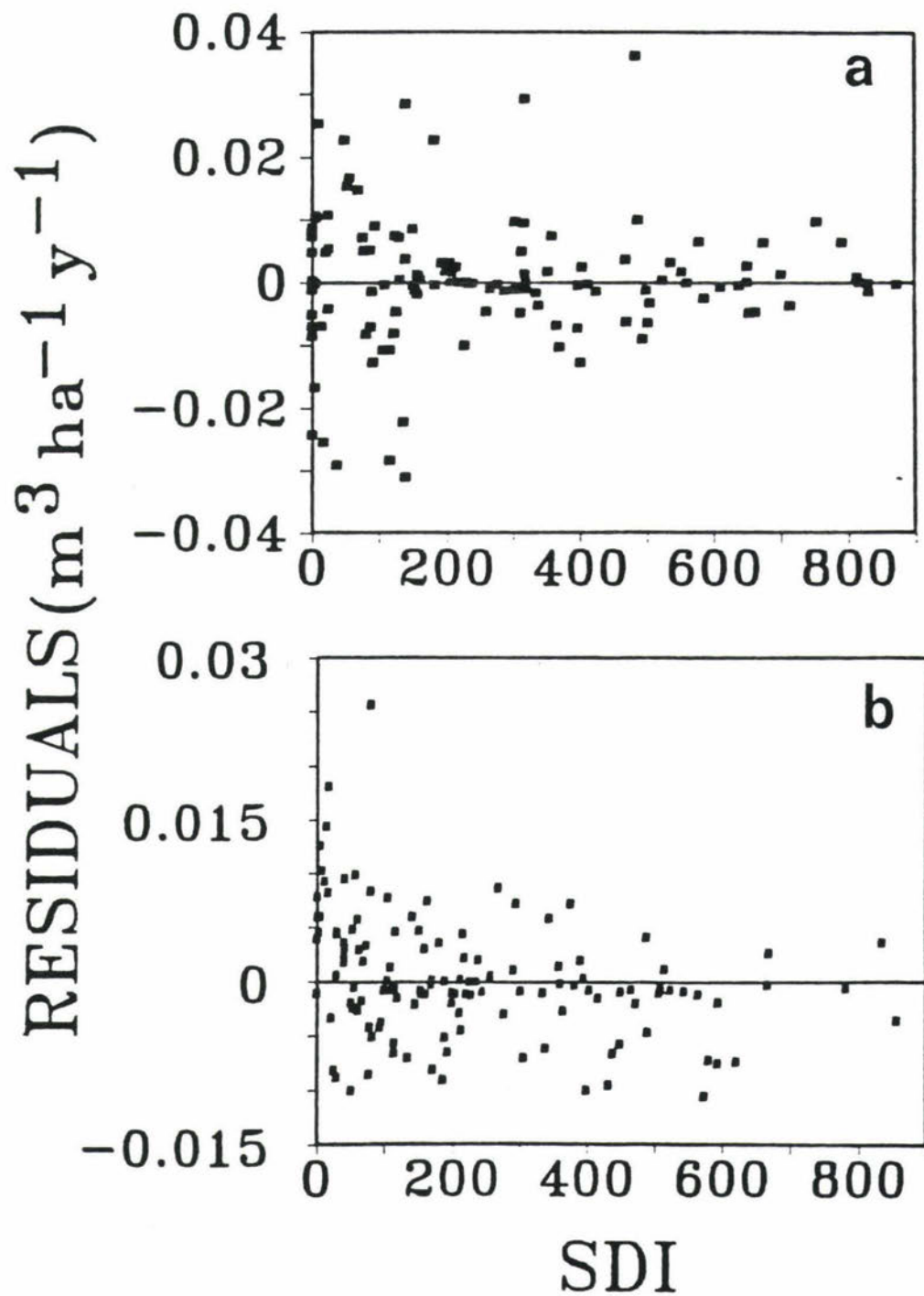


Figure 6. Residuals of the growth equations for pinyon (a) and juniper (b) plotted against the Stand Density Index (SDI) of the other species present on the plot.

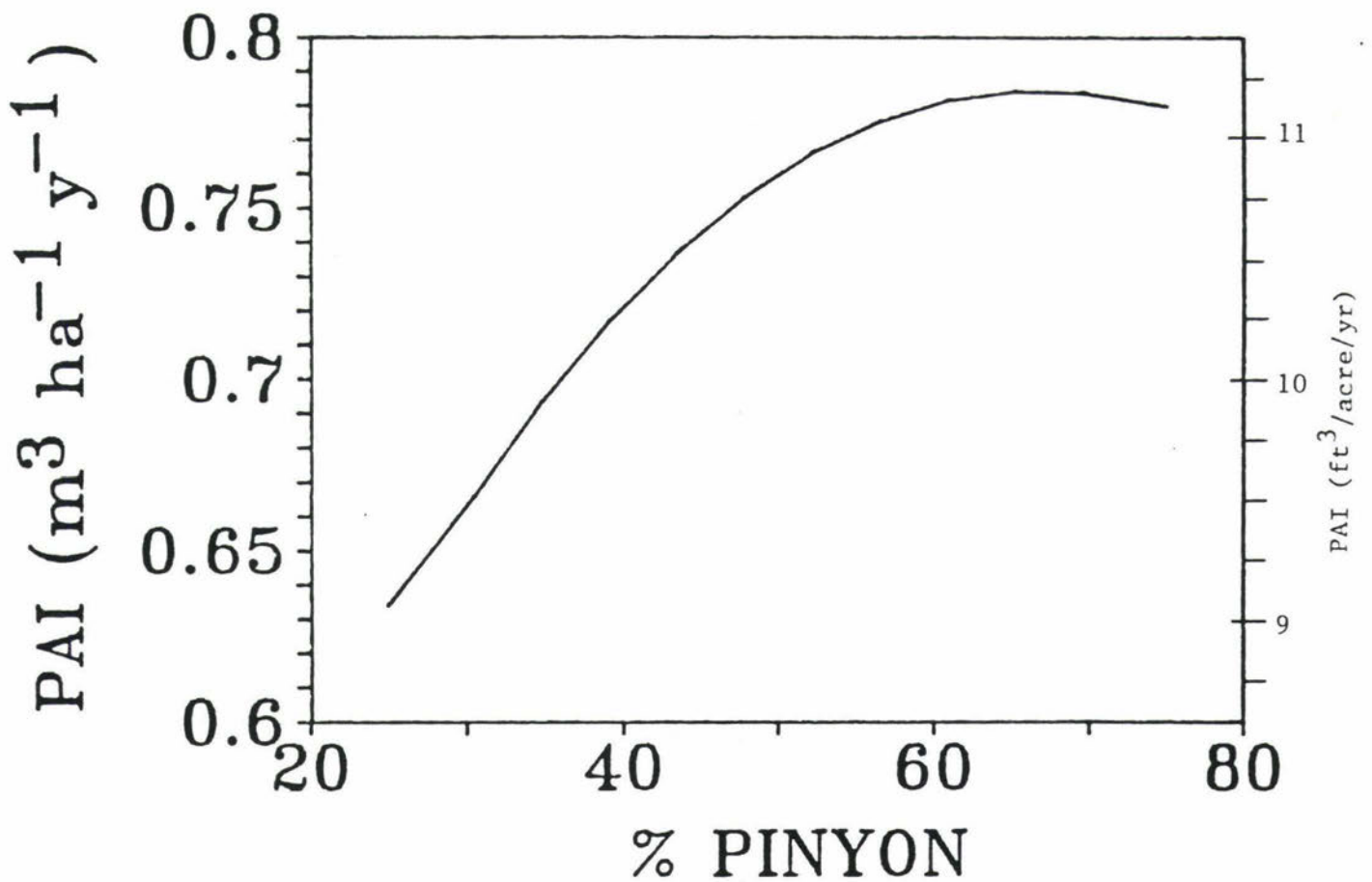


Figure 7. Estimated gross periodic annual increment (PAI) of mixed species woodlands at pinyon site index (SI_{200}) 8m where maximum woodland Stand Density Index (SDI) is 1150 and maximum pinyon or juniper SDI is 850.

SI_{200} = 26.2 ft
 maximum SDI = 465 (acre basis)
 maximum pinyon or juniper SDI = 344

growth was greater on volcanic derived soils than on sandstone derived soils when density and pinyon SI were the same (Figure 8). For example, at an SDI of 850 for juniper and a SI of 8 m, growth on volcanic derived soils is 0.34 $\text{m}^3\text{ha}^{-1}\text{yr}^{-1}$, 22% greater than for the same stand conditions on a sandstone derived soil, where growth is $0.27 \text{ m}^3\text{ha}^{-1}\text{yr}^{-1}$.

Equations described so far do not incorporate age or a measure of stand development. This is difficult to accomplish for woodlands since species, size and age class structures are complex. The relation between height at a given age and site quality was used to describe developmental stage of pinyon might be as a function of mean stand height relative to SI_{200} . Gross woodland PAI was transformed as the division of PAI by the ratio of SI_{200} and mean stand pinyon height. The relation between transformed PAI and pinyon SDI was linear:

$$\begin{aligned}
 \text{PAIT} &= 0.0446 + 0.00475 \text{ SDI} & \text{PAIT} &= 0.637 + 0.168 \text{ SDI} \\
 R^2 &= 0.79 & \text{SE} &= 0.49 & \text{where PAIT} &= \text{ft}^3/\text{acre}/\text{yr}/\text{ht}/\text{SI} \\
 & & & & \text{SDI} &= \text{acre basis}
 \end{aligned}$$

where: PAIT is $\text{PAI}/(\text{mean pinyon height}/\text{SI}_{200})$

As mean stand height of pinyon increases, estimated PAI increases. The effect of this transformation is similar to that proposed by Arney (1985) where site height increment was used to adjust PAI of even-aged Douglas fir stands for differences due to site and age. Site height has been successfully used to substitute a common stand variable for age to depict the relation between volume accretion and

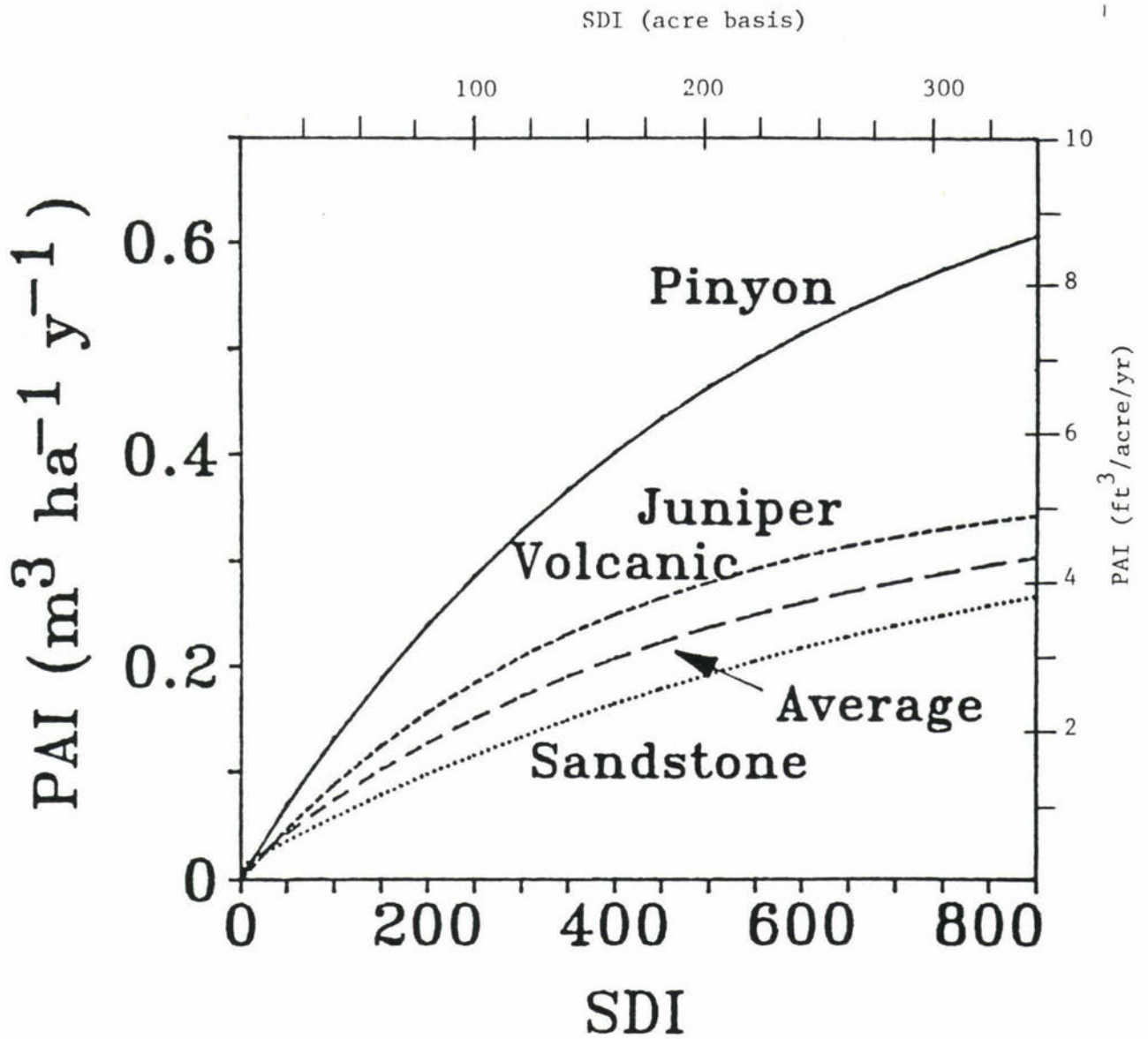


Figure 8. Differences in estimated juniper gross periodic annual increment (PAI) on soils derived from volcanic and sandstone parent materials relative to estimated average juniper and average pinyon gross PAI.

time (McCarter and Long 1986, Drew and Flewelling 1977). In contrast to the relatively simple stand structures where these techniques have been applied, pinyon-juniper woodlands are not even-aged, making a direct link between height and time or age tenuous. These results, however, do suggest that time and developmental stage have a significant influence on woodland growth rates.

CONCLUSIONS

The complex age class structure and species composition of pinyon-juniper woodlands taken with the regional environmental variability in the type has led to the assumption that site quality and yield estimation procedures used in mesic forest types are of limited use. Height-age based site index curves proved valid on a regional scale suggesting that, at least for pinyon, height growth is related to site productivity. Differences between soil types in growth of juniper at a given site index indicate that soil-site relations are important factors in site productivity. Soil-site indices should prove to be especially appropriate to woodlands since they are not dependent on the presence, age or vigor of existing vegetation.

Development of growth-growing stock relations for woodlands appears to be a tractable problem. When woodlands are broken into components by species, much of the variability in the relation between yield and density

can be accounted for. Growth-growing stock curves present an important initial tool for designing density management prescriptions for the woodland type. Densities can be chosen to realize desired levels of gross yield and to determine appropriate species mixes. Structural stage was an important influence on stand growth for pinyon, but was not incorporated in our general growth-growing stock models. Future work should clarify the influence of age or structural stage on growth and the relation between density and tree diameter.

LITERATURE CITED

- ARNOLD, J.F., D. A. JAMESON AND E.H. REID. 1964. The pinyon-juniper type of Arizona: effects of grazing, fire and tree control. USDA Prod. Res. Rep. No. 84. pp.
- ARNEY, J. D. 1985. A modeling strategy for the growth projection of managed stands. Can. J. For. Res. 15:511-518.
- ARO, R. S. 1971. Evaluation of pinyon-juniper conversion to grassland. J. Range Manage. 24:188-197.
- BRADLEY, R. T., J. M. Christie, and D. R. Johnston. 1966. Forest Management Tables. Her Majesty's Stationery Office, London. 218 pp.
- CACECI, M. S. AND W. P. CACHERIS. 1984. Fitting curves to data. Byte 9:340-362.
- CAMPBELL R. E. AND M. E. RYAN. 1982. Precipitation and temperature characteristics of forested watersheds in Central Arizona. USDA Gen. Tech. Rpt. RM-39 12pp.
- CLARY, W. P., M. B. BAKER, P. E. O'CONNELL, T. N. JOHNSON, JR., AND R. E. CAMPBELL. 1974. Effects of pinyon-juniper removal on natural resource products and uses in Arizona. USDA For. Ser. Res. Pap. RM-128. 28pp.
- CLENDONON, G. W. 1979. Gross cubic-volume equations for pinyon and juniper trees in northern New Mexico. USDA For. Serv. Res. Pap. INT-228. 21 pp.
- DANIEL, T.W., J.A. HELMS and F.S. BAKER. 1979. Principles of Silviculture. 2nd edition. McGraw-Hill C o., N.Y. 500 pg.
- DANIEL, T. W., R. J. RIVERS, H. E. ISAACSON, E. J. EBERHARD, and A. D. LeBARON. 1966. Management alternatives for pinyon-juniper woodlands. A. Ecological phase: the ecology of the pinyon-juniper type of the Colorado Plateau and the Basin and Range Provinces. Utah State Agric. Exp. Stn. 242 pp.
- DIXON, W. J. 1983. BMDP Statistical Software. University of California Press. Berkeley, California. 733 pp.
- DREW, T. J. AND J. W. FLEWELLING. 1979. Stand density management: an alternative approach and its application to Douglas-fir plantations. For. Sci. 25:518-532.

- HOWELL, J. 1940. Pinyon and juniper: a preliminary study of volume, growth and yield. 90 pp. USDA Soil Conservation Service, Regional Bulletin No. 71, Region 8.
- JAMESON, D. A. 1969. Rainfall patterns on vegetation zones in northern Arizona. Plateau. 41:105-111.
- LONG, J.N. 1985. A practical approach to density management. Forestry Chronicle 61:23-27.
- MCCARTER, J.B. and J.N. Long. 1986. A lodgepole pine density management diagram. West. J. Appl. For. 1:6-11.
- MEEUWIG, R. O. AND S. V. COOPER. 1981. Site quality and growth of pinyon juniper stands in Nevada. For. Sci. 27:593-601.
- PIEPER, R. D. 1977. The southwestern pinyon-juniper ecosystem. in Ecology, uses and management of pinyon-juniper woodlands. USDA For. Serv. Gen. Tech. Rpt. RM-39. 48 pp.
- REINEKE, L.H. 1933. Perfecting a stand density index for evenaged forests. J. Agric. Res. 46:627-638.
- RIPPEL, P. B., R. D. RYAN, AND G. A. LYMBERG. 1980. Short term vegetational response to two-way cabling in pinyon-juniper vegetation. New Mexico State Univ. Agr. Exp. Res. Pap. 410. 5pp.
- SPRINGFIELD, H. W. 1976. Characteristics and management of southwestern pinyon-juniper ranges--The status of our knowledge. USDA For. Serv. Res. Pap. RM-160. 32 pp.
- TAUSCH, R. 1980. Allometric analysis of plant growth in woodland communities. Ph.D. dissertation, Utah State University, Department of Range Science. 143p.
- TESCH, S. D. 1981. The evolution of forest yield determination and site classification. For. Ecol. Manage. 3:169-182.

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NEWSLETTER



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PINYON IN THE COLORADO FRONT RANGE

The outlier of *Pinus edulis* at Owl Canyon, about 25 km north of Fort Collins, is well known. In 1961, W. A. Weber reported 2 pinyons in Rist Canyon, some 19 km south of Owl Canyon (T. 8 N., R. 70 W., Sections 28 and 29). Since then, five other pinyon localities have been found in Larimer County: two additional areas in Rist Canyon (T. 8 N., R. 70 W., Sections 30 and 32), north fork of the Poudre River (T. 9N., R. 70 W., Sec. 15), Hewlett Gulch (T. 9 N., R 71 W., Sec. 27), and Poudre Canyon near Fort Collins Mountain Park (T. 9 N., R. 72 W., Sec. 4). The latter area is about 26 km WSW of the Owl Canyon Grove. In all these localities, only one or a few trees are present and they probably are a result of spread by jays from the main Owl Canyon Grove.

The northernmost locality of the main population of pinyon along the Front Range seems to be in southern Douglas County. Pinyon was recently collected on the west side of the Rampart Range in Missouri Gulch (T. 10 S., R. 69 W., Sec. 35), about 16 km north of Woodland Park.

The northernmost locality on the east side of the Rampart Range seems to be Douglas Creek, 5 km north of Garden-of-the-Gods, El Paso County. E. L. Little (Atlas of United States Trees, Vol. 1. Conifers and Important Hardwoods, U.S. Dept. Agric., 1971) shows a location in southern Douglas County on the east side of the Rampart Range, but this has not been confirmed.

Pinyon has also been collected in Boulder County: Boulder Canyon, 14 miles west of Boulder. Dr. Weber says that only a single tree was found (which was subsequently removed) and it was probably not native. Little shows a pinyon location in central Jefferson County, but I have not been able to confirm this report.

Any further information on the natural distribution of pinyon in the Colorado Front Range would be appreciated. Frank Hawksworth, U.S. Forest Service, Rocky Mountain Station, 240 W. Prospect St., Fort Collins, Colorado 80526.

LEBER
1965

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V. S. Hartshorn

Fossil Arc. Bull. p. 456

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Princeton
See p. 463

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PLANT GEOGRAPHY IN THE SOUTHERN ROCKY MOUNTAINS

W. A. WEBER¹

THE FOLLOWING discussion of plant geography in the Southern Rocky Mountains is an attempt to assemble impressions accumulated during eighteen years of residence in this area. The Southern Rocky Mountains, for the purposes of this discussion, are those mountain ranges lying south of the Wyoming deserts, west of the Great Plains, north of Santa Fe, New Mexico, and westward to and including the Wasatch, Uinta, La Sal, and Abajo Mountains of Utah and the San Francisco Peaks of Arizona. Floristically the area forms a unit, effectively isolated on all sides by lowlands in the form of plains, deserts, or lower mountain ranges. The major development of alpine tundra in the western United States occurs in this area. The Black Hills of South Dakota, while lying well to the northeast, are very closely related to the Southern Rockies by their strong element of the Cordilleran flora and are a key to a detailed understanding of floral migrations during the Pleistocene.

Phytogeographically the Southern Rocky Mountain region is an extremely complicated area. It harbors remnants of the ancient Tertiary flora that existed there in Florissant and Creede (late-Tertiary) times. The mountains themselves have been major highways for north-south movement of plants between the American Arctic and, according to some phytogeographers, the South American Andes. Several of the major river systems draining into the Pacific Ocean and the Gulf of Mexico originate there and provide pathways of migrations for plants, while the divides between the river systems constitute effective barriers at the same time. The mountain area now is effectively isolated on all sides from similar alpine areas by arid steppes or lowlands, but at one time or another different segments of its periphery must have been open to floristic traffic. The Southern Rockies constitute one terminus of a track that once led from the mountains of Central Asia to the Mexican Plateau. On the American continent the area holds the greatest concentration of circumpolar species at their southernmost limits.

The physical attributes of the mountains for this role are exceptional. Aside from the features already mentioned, the Southern Rockies contain the greatest concentration of high peaks, 52 over 14,000 ft (4,240 m) and the largest area of alpine tundra outside Alaska. A wide variety of life-zones, from alpine to Upper Sonoran, are telescoped locally within narrow linear distances. The Continental Divide not only reaches here its easternmost approach on the Continent, but it meets the plains by way of an abrupt escarpment that results in local climatic anomalies critical for the flora.

Several problems arise when one places the outline of the

present vegetation against the background of the Quaternary period, and these have been kept in mind, below, in making a division of the flora into its obvious "elements," or clusters of species whose geographical patterns roughly coincide, for reasons that may be part ecological, part historical. An attempt is then made to place these elements in perspective as to their wider holarctic patterns and as to the possible influences, past and present, that may bear on the history of these plant distribution patterns in the Southern Rockies.

The overriding problem concerns migration. Did the alpine flora move out of the Arctic under the influence of Continental glaciation, as Darwin (1853), Hooker and Gray (1850), Wallace (1900), and others following them have suggested, to climb the mountaintops and become stranded there following the recession of the Pleistocene climate, or did an ancient Tertiary alpine flora already exist here and in the other austral ranges of the Northern Hemisphere? Did not this old flora, aided by a climatic depression of timberline and the availability of unstable virgin soils to the north, form the present arctic flora, as suggested by Tolmachev (1959) and Hultén (1962, p. 4)?

What were the nature and the chronology of the events that have placed certain "Cordilleran" species at isolated stations in the Great Lakes Region and in eastern Canada (Fernald, 1925) and that resulted in the curious mixture of boreal, Cordilleran, eastern-deciduous-forest and Great Plains species in the Black Hills of South Dakota? And how can one explain the fact that many of these eastern species occur in a necklace-like pattern extending in mesic sites along the eastern flank of the Rockies from the Black Hills down through New Mexico and eastern Arizona?

Falling into the same general pattern in the eastern Rockies, a number of ferns, mosses, lichens, and higher plant genera occur as narrow endemics or as worldwide disjuncts. Some of these might be classed as subtropical or sub-oceanic elsewhere in the world. Are these relicts of the old Tertiary flora or have they arrived at odd times by long-distance transport from other continents?

What is the explanation for the modern absence of broad-leaved trees in an area that once supported a mixed broad-leaf-coniferous flora probably as rich as that of the southern Appalachians? Can the depletion of this flora be correlated with paleoclimatic or orogenic events?

Are the basic similarities between the floras of the Southern Rockies and the Asiatic Altai simply the result of similar climate, topography, and continental situation—each area in the long run receiving and supporting a common species pool derived by long-distance transport? Or are their floras the surviving remnants of a flora that at

¹University of Colorado Museum, Boulder, Colorado.

one time was more or less continuous over mountain ranges connecting the two areas?

How many modern plant distributions can be traced to migrations of floras ahead of an advancing ice sheet? How many must be attributed to wholesale extinction and recovery from small refugia? Can these problems be successfully attacked on a vegetational basis, or must each species be considered a problem in itself?

In the succeeding paragraphs the reader may be disappointed to find that the well-known species or dominant trees receive little consideration. This is unavoidable because the species critical to a discussion of this sort are those that are relatively homogeneous or not racially complex. Their distribution patterns are most likely to be framed within an area showing obvious correlations with climate or geochronology. Widespread species like *Pinus ponderosa*, *Pseudotsuga menziesii*, and the like are genetically very complex and racially differentiated. Their heterogeneity has enabled them to radiate adaptively into a large number of ecological situations. A knowledge of their ecology, genetics, and migrations in detail would, of course, be of great value, but at the present time, because of insufficient study, they are part of the enigma.

Taxonomic relationships are questionable, contact between American and Asiatic institutions are difficult, the major literature is hidden in monographs and revisions of isolated genera, and the physical record in the form of herbarium specimens is scattered in hundreds of museums, some of which no longer lend specimens for phytogeographical study. Because of the magnitude of this segment of the field of phytogeography, this paper will be limited to a discussion of the patterns that emerge from study of the Southern Rocky Mountain flora. Other equally important aspects, namely phytosociology, cytotaxonomy, autecology, paleontology, and physiology will be left to those who may find among these patterns problems that may be tackled by use of their disciplines.

HISTORICAL REVIEW

Phytogeographical research began in the Rocky Mountains with the historic journey across America made in 1877 by Joseph Dalton Hooker and Asa Gray. Out of this brief exposure to the living landscape of the area came one of phytogeography's classic papers, "The Vegetation of the Rocky Mountain Region and a Comparison with That of Other Parts of the World" (Hooker and Gray, 1880). In this paper Hooker established the presence of the Boreal, Asiatic, Mexican, and local elements in the Rocky Mountain flora and built the framework of all future discussions.

A few years later, in 1887, another of the greatest biogeographers of all time, Alfred Russel Wallace, spent a few days in Colorado during a lecture tour and happened to meet a young botanical novice who took him on an excursion to Gray's Peak (Wallace, 1905). His companion was a Denver schoolteacher named Alice Eastwood, Colorado's first resident botanist, who later became world-famous for her studies of the California flora and for the part she played in rescuing the type collections of the California Academy of Sciences during the San Francisco earthquake of 1906. The Gray's Peak excursion gave Wallace a num-

ber of significant phytogeographical impressions (Wallace, 1900).

Professor T. D. A. Cockerell should also be listed among the early phytogeographers, because, beginning with his sojourn in the Wet Mountain Valley in 1887-1888, he attempted to record the entire spectrum of plant and animal life in the Southern Rockies. This work was prompted by biogeographical considerations, as witnessed by the many papers he later published bearing on the field. Throughout his life Cockerell was a strong disciple of Darwin and Wallace. He published several papers analyzing the alpine vegetation of Colorado (Cockerell, 1887-1906) and was an active collector and describer of fossil plants, particularly from the late-Cenozoic floras of southern Colorado.

For many years the taxonomic philosophy of Per Axel Rydberg dominated thinking about the Rocky Mountain region, later to fall into disrepute because of his reputation as a taxonomic "splitter." Rydberg, nevertheless, was a man of remarkable perception even though his taxonomic categories often were at least one level removed from contemporary taxonomic tastes. Rydberg made substantial contributions to phytogeography, first by his analysis (1896) of the flora of the Black Hills in which he demonstrated the coexistence in that area of a Boreal, a Cordilleran, an eastern woodland-prairie, and a Great Plains element. In a paper on the origin of the alpine flora (1914a) he speculated on the origins of circumpolar species, on dispersal capacities of plants, and on disjunct vicarious species pairs. In a series of papers (1914b-1922) Rydberg analyzed the flora of the altitudinal- or life-zones of the Rockies, but these were essentially phytosociological rather than geographical in substance.

The most sophisticated and broadly based work on Rocky Mountain phytogeography was contributed by the Danish-American botanist Theodore Holm, whose forgotten paper, "Alpine Vegetation of Colorado" (Holm, 1923), is really a classic. Holm spent two summers in Colorado, in 1896 and 1899, and brought to the area personal field experience gained from three Danish arctic expeditions. Holm published tables listing the occurrence of Colorado alpine species in twelve major arctic-alpine regions of the Northern Hemisphere and in many ways anticipated the monumental style of Hultén.

Holm first recognized that a number of Colorado "endemics" were in fact conspecific with Asiatic species or circumpolar species, and he perceived that the alpine species of such genera as *Trifolium* were more closely related to species of the Old World alpine than to local lowland groups: he pointed out the probable Old-World relatives of certain alpine endemic genera such as *Oreoxis* and *Chionophila*. Holm also made significant contributions to the taxonomy and phytogeography of alpine grasses and sedges, which, unfortunately, have not been given full consideration up to the present time. He discovered the arctic-alpine *Juncus biglumis* L. for the first time in the Southern Rockies, but the report went unnoticed until years later when the plant was rediscovered (Weber, 1955). It is a pity that Holm's field work in the region was so brief, for he had the background necessary to make a major contribution.

In August, 1919, the International Phytogeographical

Excursion, under the leadership of Eduard Rübel, was held in the United States. In Colorado the party visited the Pikes Peak area. A photograph was recently published showing a trio of famous botanists—Adolf Engler, Carl Schröter, and Rübel—on the trail near Minnehaha (Lüdi, 1961). It was on this excursion that the Danish botanical explorer, Ove Paulsen, collected the arctic annual *Koenigia islandica* L. for the first time in America outside the Arctic. Incredibly, this record was never published, and the specimen was only discovered in the Copenhagen Herbarium shortly after the writer published his discovery of the species in 1953 (Weber, 1955, 1961).

The Alpine Laboratory of F. E. Clements on Pikes Peak attracted many ecologists and some phytogeographers to the area, including G. Einar DuRietz, who visited it in 1926. The University of Colorado's Institute of Arctic and Alpine Research provides current facilities for research in its subalpine and alpine stations near Boulder. The hemispheric ramifications of plant relationships in the Rockies are very complex, and through visits and exchanges of research workers from the far-flung mountain areas of the northern world much correlative information can be gained and new understandings reached.

Recent local phytogeographical activity has been principally accessory to the publication of up-to-date floras. Modern floras are now available for Colorado (Harrington, 1954), Arizona (Kearney and Peebles, 1960), Idaho (Davis, 1952), and the Pacific Northwest (Hitchcock *et al.*, 1955-1961), while floras are in preparation for Wyoming (Porter), Utah (Holmgren *et al.*), Montana (Booth, 1950), and New Mexico (Dittmer *et al.*). New discoveries of plants in Colorado are reported by Weber (1955, 1961). The Beartooth Plateau of northern Wyoming and adjacent Montana has recently been found to be rich in arctic-alpine rarities (Johnson, 1962), and the Convict Creek area of the southern Sierra Nevada, while outside our area, contains alpine-arctic disjuncts pertinent to our flora (Major and Bamberg, 1963). It would be most desirable to have available annotated lists for the alpine floras of the Uinta and La Sal Mountains of Utah, the high Rockies of New Mexico, and the Beartooth Plateau. A thorough revision of the Black Hills flora is also long overdue.

Professor Hultén's distribution maps (Hultén, 1958, 1962) of the circumpolar flora are of immense importance in clarifying the greater distributional areas of Rocky Mountain plants. As late as 1958, however, the Rocky Mountains was a particularly difficult area for him since many circumpolar species occurring there have passed as local endemics, thus making it hard to recognize them in the literature. In 1959, however, Hultén was able to spend several weeks in the Colorado alpine area, and his visit, together with succeeding visits by other foreign specialists, has helped to clarify taxonomic relationships and microhabitat questions.

Taxonomic monographs usually contain detailed dot-maps, and these are most useful phytogeographical tools. Editorial policy, however, often eliminates documentation of these maps in favor of a perfunctory list of "representative specimens." This, plus the growing reluctance of the major herbaria to lend material for phytogeographic purposes,

impedes the progress of research in the field at a time when detailed work should be encouraged. Regional floras, with notable exceptions (Deam, 1940; Jones and Fuller, 1955) provide neither dot-maps nor detailed distributional outlines; such works could be of great value if the importance of local distribution could be brought home to the authors. Careful outlines of local distribution are, of course, more useful than the usual vague compilations of world distribution.

A mapping program for the entire North American flora should be high on the agenda of cooperative taxonomic projects. The enormous number of herbaria on this continent makes mapping particularly difficult, but this is an area where computer methods would make possible a clearing-house for phytogeographical data.

LATE-CENOZOIC FOSSIL PLANT RECORDS FOR COLORADO²

The late-Cenozoic vegetation and flora of Colorado is known from only a limited number of localities, but inferences from these and from fossil localities in nearby states are summarized in this brief section.

LATE-TERTIARY FLORA OF COLORADO

A late-Oligocene flora from the Florissant Lake Beds, west of Pike's Peak in central Colorado, is well known. This flora was examined by Lesquereux (1883) and others and later studied intensively by MacGinitie (1953), who described 114 species, comprising 87 genera in 47 vascular plant families. MacGinitie characterized the Florissant flora ecologically as including several types of plants: (1) coriaceous-leaved oaks and genera of pine, scrub, and chaparral, which probably grew locally on dry foothills; (2) a riparian or lakeshore assemblage including *Salix*, *Fagopsis*, Cyperaceae, *Sequoia*, and certain broad-leaved trees (*Carya*, *Ulmus*, *Zelkova*, *Tilia*, *Castanea*) that probably occupied the wet valley margins; and (3) conifers that grew locally on higher peaks.

From the present distribution of genera and species identified from leaves at Florissant, MacGinitie concluded that the vegetation at the site was similar to that which now grows in subhumid warm-temperate areas in the northern Sierra Madre of northeastern Mexico, in part including forms similar to subxeric living species now growing in western Texas and northeastern Mexico. He inferred that the rainfall was not adequate to support a true forest except along streams where ground-water was close to the surface.

In contrast to earlier Tertiary floras of the state, which include subtropical and tropical elements, this flora suggests a warm-temperate and subxeric environment. Other mountainous areas in the state presumably also supported a relatively xeric vegetation during the late Oligocene.

A study of the Florissant pollen and spores (Leopold, unpublished data) identifies other xeric genera (*Eleagnus*, *Sarcobatus*, and *Xylonagra*) and also additional broad-leaved trees (*Eucommia*, *Juglans*, and *Fremontodendron*).

The Florissant flora contains a rather large percentage of

²This section is by Estella B. Leopold, U.S. Geological Survey, Denver, Colorado. Publication authorized by the Director, U.S. Geological Survey.

angiosperm genera that do not grow now in the Rocky Mountain Province (ca. 60%), and thus it differs from late Oligocene floras on the Pacific Coast (72-74% exotic genera; Wolfe and Barghoorn, 1960) that have a more subtropical aspect. However, it resembles a flora of the same age from the Ruby Valley in Montana (Becker, 1961).

Miocene and Pliocene floras of Colorado are less rich than the Oligocene flora, but include relatively more genera still native to Colorado. A leaf flora from Creede in southwestern Colorado in the San Juan Mountains (MacGinitie, 1953, p. 73) is thought to be either Miocene or Pliocene in age. Forms identified by MacGinitie and R. Brown (written communication, 1957), plus those found as fossil pollen and spores (Leopold, unpublished data) are: *Selaginella* cf. *densa*, *Potamogeton*, *Pinus florissanti*, *Picea*, *Abies longirostris*, *Ephedra* cf. *E. torreyana*, cf. *E. nevadensis*, *Juniperus*, cf. *Tsuga*, cf. *Larix*, *Populus*, *Salix*, *Alnus*, *Quercus*, *Jamesia* (= *Edwinia*), *Acer*, *Cercocarpus myricaefolia*, *Oenotheraceae*, *Sarcobatus*, *Eleagnus*, *Mahonia marginata*, *Carya*, *Ulmus* and/or *Zelkova*, *Crataegus*, and *Artemisia*.

Only two of the Creede genera (or 10%) are now foreign to the Rocky Mountain area (*Carya* and *Ulmus-Zelkova*). Except for *Ephedra*, which now grows in very dry sites not much farther west in the pinyon-juniper association and on desert margins, the others are common in the San Juan Mountains today.

The Troublesome Formation (middle Miocene) in Middle Park, north-central Colorado (Izett and Lewis, 1963), yields a pollen assemblage consisting of the following flora (Leopold, unpublished data): *Picea* cf. *engelmanni*, *Pinus*, *Picea*, *Abies*, *Ephedra*, *Alnus*, *Ulmus-Zelkova*, *Arceuthobium*, *Carya*, *Sphaeralcea*, *Eleagnus*, *Compositae* cf. *Xanthium*, *Artemisia*, *Gramineae*, *Symphoricarpos*, *Sarcobatus vermiculatus*, and *Chenopodiaceae* undet.

Like the Creede flora, the assemblage is composed overwhelmingly of pine and spruce pollen. The pollen assemblage resembles the present pollen rain in the area, with the exception of *Ulmus* (or *Zelkova*), *Carya*, and *Juglans*, which are now exotic to Colorado. Thus, the Mio-Pliocene floras of this region contain only a few broad-leaved trees that are late-Tertiary relicts. None of these is known to persist in the Colorado flora after the Pliocene. Pliocene floras from Wyoming, Idaho, and Arizona have a generic aspect similar to those from Colorado.

THE PLIO-PLEISTOCENE BOUNDARY IN SOUTHERN IDAHO

With respect to palynology or paleobotany, the Plio-Pleistocene boundary has not been studied in Colorado, but evidence from south-central Idaho (Axelrod, 1964; Leopold and Brown in Mapel and Hail, 1959) may be pertinent. The middle-Miocene (or early-Pliocene) flora at Trapper Creek (Beaverdam Formation of Axelrod, 1964) contains forms such as *Sequoia*, *Fraxinus*, *Carya*, *Ulmus*, *Zelkova*, *Persea*, *Nyssa*, and *Ilex*, which are now foreign to the region, plus many forms now characteristic, e.g. *Pinus*, *Picea*, *Tsuga*, *Abies*, *Ephedra*, *Alnus*, *Quercus*, *Acer*, *Populus*. The flora of the Salt Lake Formation (early Pliocene; Mapel and Hail, 1959) and of the Banbury Basalt (middle Pliocene; Leopold, unpublished data) are greatly impoverished compared with the Trapper Creek flora. Broad-leaved trees,

for example, are represented only by *Carya*, *Juglans*, and *Ulmus-Zelkova* in the Salt Lake, and only by *Carya* and *Ulmus-Zelkova* in the Banbury.

A diverse pollen flora from the Glens Ferry Formation of Blancan age (latest Pliocene and earliest Pleistocene) in the western Snake River Plain represents plants now native to Idaho, except for rare pollen of *Carya* and *Ulmus-Zelkova* (see stratigraphic summary by Malde, this volume). The flora is dominated by various genera of Pinaceae and includes *Celtis*, *Populus*, and several xeric shrubs, in addition to water plants and herbs. It suggests a climate slightly wetter than today's (annual precipitation now about 10 in.), which permitted low montane vegetation to grow in this now treeless area. Pollen from the overlying Bruneau Formation (middle Pleistocene) is mainly of the Pinaceae and includes no late-Tertiary relict genera. It suggests a climate somewhat cooler and wetter than today's.

The succession of Miocene, Pliocene, and Quaternary pollen floras from southern Idaho demonstrates gradual loss of broad-leaved tree genera that still persist in central and eastern United States and along the Pacific Coast. This may be expressed in terms of the percentage of the identified flora that is lost progressively with time (Wolfe and Barghoorn, 1960).

For Idaho, the middle-Miocene (or early-Pliocene) Trapper Creek flora contains 35% of genera that are now foreign to the central Rocky Mountain region. The Pliocene floras contain only 2 or 3 genera that are now exotic to the region, but these genera represent about 25% of the total. In the Blancan (Plio-Pleistocene) interval, these exotic genera (including only *Carya* and *Ulmus-Zelkova*) make up only 9% of the flora. Younger pollen floras that have been examined contain no genera that are now foreign to the present regional flora.

The loss of broad-leaved trees from the flora of the central Rocky Mountains was undoubtedly progressive, owing to gradual changes in regional climate and the rise of mountains (particularly the Cascade Range and the Sierra Nevada). The consequent decrease in mesic conditions permitted only a few broad-leaved trees to survive in Idaho and Colorado (e.g. *Populus*, *Acer grandidentatum*, and *Betula papyrifera*), though shrubby species of many dicotyledonous tree genera are also represented (*Quercus*, *Celtis*, *Acer*, *Alnus*, etc.).

LATE-QUATERNARY POLLEN RECORDS

The reported late-Quaternary pollen records in Colorado are limited to two late-Pinedale and postglacial bog deposits in the San Juan Mountains (Maher, 1961) and four deposits in the Rocky Mountain Front Range west of Boulder (Pennak, 1963).

In the San Juan Mountains, Maher (1961) studied two sites in the subalpine vegetation zone at an elevation of about 3,200 m, or about 300 m below the present tree line. The pollen sequence is as follows. An early interval of clayey sediments is characterized by dominance of *Artemisia* (40-70% of total pollen) and *Pinus*. A radiocarbon date of $15,450 \pm 220$ years (Y-1147) was obtained from near the top of this zone. Overlying organic sediments, with a date of $13,360 \pm 120$ (Y-1437) at the very base, are character-

ized by pollen of many montane forms—*Pinus*, *Picea*, *Abies*, *Pseudotsuga*, *Betula*, and *Quercus*, and various non-tree taxa. *Ephedra* pollen also was found, but it is thought to represent long-distance transport from arid lowlands. Tundra was apparently replaced locally by subalpine forest about 13,500 years ago. According to data from modern pollen surface samples, Maher (1961, 1963) concluded that before this forestation took place tree-line stood at least 600 m lower than now.

In the Front Range, Pennak (1963) studied four sites ranging in altitude from 2,617 to 3,247 m. C^{14} dates indicate that the oldest sediments are nearly 6,700 years old. Pollen diagrams from the four sites have individual features, but the two oldest may bear on interpreting past climate. *Artemisia* pollen is fairly high (ca. 30% of the total pollen) in sediments from 6,700 to about 6,000 years old. Otherwise, *Pinus* pollen is dominant. A predominance of grass pollen lasting from 6,000 to 3,000 years ago occurs in one pollen profile. Pennak thought this recorded a warm, dry period, but it could represent local edaphic conditions at a single site.

SUMMARY

The late-Tertiary floristic history of Colorado, reconstructed from a meager fossil record, indicates that a rich temperate flora became impoverished during the Miocene and Pliocene Epochs in Colorado—a pattern common to several western states. Although the post-Blancan Quaternary plant record of Colorado is also scant, no generic extinctions are known within this flora after the Tertiary.

THE ORIGIN OF THE MODERN FLORA

The modern flora of the Southern Rockies forms a complicated patchwork of overlays, the base consisting of what remnants there are from the Oligocene flora as recorded at Florissant, Colorado (MacGinitie, 1953). At the lower altitudes this flora is distinctly of Madro-Tertiary derivation (Axelrod, 1948), but in the high mountains occur remnants of what must have been a more or less continuously distributed high-mountain flora extending from this area across Beringia into the mountain regions of Central Asia—the Boreal-Asiatic element discussed later. The alpine areas are dominated by circumpolar species, which were either in place there before the Pleistocene or migrated there during the Ice Ages.

Modern plant-distribution patterns in the Southern Rockies suggest that the Cordilleran flora once extended considerably down-slope and eastward, possibly coincident with a depression of timberline during cold periods, and that the eastern woodland flora extended westward, probably along the major watercourses, and mingled with the Cordilleran flora along a wide area of the western Great Plains. Today the Cordilleran flora has retreated into the higher areas, leaving relicts in the Black Hills and at scattered points on the Great Plains, while the eastern flora has retreated eastward or been exterminated on the Great Plains, leaving reciprocal relict colonies along the mesic eastern front of the mountains.

Former connections of the Southern Rockies to the north-westward have been severed by the development of the

deserts of southern Wyoming, but relict stands of north-western species provide traces of the old connection. The Madro-Tertiary xeric floral elements of the Great Basin and Colorado Plateaus have penetrated far into the mountains on the west by way of the warm river valleys and deep canyons, and on the southeast a clearly defined invasion by the west Texas-western New Mexico flora (here called the Chihuahuan element) is actively encroaching on the eastern flanks of the mountains.

The most widely accepted explanation for the presence of boreal and arctic species in the Rocky Mountains was advanced by Darwin (1883), and adopted with little change by Hooker and Gray (1880) and Rydberg (1914c, p. 89). The southward penetration of the Pleistocene climate caused successive vegetational zones to replace each other southward so that a vast displacement and telescoping of the flora occurred. As the ice retreated northward, arctic species found congenial habitats on the mountaintops of the southern mountain ranges, where they now exist widely disjunct from their relatives that moved back to the Arctic. Constant repetition of this idea has given it the aura of truth. However, in recent years Tolmatchev (1959a, b) and Hultén (1962) have attacked it as rather naïve and over-simplified.

The influence of a Mexican reservoir in stocking the floristic "streams" of the American Southwest was appreciated very early by Hooker and elaborated by Watson (1890). Hooker and Gray (1880, p. 62) stated: "We infer that the Pacific region, while preserving through all vicissitudes a moderate number of boreal types and receiving a few Eastern Asiatic ones probably at a later date, has been mainly replenished from the Mexican Plateau, and at a comparatively late period. A large part of the botany of California, still more of Nevada, Utah, and western Texas, and, yet more, that of Arizona and New Mexico, may be regarded as a northward extension of the botany of the Mexican Plateau."

Axelrod (1948, p. 139) sums up succinctly his interpretation of the historic events that have resulted in the present-day Rocky Mountain flora: "The histories of montane forest, woodland, chaparral and desert vegetation outlined . . . indicate that the major Tertiary floras of the western United States were differentiated into communities of essentially modern aspect largely by Middle Pliocene and succeeding climates. Differentiation apparently was in response to a trend to lowered yearly rainfall, shifting seasonal distribution of rain, and increased ranges and extremes of temperature. Under the impact of these accelerated post-lower Pliocene climatic changes the Areto-Tertiary and Madro-Tertiary floras lost their identity, since species formerly shared with other regions became extinct in certain areas of their early Pliocene distribution. As montane forest, woodland, chaparral and arid subtropical scrub were restricted in range as rainfall lessened, open steppe and subdesert environments of subcontinental extent came into existence over the warm-dry and cold-dry regions. Herbaceous and semi-woody plants which had a restricted distribution on the borders of Miocene and early Pliocene communities apparently spread widely and evolved rapidly as these new regional environments were initiated. Only in latest Ceno-

zoic times, in response to the development of more localized environments, were the modern plant formations fully segregated into the regional climaxes, the subregional associations and the more localized communities that now characterize western North America. . . .

"The floristic evolution initiated during the Middle Pliocene has not been completed, but is continuing at the present time. This is shown by inter-relationships displayed by the various modern communities of each plant formation over this region. The relationships between these living derivative communities of Late Tertiary vegetation are expressed by the modern patterns of plant distribution. They occur not only in North America, but extend beyond to other continents in both latitudinal and meridional directions. These distributional patterns are considered to reflect the former occurrence of ancestral Tertiary Floras across the intervening areas. The modern patterns seem to have resulted from world-wide late Cenozoic climatic changes which differentiated generalized Tertiary floras into communities now having more restricted ranges."

PRESENT-DAY COINCIDENT PATTERNS AND THEIR RELATIONSHIPS TO PAST EVENTS

Plant species have genetically determined ranges of tolerance to environmental characteristics, and they are bound to specific areas in which a tolerable set of environmental factors operates. Plant-distribution patterns thus are maps of the environments of the world.

The application of plant-distribution patterns to problems involving long-term climatic changes, orogenies, and continental displacement is based upon the assumption that plants are not capable of quickly colonizing every land area that is suitable for them but are limited by their innate dispersal capacity, competitive ability, and genetic structure (individual and populational) and by physiographic and climatic barriers to their spread. Because of this, the actual distribution patterns of plant species always tend to lag behind geologic evolution, and modern plant-distribution patterns in greater or lesser degree provide "fossil" evidence of ancient distribution patterns.

Mason (1946), in a very important paper on the edaphic factor in narrow endemism, analyzed the dynamics of geographic distribution in plants. He showed that distribution patterns result from the interaction of the physical environment with the physiological reactions and genetic processes of individuals and populations. He insisted that "area as such has no historical significance in vegetation. . . . The pattern of distribution is determined by causes inherent in the locality and most probably has had no correlative relationship with the history of the flora over any wide area. . . . The size and shape of the area occupied are the product of today's facts, both genetic and environmental."

Mason here was attacking the oversimplifications of Willis' "Age and Area" hypothesis, Hultén's model of the "equiformal progressive area," and other phytogeographical dicta concerning the center of origin and dispersal. It is difficult to believe that Mason would deny the historic implications for those classic distribution patterns linking eastern Asia with the southern Appalachians, the Chilean flora with

that of Australasia, or the well-known transatlantic biological connections.

Botanical evidence has played an important role in suggesting theories of land bridges between continents, continental drift, and the various other notions of geologic evolution. In this discussion we are concerned only with the presence in the Rocky Mountains of "coincident distribution patterns." These represent assemblages of species with generally homologous areas or with ranges radiating from a more or less restricted area toward other parts of the world, the implication being that these patterns represent traces of past continuities of distribution or paths of migration to or from those regions.

The following analysis of modern distribution patterns is inspired by the more comprehensive work of Hultén, who is mapping the distribution patterns of the entire holartic flora.

Hultén (1937) proposed a theory of "equiformal progressive areas," briefly described below, which he hoped would provide detailed explanations of the recolonization of the ice-denuded portions of the North following the last glacial period. In essence, he postulated a bare circular area of uniform climate seeded with a number of species and characterized by minimum competition. Depending on the dispersal potential of the various species, these would radiate from the center where they were introduced and eventually develop "equiformal" circular areas that in the end would occupy the total area available. The model is never realized because of the complex biology of plant species, their competitive relations, unequal dispersal capacities, and environmental complexity. But Hultén showed that the theoretical situation could be approximated with maps of the total areas of a large number of species, and in so doing he located a number of centers of these "equiformal progressive areas."

In the Southern Rocky Mountains the historical background is very different from that of the arctic regions with which Hultén was concerned. The region was not affected directly by continental glaciation, and at no time were large land areas completely devoid of plants. Present distribution patterns reflect events much older than Pleistocene, and the flora is much larger than that of the North. Except for a relatively small number of species endemic to this area, the patterns with which one deals represent only the termini of distribution areas of great magnitude. For example, from almost all sides, major distribution patterns converge upon the Southern Rockies. The northern limits of the Mexican Plateau flora are there, as are the southern limits of the arctic flora, the eastern limits of the Great Basin flora, the western limits of the Great Plains flora. Unfortunately, although the patterns are clear, the detailed information from climatology, geology, and paleontology that might justify and explain them has not yet been integrated. The patterns are outlined here in the hope of stimulating investigation and of thus securing the needed information from the other branches of biology and from geology.

In the short time available it has been impossible to provide a complete analysis of the 4,000 or so species of higher plants, not to mention the cryptogams, of the Southern

Rocky Mountain flora. For one thing, our knowledge of distributions is still too incomplete to permit this. At the risk of seeming to bias the record in favor of the proposed hypotheses, those species that have been selected exemplify the patterns, and it is left to future research to determine whether the coincident patterns are real or not.

Hultén (1937) pointed out some of the difficulties in this work. Among the most pertinent is the fact that nothing less than total distribution must be shown, because, whereas one might imagine that a generalized pattern should be adequate, it is the isolated outlier that is often most critical to an understanding of ecological tolerances or history of migration.

Hultén was especially critical of studies that use a single species to solve a biogeographic problem and of ones that concern themselves with only a segment of a distribution pattern. The present analysis is open to criticism on the latter count because very different distribution patterns may have homologous radiant arms into the Rocky Mountains. With some attention to the broader distributional area, some separation of these elements may be effected, but oversimplifications are bound to creep in.

Because the areas being considered here are only portions of the greater world areas, and because no inference is made to "center of dispersal," or direction of migration, the writer prefers not to use Hultén's term, "equiformal progressive areas." Instead the areas described herein are called "coincident areas." A group of species having a coin-

cident area constitutes an *element*. Elements may be further subdivided into sub-elements. Coincident areas are either well-marked or vague to the extent that the species coincide in their ranges to a more or less marked degree.

THE CIRCUMPOLAR ELEMENT AND RELATED CORDILLERAN PATTERNS

It has long been known that many plants of the Northern Hemisphere are found in an almost continuous ring on the fringes of North America, Eurasia, and the intervening islands (see Fig. 1). The occurrence of some of these species in the southern mountains of both continents, either with a continuous connection or as disjunct populations, is also a fact that was obvious to the earliest phytogeographers. Yet the details of their distribution and the sorting of these patterns into groups reveal that there are significant gaps both in their meridional and latitudinal aspects. The circumpolar plants are being mapped by Hultén (1958, 1962, and unpublished), who has presented in some detail (Hultén, 1958, p. 3-6) the theory of the origin and migration of this flora.

Hultén (1958) presents a significant departure from the time-honored concept of the origin of the alpine flora as postulated by Darwin, Hooker, and subsequent investigators (cited earlier in this chapter). He postulates a warm and genial Tertiary climate over the northern world, conducive to circumpolar distributions of many groups now considered to be temperate or subtropical. The onset of the Ice Ages

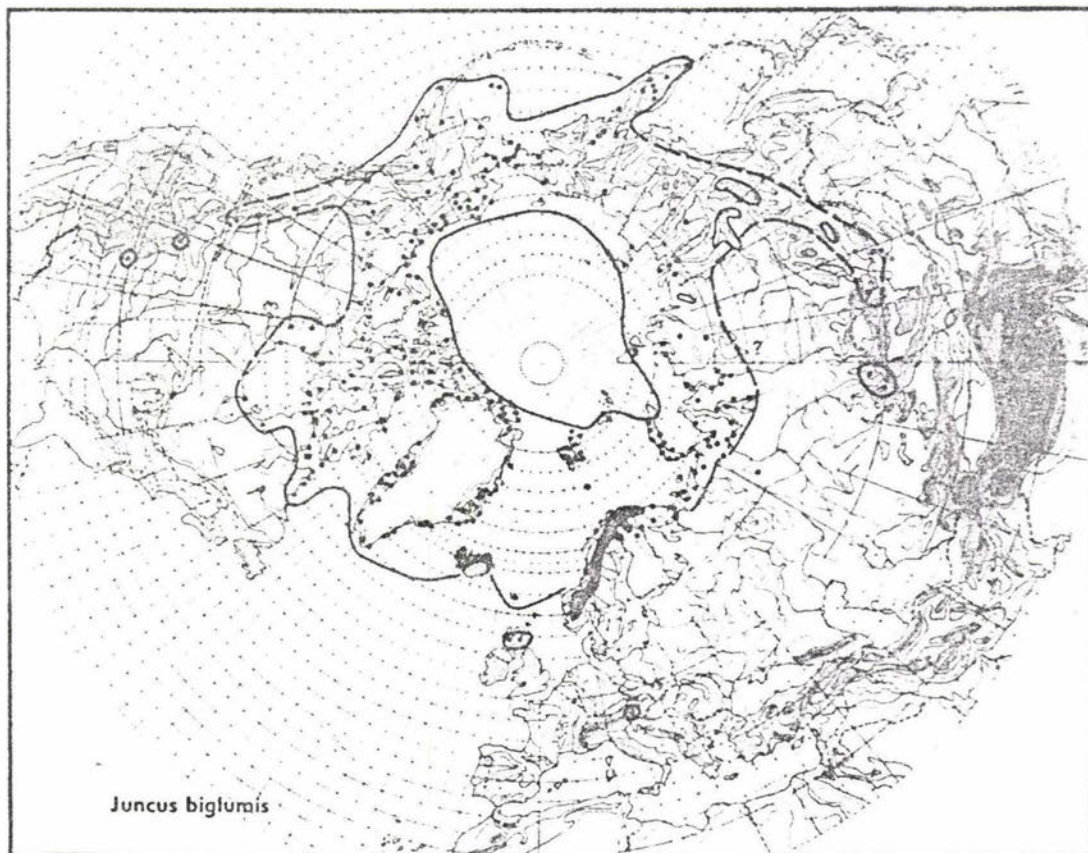


Figure 1. Distribution of *Juncus biglumis*, a typical circumpolar pattern with southern outliers. From Hultén (1962).

not only exterminated many of these plants in their northern areas but eliminated them from even more southerly intermediate areas. The circumpolar areas were broken up, leaving isolated fragments. Hultén does not insist that the present alpine flora migrated out of the Arctic at all but implies that the alpine floras of the Northern Hemisphere, originally more or less circumpolar, were also fragmented by the climatic changes and persisted as isolated remnants in the southern mountains. Comprehensive accounts of the circumpolar species are found in Hultén (1958-1962).

It is likely that the present low-altitude circumpolar arctic flora reached that area by outward migration onto virgin areas left bare by the ice; this migration led them away from the mountain regions where they had been surviving as fragmented populations of the old montane segment of the circumpolar Tertiary flora.

In the Southern Rockies the richest alpine communities are situated where high ranges trending east-west lie between or connect the principal north-south ranges. These ranges are all similar in that they are more constantly mesic throughout the year than the contrasting north-south mountains. Here the diurnal insolation through the summer months seems to be less direct or of shorter duration, resulting in a slow run-off, later snow beds, and development of small bogs and lakes at high elevations. These ranges probably escape the severe effects of the winter "Foehn" winds that dry out the slopes of the north-south ranges. Rare species in these places may occur on either north-facing or south-facing slopes, not necessarily on the summits but at some distance below. Cold-air drainage basins are also important relict areas. South Park, for example, harbors a colony of *Salix candida* Flügge, *Primula egaliksensis* Wormskj., and *Halimolobos virgata* (Nutt.) Schulz, and Middle Park supports stands of *Rubus acaulis* Michx., *Cystopteris montana* (Lam.) Bernh., and *Parnassia kotzebuei* Cham. & Schl.

A list of the especially rich alpine areas of Colorado, together with their special attractions, is given below:

1. Mount Evans: *Saxifraga foliolosa* R. Br., *Phippsia algida* (Phipps) R. Br., *Koenigia islandica* L., *Hydrogymnia mollis* (B.S.G.) Loeske, *Oreas martiana* (Hoppe & Hornsch.) Brid., *Cetraria commixta* (Nyl.) Th. Fr., *Stereocaulon rivulorum* Magn.

2. Hoosier Pass: *Eutrema penlandii* Rollins, *Saussurea weberi* Hultén, *Festuca brachyphylla* Schultes, *Braya humilis* Robinson, *Armeria maritima* (Mill.) Willd., *Oxytropis podocarpa* A. Gray.

3. Elk Mountains: *Erigeron humilis* Grah., *E. lanatus* Hook., *Stellaria irrigua* Bunge, *Senecio porteri* Greene, *Eriophorum scheuchzeri* Hoppe, *E. russeolum* Frise. This area is unusual in its concentration of species that are Canadian Rocky Mountain types.

4. San Juan-San Miguel Range near Silverton: *Cladonia mitis* Sandst., *Adiantum pedatum* L., *Eriophorum scheuchzeri* Hoppe, *Parnassia kotzebuei* Cham. & Schl.

Much of our mountain vegetation can be related, directly or indirectly, to the Circumpolar Element. Local endemics can be linked to relatives that are Northern Rocky Mountain

types; these in turn are related to species that have radiated across Boreal America, and these in turn to circumpolar types. The sorting of patterns into sub-elements is accomplished with this understanding always in mind. These sub-elements are listed below, in order of increasing area:

- A. Southern Rocky Mountain endemics, derived from Circumpolar Elements
- B. Central Rocky Mountain-Pacific Northwest
- C. Northern Rocky Mountain
- D. American radiants
- E. Boreal-Asiatic
- F. Circumpolar

Boreal-Asiatic sub-element. The Boreal-Asiatic sub-element comprises species of the general circumpolar distribution that tend to be concentrated in the mountains of western America, Asia, and southern Europe, rare or absent in the American Arctic, and generally absent from Scandinavia. This extremely interesting group in our flora contains the following types:

1. Genera with close relatives in Central Asia: e.g. *Besseyia* (Scrophulariaceae), related to Eurasian *Wulfenia* and *Picrorhiza* (fide Pennell, 1933); *Chionophila* (Scrophulariaceae), related to *Chelone*?; *Oreoxis* (Umbelliferae), related to *Ligusticum*?

2. Genera with endemic species in the Rockies and different endemics in Eurasia; e.g. *Aquilegia* (Ranunculaceae), several blue-flowered species in Rockies with counterparts in Asia; *Eritrichium* (Boraginaceae), two or three species in the western Cordillera and the rest scattered in alpine and Arctic Eurasia (Fig. 2); *Helictotrichon* (Gramineae), two species in the Rockies, many in Eurasia.

3. Rocky Mountain forms only racially distinct from Eurasian counterparts: *Androsace chamaejasme* Host., *Aster alpinus* L., *Braya humilis* (C. A. Mey.) Rob., *Artemisia arctica* Less.

4. Highly uniform species isolated in widely disjunct areas of the Rocky Mountains and Asia: *Stellaria umbellata* Turcz., *S. irrigua* Bunge, *Draba fladnizensis* Wulf., *Ranunculus gelidus* Kar. & Kar., *Crepis nana* Rich., *Gentiana prostrata* Haenke.

The Boreal-Asiatic sub-element of the circumpolar flora is probably a very old Tertiary one; it has radiated at various times to produce circumpolar types. For example, *Cerastium beeringianum* Cham. & Schlecht., studied by Hultén (1956), has a fairly typical Boreal-Asiatic distribution reinforced in the general area by the related *C. fischerianum* and *C. jenesiense*, which are Amphi-Beringian and Eastern Asiatic respectively. Other related species in the same group have reached and now occupy segments of the northeast America-Greenland-Scandinavia areas.

Eritrichium arctioides (Cham.) DC. (Boraginaceae), typifies the pattern of Boreal-Asiatic distributions in our area. Lechner-Pock (1956) reviewed the species of the *E. nanum* group (Fig. 2), to which this belongs and showed that the group as a whole occupies four major areas: (1) an Arctic belt in Eurasia with outlying stations as far west

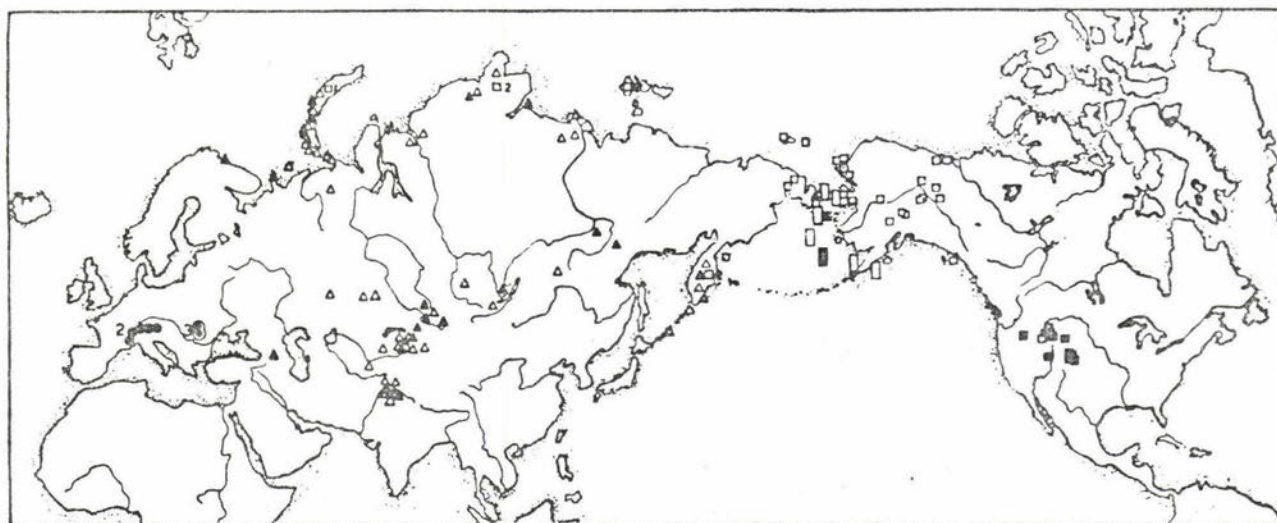


Figure 2. Distribution of the *Eritrichium nanum* group, a Boreal-Asiatic pattern. From Lechner-Poek (1956). Symbols represent different taxa.

as Kola Peninsula; (2) the mountainous regions of Central Asia and Central Europe; (3) the lands on either side of the Bering Sea (Kamchatka, eastern Siberia, and Alaska); and (4) the Rocky Mountains. Thus there are major disjunctions of the same or related species between (1) and (2) on the one hand and (3) and (4) on the other. The group is absent from the American Arctic east of Alaska. Five species comprise the subgenus; three of these are Eurasian: *E. nanum* (Alps), *E. jankae* (Carpathians), and *E. villosum* (Asia, Caucasus, Arctic Europe), and two are American-East Asian: *E. aretioides* (discussed above) and *E. chamissonis* (Bering Strait).

The Boreal-Asiatic sub-element, as far as it seems to be composed of species with close relatives in Asia, tends to be alpine. However, if one extrapolates this element to related genera that are now endemic in western North America, there is a suggestion that this element "seeded" the southwestern desert areas with these groups. It seems likely that *Cryptantha*, *Onosmodium*, *Mertensia*, and other such genera are ultimately related to ancient Asiatic genera.

The alpine members of the Boreal-Asiatic element include species that vary from common and widespread to rare and highly disjunct. This element includes conservative species that appear to be much like their Asiatic counterparts, "raucy" species forming intercontinental chains of subspecies, and those species whose relationships to Asiatic counterparts are probably close but untested.

Boreal-American sub-element. A few alpine species belong to a group that has radiated into Boreal America but no farther (Fig. 3). However, all of these are clearly related to Boreal-Asiatic groups, on the one hand, and to circumpolar species on the other. These include: *Arenaria obtusiloba* (Rydb.) Fern., *Carex stans* Drejer, *Festuca baffinensis* Polunin, *Geum rossii* (R. Br.) Ser., *Oxytropis podocarpa* A. Gray, *O. viscida* Nutt., *Potentilla hookeriana* Lehm., *P. rubricaulis* Lehm., and *Stellaria monantha* Hultén.

Central Rocky Mountain-Pacific Northwest sub-element. A small group of Central Rocky Mountain-Pacific North-

west species, isolated from the next northern area of distribution by the Wyoming deserts, occurs in the Park Range north of Steamboat Springs, Colorado, with outliers as far south as Rocky Mountain National Park and Rabbit Ears Pass. This pattern is characterized by *Rhododendron albiflorum* Hook. and *Trillium ovatum* Pursh, which are quite obviously derivatives of Tertiary relicts. This group of species must have had a continuity of range northwestward prior to the desiccation of the southern Wyoming high desert. The assemblage imparts a characteristic northwestern flavor to this regional flora. The environment is considerably more mesic than in the mountains to the south, and the area supports an isolated population of the wood frog, *Rana sylvatica cantabrigensis* Baird (Maslin, 1959). This sub-element includes: *Antennaria luzuloides* T. & G., *Botrychium multifidum* ssp. *coulteri* (Underw.) Clausen, *Cypripedium fasciculatum* Kellogg, *Fritillaria pudica* (Pursh) Spreng., *Ivesia gordonii* (Hook.) T. & G., *Lewisia triphylla* (S. Wats.) Robinson, *Mimulus lewisii* Pursh,

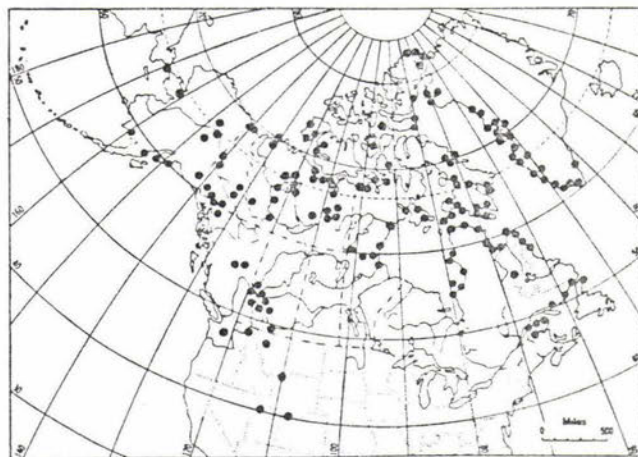


Figure 3. Distribution of *Stellaria monantha*, a Boreal-American pattern. From Porsild (1963). Colorado stations not shown.

M. moschatus Dougl., *Polygonum minimum* S. Wats., *Potentilla glandulosa* Lindl., *Rhododendron albiflorum* Hook., *Trillium ovatum* Pursh, *Viola purpurea* Kellogg, *Wyethia amplexicaulis* (Nutt.) Nutt., and *Bryum sandbergii* Holz.

Northern Rocky Mountain sub-element. In Colorado, the essentially east-west-trending San Juan Range, Elk Mountains, and Hoosier Ridge support populations of a number of species disjunct from the Northern Rocky Mountains. This small group includes: *Adiantum pedatum* L., *Crepis nana* Rich., *Erigeron lanatus* Hook., *Senecio porteri* Greene, *Eutrema penlandii* Rollins (aff. *E. edwardsii*), and *Sausurea weberi* Hult. (aff. *S. viscida*).

MADRO-TERTIARY ELEMENT

The Madro-Tertiary flora has been discussed in as much detail and for as long a time as the circumpolar flora. Hooker had much to say about the Mexican Plateau source of the southwestern flora. Watson (1890) and Abrams (1913) also discussed the origins of southwestern plants, and Axelrod (1948) has developed a general theory of the history of this ancient element in our flora. Locally, MacGinitie's (1953) work on the Florissant fossil flora is a basic source of information on the flora and climate of Oligocene times in Colorado, and Hay (1939) has analyzed the Mexican element in the Colorado flora.

These southern elements are of peripheral importance to a study of the Rocky Mountain flora because few species reach very high altitudes. However, the foothills flora contains a woody element not unlike a portion of that found by MacGinitie in the Florissant formation. These are discussed under "Tertiary Relicts." There is furthermore a strongly developed coincident area of species that appear to be actively encroaching northward along the mountain base on the eastern slope. This element centers in West Texas, eastern New Mexico, and Chihuahua and may be called the Chihuahuan sub-element. On the western side of the mountains a number of Great Basin and Southwest Desert species penetrate far into the mountainous area by way of the deep, warm canyons. These may be called the Sonoran-Great Basin sub-element. A fourth group consists of a few genera that have given rise to alpine races of local desert species.

Tertiary Relict sub-element. This element is epitomized by *Jamesia americana*. *Jamesia* is a monotypic genus of the Hydrangeaceae with no close relatives in the modern flora of this region, but probably closely related to Asiatic species of *Deutzia*. Leaves of *Jamesia* have been reported from the Creede (Mio-Pliocene) flora by Stewart (1940). The modern distribution of *Jamesia* consists of a continuous area in the eastern foothills of the Colorado Rockies, south to northern New Mexico, and discontinuous areas in the mountains of southern New Mexico to the southeastern corner of Arizona. The species also reappears locally on the east slope of the southern Sierra Nevada of California.

Rubus deliciosus Torr. is similarly restricted to the east slope of the Rockies but has an outlying relative in western Colorado and Utah. *Selaginella weatherbiana* Tryon is limited to cool north-facing canyonsides in the eastern foothills from northern Colorado to southern New Mexico. The umbelliferous genera *Aletes*, *Neoparrya* (Fig. 4), and *Harbouria* have essentially the same distribution, although *Aletes* also has a Colorado Plateau member.

It is significant that a number of the species displaying this distribution are types that have a worldwide Tertiary Relict status. This is especially true of the ferns, some bryophytes, and lichens. The ferns *Asplenium septentrionale* (L.) Hoffm., *A. adiantum-nigrum* L., *Dryopteris filix-mas* (L.) Schott, the moss *Anacolia laevisphaera* (Tayl.) Flowers, and the lichens *Normandina pulchella* (Borr.) Nyl., *Cetraria glauca* (L.) Ach., *Cetraria chlorophylla* (Willd.) Vain., *Sticta weigelii* (Ach.) Vain., *Anaptychia leucomelaena* (L.) Vain. are quite out of place in the present Rocky Mountain flora but show interesting world distributions involving more oceanic or subtropical regions.

This group includes species of peculiar ecological requirements. They evidently were once widespread in the foothill flora of the West but have been eliminated with increasing aridity, leaving isolated remnants in three principal areas: the east slope of the Rockies, the Colorado Plateaus, and the eastern Sierra Nevada. Many of these species are cliff-dwelling types that may combine high water requirements with obligate saxicolity or low competitive ability. On the eastern slope of the Rockies this ecological combination is fulfilled by the steep escarpments which, combined with

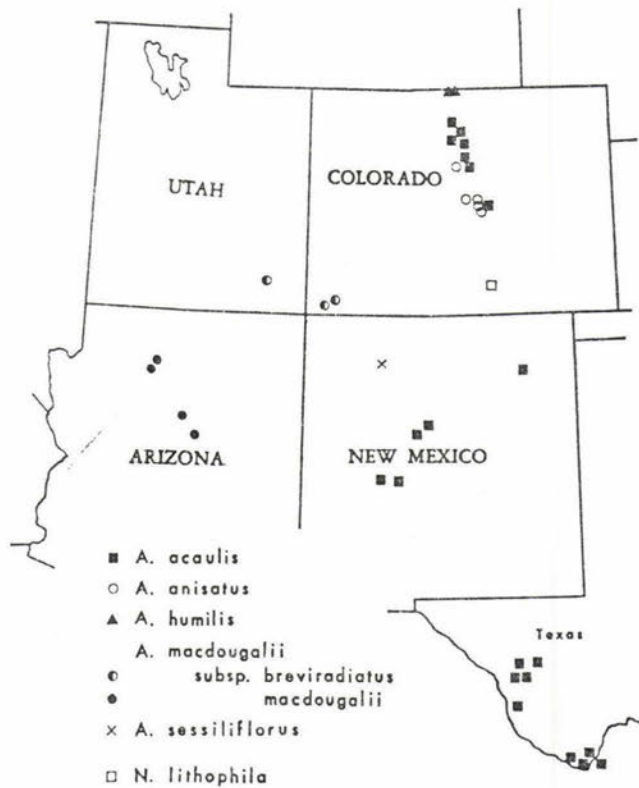


Figure 4. Distribution of *Aletes* and *Neoparrya*, genera with Madro-Tertiary relict patterns. (*Aletes acaulis*, black squares, falls into the Chihuahuan sub-element.) From Theobald *et al.* (1964).

local atmospheric peculiarities, produce a cloud veil that results in local pockets of temporary high humidity (Ives, 1938).

Several additional species belonging to this old mesic Tertiary flora have persisted in much larger areas in the forested regions. *Pachystima myrsinites* (Pursh) Raf., *Mahonia repens* Lindl., *M. fremontii* (Torr.) Fedde and species of *Populus*, *Ribes*, and *Cercocarpus* represent the more successful survivors of this group. Other Tertiary Relicts include: *Acer grandidentatum* Nutt. ex T. & G., *Asplenium adiantum-nigrum* L., *Asplenium septentrionale* (L.) Hoffm., *Dryopteris filix-mas* (L.) Schott, *Epipactis gigantea* Dougl. ex Hook., *Jamesia americana* T. & G., *Pachystima myrsinites* (Pursh) Raf., *Philadelphus microphyllus* A. Gray, *Ptelea trifoliata* L., *Rhamnus smithii* Greene, *Robinia neomexicana* A. Gray, *Rubus deliciosus* Torr., *Selaginella weatherbiana* Tyron, *Harbouria trachypleura* (A. Gray) C. & R., *Neoparrya lithophila* Mathias, *Aletes acaulis* (Torr.) C. & R., *Aletes humilis* C. & R., and *Aletes macdougali* C. & R.

Chihuahuan sub-element. In the Chihuahuan sub-element is included a group of species that occupy west Texas, eastern New Mexico, and usually Chihuahua and that show a coincident area extending northwest into Colorado along the Arkansas drainage system. Probably this pattern contributes a good number of species to the flora of the southern Great Plains, and in some instances to southeastern United States. It appears to be a more or less distinct group because the species in Colorado are decidedly "eastern" and do not occur in the southwestern corner, nor do most of them occur west of southeastern Arizona.

South from the Boulder area, the flora changes dramatically in several stages. Just south of Denver one encounters the first stands of *Quercus gambelii* Nutt., which becomes an important species to the south. Just north of Colorado Springs, *Pinus edulis* Engelm. appears, and a few miles to the south of that city the candelabra cactus, *Opuntia arborescens* Engelm. becomes conspicuous. Near Walsenburg *Juniperus monosperma* (Engelm.) Sarg. makes its appearance, and when the Arkansas River is reached a number of herbaceous plants and suffruticose species of southern affinities add to the pattern. The number of species belonging to the distribution pattern characteristically including West Texas, eastern New Mexico, and the Chihuahuan desert increases southeastward along the Arkansas River drainage until at the southeastern corner of Colorado the entire flora is dominated by this element.

The distribution pattern of *Pinus edulis* indicates that it belongs to the Madro-Tertiary element, which with Chihuahuan sub-element, appears to fill an expanding rather than a retreating area in eastern Colorado. This peculiarity is explained by Cain (1944): "An expanding area tends to have a relatively continuous boundary and a homogeneous topography, whereas a contracting area tends to have a relatively discontinuous boundary and an irregular and broken topography. . . . The principal reasons for the above relationships are the fact that the expanding area has not reached effective barriers and that the contracting area leaves behind relict colonies in local situations where

frequently edaphic or microclimatic conditions provide at least temporary compensation for a general climatic unfavorableness."

It does not seem necessary to the argument to insist that effective barriers have not been reached, for it is quite obvious that in our flora, at least, the barriers exist and have been reached by many species in this pattern. However, the barriers themselves are very likely moving northward, permitting a slow encroachment, and the differential extensions of the various species indicate that different species are limited in their spread by different combinations of climatic extremes.

In the Southern Rocky Mountains *Pinus edulis* reaches the Wyoming state line (Peterson, 1962) on the west side of the mountains, but on the east slope its limit of maximum continuous distribution is in the Colorado Springs region westward to Monarch Pass. It is therefore anomalous to find a colony of piñon pine about 250 km to the north, in Owl Canyon, 50 km northwest of Fort Collins. This population has been regarded by many botanists as a relict population; this interpretation would be out of harmony with the general theory proposed here and would place it in the general Cordilleran pattern, which is a contracting area. Does this colony really represent the remnant of an ancient extension of the species? Or is there some other explanation?

Wright (1952) mapped the stand, took borings of the trees, and listed the associated vegetation. He found that the age of the six largest trees ranged from 317 to 372 years and that the population radiates out from a small group of old trees in the northwest corner of the grove. In other words, the population can be projected back only 300 years to a small cluster of trees all concentrated in one gully. The associated vegetation contains no species pointing to a southern relict stand; even the juniper associated with this piñon stand is *Juniperus scopulorum* rather than *J. monosperma*, the usual associate of piñon on the eastern slope. Wright held that this isolated stand, instead of representing a relict stand, represents a chance introduction, possibly through the agency of animals that might have rifled supplies of Indians carrying the nuts from place to place. The survival of the piñon on this site may be attributed, in its turn, to a combination of calcareous substrate, eastern exposure, and an open community present in the beginning. In recent times, the piñon has been spread to several nearby localities, probably by jays (Weber, 1961), where isolated individuals ranging from a few years to 100 years old have been found.

Species of the Chihuahuan sub-element include: *Abutilon incanum* (Link) Sweet, *Andropogon saccharoides* Sw., *Argemone squarrosa* Greene, *Asclepias macrotis* Torr., *A. oenotheroides* Cham. & Schlecht., *Asplenium resiliens* Kunze, *Berlandiera lyrata* Benth., *Bouteloua barbata* Lag., *B. eriopoda* (Torr.) Torr., *Cheilanthes eatonii* Baker, *C. wootonii* Maxon, *Croton texensis* (Klotzsch) Muell. Arg., *Cucurbita foetidissima* H.B.K., *Dalea lanata* Spreng., *D. nana* Torr., *Desmanthus cooleyi* (Eaton) Trel., *Engelmannia pinnatifida* T. & G., *Eragrostis oxylepis* (Torr.) Torr., *Eriochloa contracta* Hitchc., *Gaillardia pulchella* Foug., *Hoffmanseggia densiflora* Benth., *H. drepanocarpa* A. Gray, *H. jamesii* T. & G., *Juniperus monosperma* (Engelm.) Sarg.,

Krameria spp., *Melampodium cinereum* DC., *Mimosa borealis* A. Gray, *Palafoxia* spp., *Pericome caudata* A. Gray, *Sapindus saponaria* L., *Sarcostemma crispum* Benth., *Stillingia sylvatica* Gard., and *Thelesperma* spp.

Sonoran-Great Basin sub-element. The desert flora that penetrates far into the Rockies by way of the warm river valleys, canyon walls, and arid plateaus is a conspicuous element in Western Colorado, represented by hundreds of species, of which it is sufficient to name only a few genera: *Astragalus*, *Atriplex*, *Cryptantha*, *Phacelia*, and *Gilia*. These groups are evidently elaborations of the old Tertiary flora that radiated into the Great Basin from a Mexican reservoir. The low divides in southern Wyoming and northern New Mexico have permitted a number of species of this western group to overflow into favorable sites on the eastern face of the Rockies, particularly those species that are adapted to shale outcrops. The Pierre and Niobrara shales along the eastern foothills support local stands of essentially western species, e.g., *Physaria australis* (Pays.) Rollins, *Eriogonum campanulatum* Nutt., and *Erigeron canus* A. Gray.

A discussion of this large and complicated group is outside the scope of this paper, because the flora is not chiefly Rocky Mountain in composition. The importance of this element arises from the fact that the Great Basin flora has contributed several species to the Rocky Mountain alpine flora, which will be discussed next.

Alpine-Desert disjunct vicariads. One of the distinct differences between the alpine areas of the Southern Rockies and of the Sierra Nevada of California is the almost total lack of desert annuals in the former. In fact, the Southern Rockies boast a single alpine annual, *Koenigia islandica* L., and this is not at all related to the local desert element but belongs to the circumpolar arctic flora.

On the other hand, several of the common desert perennials are represented in the alpine zone by subspecies or closely related species. Since their distribution from desert

to alpine zone is interrupted by the forested belt they may be said to be disjunct races. The presence of such desert types as *Hymenoxys*, *Gilia* (*Ipomopsis*), *Lesquerella*, and *Paronychia* in the alpine flora imparts an anomalous aspect to the tundra. Following is a list of desert species with their alpine counterparts: *Hymenoxys acaulis* (Pursh) Parker and *H. acaulis* var. *caespitosa* (A. Nels.) Parker; *Oreoxis alpina* ssp. *puberulenta* W. A. Weber and *O. alpina* ssp. *alpina* (A. Gray) C. & R.; *Paronychia sessiliflora* Nutt. ssp. *sessiliflora* and *P. sessiliflora* ssp. *pulvinata* (A. Gray) W. A. Weber; *Erysimum capitatum* (Dougl.) Greene and *E. nivale* (Greene) Rydb.; *Gilia spicata* Nutt. and *G. globularis* Brand; *Eriogonum jamesii* Benth. and *E. flavum* Nutt.

The enlargement of this list to include other alpine species belonging to genera found in the adjacent deserts must be done very cautiously. The alpine species of *Trifolium*, for example, are much more closely related to Eurasian alpine counterparts than to local desert-steppe species, and the alpine *Phlox condensata* (A. Gray) A. Nels. is evidently much closer to the western Arctic-eastern Asiatic *Phlox sibirica* or *P. richardsonii* than it is to local species.

EASTERN WOODLAND-PRAIRIE ELEMENT

Along the east face of the Front Ranges of Colorado and New Mexico, and at scattered points in a southwesterly direction into southeasternmost Arizona, characteristic members of the flora of the northeastern United States occur in favorable mesic localities. These localities include forested northeast-facing ravines in the foothills, moist gulches at the junction with the plains, prairie remnants, and open pine forests of gentle topography abutting on the plains. Livingston (1952) was concerned with this group as a problem in ecology rather than historical phytogeography.

Several facts concerning these plants are noteworthy. Most or all of the species also occur in the famous mixed Cordilleran-Boreal-eastern forests and prairies of the Black Hills of South Dakota, and the present distribution in the Rocky Mountains (see Fig. 5) may be considered a fragmentary remnant of this old pattern along the flanks of the Rocky Mountains. In Colorado, the Continental Divide acts as a complete barrier to the westward extension of this pattern, which suggests that the distribution postdates the last uplift of the area.

The mixing of these species with the Cordilleran flora at their present locations might be explained by an extension of the Cordilleran flora along highlands eastward during the Pleistocene, encouraged by the climatic changes at the lower altitudes and the depression of timberline above, accompanied by a westward extension of the eastern flora along the principal watercourses. Postglacial events would have caused each element to retreat toward its original center, leaving remnants in the most favorable sites at each end of the farthest extension. The mixture of Rocky Mountain, Boreal, and eastern elements is most pronounced in the Black Hills. Southward, where increasing aridity has eliminated all but a few species, the pattern occurs in smaller and more widely isolated patches.

The eastern species are favored in areas where the transition from high plains to mountains is especially abrupt. In

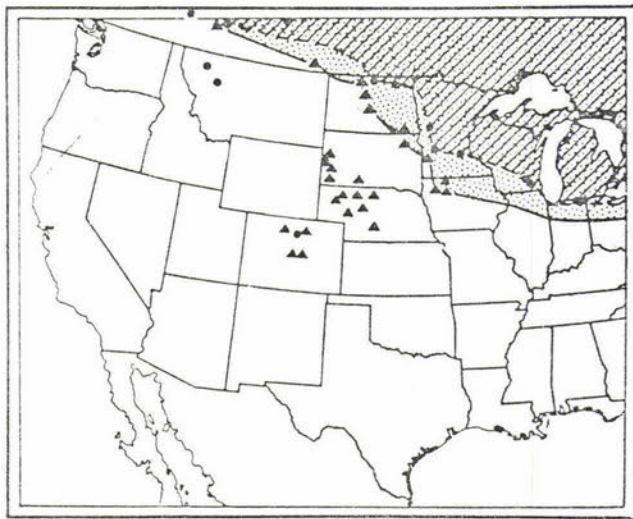


Figure 5. Distribution of *Salix serissima* (hatching and large dots) and *S. petiolaris* (fine dotting and triangles), two eastern woodland species. From Ball (1949).

such areas, exemplified by the prominent face of Green Mountain near Boulder, Colorado, the almost vertical escarpment provides a wall rising from 1,600 m to over 2,400 m. This wall provides steep, cool, sheltered northeast-facing ravines and at certain times of the year intercepts air masses in such a way as to produce a local cloud veil. The concomitant increase of humidity protects eastern relicts of high moisture requirements and encourages the development of local pockets of vegetation quite unlike that in the surrounding foothills. It is interesting to find that this "eastern" element is drawn from the entire taxonomic spectrum, from the lichens on up to the phanerogams.

Probably some of these species were nearly extinct in this area at the time of the arrival of white men. But the white man soon introduced irrigation, and as a result some of these species have spread along the irrigation ditches. It is also possible that some species of eastern distribution have actually been introduced by the early settlers themselves in this way, or have escaped from nurseries featuring wild species.

In some instances it is almost impossible to tell whether a plant was originally native here or was introduced. *Thalictrum dasycarpum* Fisch. & Lall. and *Eupatorium maculatum* L. are almost unquestionably natives and are now established locally along ditches. But it is hard to decide whether this is also true of *Impatiens capensis* Meerb., *Acorus calamus* L., and *Leersia oryzoides* (L.) Sw.

SPECIAL PROBLEMS

ENDEMISM

For such an apparently diversified area, the striking absence of narrow endemism is a remarkable feature of the flora. The reasons for this are complex and little studied.

The following is a reasonably complete list of the high mountain endemics of the southern Rockies; most of these seem to be related to Great Basin species: *Aquilegia saximontana* Rydb., *Arenaria macrantha* (Rydb.) A. Nels., *Artemisia pattersonii* A. Gray, *Astragalus molybdenus* Barneby, *Castilleja haydenii* (A. Gray) Cockerell, *C. occidentalis* Torr., *C. puberula* Rydb., *Chionophila jamesii* Benth., *Draba crassa* Rydb., *D. exunguiculata* (Schulz) C. L. Hitchcock, *D. graminea* Greene, *D. grayana* (Rydb.) C. L. Hitchc., *D. streptocarpa* A. Gray, *Erigeron melanocephalus* A. Nels., *Eriogonum coloradense* Small, *Eutrema penlandii* Rollins, *Gilia globularis* Brand, *Haplopappus clementis* (Rydb.) Blake, *Haplopappus pygmaeus* (T. & G.) Gray, *Helictotrichon mortonianum* (Scribn.) Henr., *Kobresia macrocarpa* Clokey, *Mertensia alpina* (Torr.) G. Don, *Oreoxis bakeri* C. & R., *O. humilis* Raf., *Penstemon hallii* A. Gray, *P. harbourii* A. Gray, *Podistera eastwoodae* (C. & R.) Math. & Const., *Ranunculus macauleyi* A. Gray, *R. adoneus* A. Gray, *Saussurea weberi* Hultén, *Senecio soldanella* A. Gray, *S. taraxacoides* (A. Gray) Greene, *Townsendia rothrockii* A. Gray, *Trifolium attenuatum* Greene, and *T. brandegei* S. Wats.

Most of the endemics of lower elevations are plants of arid lands in the Colorado Plateau country (*Lomatium*, *Astragalus*, *Cryptantha*, *Penstemon*, *Townsendia*). A few of the mountain endemics (*Gilia globularis*, *Mertensia al-*

pina, *Haplopappus clementis*, *Hymenopappus newberryi*, are obviously derived from the surrounding desert flora, in most instances easily matched to their respective vicariads.

A small remainder are obviously related to arctic species (*Luzula subcapitata*, *Eutrema penlandii*) or to northern Cordilleran types with further relationship westward across Beringia (*Saussurea weberi* Hultén, aff. *S. viscida* Hultén of Alaska; *Kobresia macrocarpa* Clokey, aff. *K. hyperborea* Forsild). A very few represent remnants of the old Tertiary flora. These are well illustrated by the monotypic genus *Neoparrya*, and by *Rubus deliciosus* Torr., *Aletes anisatus* and *A. humilis*, *Selaginella weatherbiana*, and the lichen *Candelariella spraguei*, all of which are endemic along the eastern foothills in a line leading from southern Wyoming to northern New Mexico. The list is necessarily somewhat incomplete because of judgment decisions on the "narrowness" of the endemism.

The general problem of edaphic endemism has been thoroughly elaborated by Mason (1946), and specific parts of the problem have been discussed by Trelease and Beath (1949), Johnston (1941), and Persson (1956).

Trelease and Beath's study (1949) of seleniferous plants has particular importance in our area, because a number of species are limited in their distribution by the outcrops of rocks containing selenium. Some species of *Astragalus*, *Machaeranthera* (*Xylorhiza*), and *Stanleya*, are thus affected, and these plants have played an important part in the history of the cattle industry because of the poisonous qualities of plants containing selenium. *Haplopappus fremontii* A. Gray, *Eriogonum lachnogynum* Torr., and *Parthenium alpinum* (Nutt.) T. & G. appear to be selenophiles in our flora.

Johnston (1941) discusses the occurrence and restriction of plants on gypsum soils in Mexico. In the Rocky Mountain flora, *Cryptantha paradoxa* (A. Nels.) Payson, *Frankeia jamesii* Torr., and *Townsendia annua* Beaman appear to be restricted to gypsum outcrops.

In many parts of the world limestone and calcareous soils are of great importance in plant distribution. It is therefore of interest that many species that are proved to be calciphiles in northern Europe, e.g. *Dryas octopetala* L. and *Kobresia simpliciuscula* (Wahlenb.) Mack., are not so in the Southern Rockies. This is a problem that needs study. Furthermore, the limestone outcrops do not appear to be critical from the standpoint of fern distribution, as they often are in eastern North America. However, certain lichens (*Acarospora glaucocarpa* (Wahlenb.) Koerb., *Placynthium nigrum* (Huds.) S. Gray and certain bryophytes (*Orthotrichum jamesianum* Sull. & Lesq., *Didymodon* spp.), being much more closely tied to substrates, are limited to limestone.

CRYPTOGAMIC DISTRIBUTION PATTERNS

Some information is now available concerning the extent to which the mosses, hepatics, and lichens mirror the distribution patterns of the higher plants. Generally speaking, the ranges of most cryptogams are broader than those of phanerogams, and many more species are widely disjunct over the world. But the reasons for this are not necessarily related to the ease of dispersal by spores or soredia. The striking discontinuities of the desert and subtropical mosses

and many crustose lichens argue for Tertiary or older origins for these species, as well as for extraordinary genetic stability.

In the Southern Rockies almost all the bryophyte species in the mountains are well-known circumpolar types. The flora of the alpine and subalpine regions can be analyzed with the help of any of the standard Scandinavian manuals. There is virtually no high-altitude endemism in our moss flora. On the other hand, in the foothills and desert areas one encounters species belonging to the Madro-Tertiary flora, many of which range into Mexico, while some are common to the deserts of America, Central Asia, and North Africa.

The lichen flora is much the same. The mountains have a very strong circumpolar or arctic-alpine element. Somewhat higher percentages of Cordilleran endemism occur, although this may be an illusion, because we know little of the crustose flora of the high mountains of Asia. In the eastern foothills, a few species occur that seem to be correlated with the Eastern Woodland-Prairie element discussed earlier (e.g. *Parmeliopsis placorodia*, *Umbilicaria pustulata*, and *U. pensylvanica*). The cloud veil so often present on the eastern escarpment of the Front Range creates conditions mesic enough to support several species of high moisture requirement, whose occurrence is extremely unusual so far distant from the coastal influence (*Cetraria glauca*, *Cetraria chlorophylla*).

One of the striking negative aspects of the lichen flora is the scarcity of epiphytic macrolichens on the coniferous trees of the higher foothills and mountains. Their absence may be associated with the very low humidity of these areas. The intermountain parks, which are cold-air drainage basins, on the other hand, support adequate corticolous elements. The cryptogam-barren upper foothills of the Rockies contrast sharply with the same areas in southern New Mexico and Arizona, where periodic cloud cover on the higher slopes, probably resulting from proximity to moisture-laden air from the Gulf of California, results in a very rich corticolous lichen flora.

CONCLUSION

The elucidation of coincident distribution patterns is only a first faltering step in the elaboration of local phytogeographical theory. As Faegri (1963, p. 221) says: "A common distribution area does not in itself explain anything. On the contrary, it is a problem in itself, and what is generally done, is to consider the hypothetical explanation of the reason why a group of plants occur together as a fact to be used in the analysis of other problems as well. But in nature there is nothing like a flora element behaving as a collective unit. There are only individual plants (not plant species!) reacting each in an individual way. And the more or less fortuitous occurring together may be the result of widely differing histories and ecologic demands."

The foregoing discussion merely draws attention to some obvious patterns of plant distribution in the Southern Rocky Mountains and relates these to some fairly well-established events in Quaternary and Tertiary times. No questions have been answered and few have been raised. Plant-geographical research has only begun, and there is

much to do before the region will take its place among those that may be said to be botanically well known. Future progress will depend upon advances in the fields of traditional taxonomic methodology, mapping, cytology, autecology, and geology in many of its forms.

1. Traditional Taxonomic Methodology. The strong connections between the Southern Rocky Mountain flora and the floras of several widely separated areas necessitate a broad exchange policy for herbarium collections. Cooperation and interest is greatly needed from workers well-informed about the Alps, Pyrenees, Caucasus, and the mountains of the Soviet Union.

2. Mapping. Although the great mapping project of Hultén on the circumpolar plants will be valuable, local mapping projects should be designed to refine the world patterns. In the United States detailed mapping has been left to monographers instead of floristic workers, with the result that many common species have not been mapped simply because they present no taxonomic problems.

Ideally, a major herbarium in each state should be designated as a clearing-house for accurate taxonomic and geographical data, and uniform sets of base maps should be selected for the mapping of the flora on the local level.

3. Cytology. Hultén points out that in many instances Rocky Mountain species seem to be more closely related morphologically to their Eurasian mountain counterparts than they are to their American Arctic counterparts. An analysis of chromosome numbers and polyploidy levels for these species in all segments of their areas would go far to develop a general theory of origin and migrations.

4. Autecology. The strong dominance of community studies in American ecology should be balanced by an equally strong analysis of the ecology of species.

5. Geology. Plant geographers need to know from the physical geologist and geographer the extent, altitude, and time spans of local land masses in detail, as well as information bearing on the ancient climates, presence of highland migration bridges, and barriers. At the present time much of the information available is too general to be of much value to the phytogeographer. It is hoped that the present discussion has suggested points that might lead to a continuing dialogue between botanists and geologists and between botanists concerned with the present flora and paleobotanists concerned with the Pleistocene and Tertiary flora.

REFERENCES

- Abrams, LeRoy, 1913, Deserts and desert flora of the West, in *Nature and science on the Pacific Coast*: San Francisco, Paul Elder & Co., p. 168-176
- Axelrod, D. I., 1948, Climate and evolution in western North America during middle Pliocene time: *Evolution*, v. 2, p. 127-144
- 1964, The Miocene Trapper Creek flora of Southern Idaho: Berkeley, Univ. California Publ. Geol. Sci., v. 51, 148 p.
- Ball, C. R., 1949, Two problems in *Salix* distribution: *Madrono*, v. 10, p. 81-87
- Becker, H. F., 1961, Oligocene plants from the Upper Ruby Basin, southwestern Montana: *Geol. Soc. Amer. Mem.*, v. 82, 127 p.

- Booth, W. E., 1950, Flora of Montana. I, Monocots: Bozeman, Montana State College, 232 p.
- Cain, S. A., 1944, Foundations of plant geography: New York, Harper & Brothers, 556 p.
- Cockerell, T. D. A., 1887, British plants in America: Science Gossip, v. 23, p. 214
- 1888, The boreal flora in Colorado: Science Gossip, v. 24, p. 189
- 1891, The effect of altitude on plants: Nature Notes (Selborne Society), v. 2, p. 13-15
- 1906, The alpine flora of Colorado: Amer. Naturalist, v. 40, p. 861-873
- Darwin, Charles, 1883, Origin of species: New York, D. Appleton and Co., 458 p.
- Davis, R. J., 1952, Flora of Idaho: Dubuque, Iowa, Wm. C. Brown Co., 828 p.
- Deam, C. C., 1940, Flora of Indiana: Indianapolis, Dept. Conservation, 1236 p.
- Faegri, Knut, 1963, Problems of immigration and dispersal of the Scandinavian flora, in Löve, Askell, and Löve, Doris, North Atlantic biota and their history: New York, Pergamon Press, p. 221-232
- Fernald, M. L., 1925, Persistence of plants in unglaciated areas of boreal America: Amer. Acad. Arts Sci. Mem., v. 15, p. 237-342
- Harrington, H. D., 1954, Manual of the plants of Colorado: Denver, Sage Books, 666 p.
- Hay, Dorothy, 1939, The Mexican element in the Colorado flora: Univ. Colorado M.S. thesis, 107 p.
- Hitchcock, C. L., Cronquist, Arthur, Ownbey, Marion, and Thompson, J. W., 1955-1961, Vascular plants of the Pacific Northwest: Seattle, Univ. Washington Press, v. 3-5
- Holm, Theodore, 1923, The vegetation of the alpine region of the Rocky Mountains in Colorado: Nat. Acad. Sci. Mem., v. 19, p. 1-45
- Hooker, J. D., and Gray, Asa, 1880, The vegetation of the Rocky Mountain region and a comparison with that of other parts of the world: U.S. Geol. Surv. Terr., v. 6, p. 1-62
- Hultén, Eric, 1937, Outline of the history of arctic and boreal biota during the Quaternary period: Stockholm, A/B Thule, 168 p.
- 1956, The *Cerastium alpinum* complex, a case of worldwide introgressive hybridization: Svensk Bot. Tidskr., v. 50, p. 411-495
- 1958, The Amphi-Atlantic plants and their phyto-geographical connections: Kgl. Sv. Vetensk.-Akad. Handl., ser. 4, v. 7, 340 p.
- 1962, The Circumpolar plants. I, Vascular cryptogams, conifers, monocotyledons: Kgl. Sv. Vetensk.-Akad. Handl., ser. 4, v. 8, 275 p.
- Ives, R. L., 1938, Weather phenomena of the Colorado Rockies: Franklin Inst. J., v. 226, p. 691-755
- Izett, G. A., and Lewis, G. E., 1963, Miocene vertebrates from Middle Park, Colorado: U.S. Geol. Surv. Prof. Pap. 475-B, p. 120-122
- Johnson, P. L., 1962, The occurrence of new Arctic-Alpine species in the Beartooth Mountains, Wyoming-Montana: Madrono, v. 16, p. 229-233
- Johnston, I. M., 1941, Gypsophily among Mexican desert plants: Harvard Univ., Arnold Arbor. J., v. 22, p. 145-170
- Jones, G. N., and Fuller, G. D., 1955, Vascular plants of Illinois: Urbana, Univ. Illinois Press, 593 p.
- Kearney, T. H., and Peebles, R. H., 1960, Arizona flora: Berkeley, Univ. California Press, 2nd ed., 1085 p.
- Lechner-Pock, Lore, 1956, *Eritrichium nanum* (Amann) Schrader und seine Verwandten: Phyton, v. 6, p. 98-206
- Lesquereux, L., 1883, Contributions to the fossil flora of the western territories. III, The Cretaceous and Tertiary floras: U.S. Geol. Survey Terr. Rep., v. 8, 279 p.
- Livingston, L. B., 1952, Relict true prairie communities in central Colorado: Ecology, v. 33, p. 72-86
- Lüdi, Werner, 1961, Eduard August Rubel, 1876-1960: Zürich, Geobot. Inst. Eidg. Techn. Hochschule Stiftung Rübel Ber., v. 32, p. 5-24
- MacGinitie, H. D., 1953, Fossil plants of the Florissant beds, Colorado: Carnegie Instn. Publ. 599, 198 p.
- Maher, L. J., 1961, Pollen analysis and postglacial vegetation history in the Animas Valley Region, Southern San Juan Mountains, Colorado: Univ. Minnesota Ph.D. thesis, 85 p.
- 1963, Pollen analyses of surface materials from the southern San Juan Mountains, Colorado: Geol. Soc. Amer. Bull., v. 74, p. 1485-1504
- Major, J., and Bamberg, S. A., 1963, Some Cordilleran plant species new for the Sierra Nevada of California: Madrono, v. 17, p. 93-109
- Maide, Harold E., this volume, Snake River Plain
- Mapel, P., and Hail, J., 1960, Tertiary geology of the Goose Creek district Cassia County, Idaho, Box Elder County, Utah, and Elko County, Nevada: U.S. Geol. Surv. Bull., 1055-H, p. 217-254
- Maslin, T. P., 1959, An annotated check list of the amphibians and reptiles of Colorado: Univ. Colorado Stud., v. 6, p. 1-98
- Mason, L., 1946, The edaphic factor in narrow endemism: Madrono, v. 8, p. 209-226, 241-257
- Pennak, R. W., 1963, Ecological and radiocarbon correlations in some Colorado Mountain lake and bog deposits: Ecology, v. 44, p. 1-15
- Persson, Herman, 1956, Studies in "Copper Mosses": Hattori Bot. Lab. J., v. 17, p. 1-18
- Peterson, R. S., 1962, Wyoming pinyon revisited: Madrono, v. 16, p. 269-270
- Porsild, A. E., 1963, *Stellaria longipes* Goldie and its allies in North America: Nat. Mus. Canada Bull., v. 186, p. 1-35
- Rydberg, P. A., 1896, Flora of the Black Hills of South Dakota: U.S. Nat. Herbarium Contr., v. 3, p. 463-536
- 1914a, Phytogeography and its relation to taxonomy and other branches of science: Torreya, v. 12, p. 73-85
- 1914b-1922, Phytogeographical notes on the Rocky Mountain region: Torr. Bot. Club Bull. 1914b, Pt. I, Alpine region: v. 40, p. 677-686; 1914c, Pt. II, Origin of the alpine flora: v. 41, p. 89-103; Pt. III, Formations of the alpine zone: v. 41, p. 459-474; Pt. IV, Forests of the subalpine and montane zones, v. 42 (1915), p. 11-25; Pt. V, Grasslands of the subalpine and montane zones: v. 42, p. 629-642; Pt. VI, Distribution of the subalpine plants: v. 43 (1916), p. 343-364; Pt. VII, Formations in the

- subalpine zone: v. 44 (1917), p. 431-454; Pt. VIII, Distribution of the montane plants: V. 46 (1919), p. 295-327; Pt. IX, Wooded formations of the montane zone of the Southern Rockies: v. 47 (1920), p. 441-454; Pt. X, Grasslands and other open formations of the montane zone of the Southern Rockies: v. 48 (1922), p. 315-326
- 1916, Vegetative life zones of the Rocky Mountains: New York Bot. Garden Mem., v. 6, p. 477-499
- Stewart, B. K., 1940, Plant ecology and paleoecology of the Creede Valley, Colorado: Univ. Colorado, Ph.D. thesis, 154 p.
- Theobald, W. L., Tseng, C. C., and Mathias, M. E., 1964, A revision of *Aletes* and *Neoparrya* (Umbelliferae): Brittonia, v. 16, p. 296-315
- Tolmachev, A., 1959a, Sur l'origine de la flore arctique: Quant, ou, et comment surgit la flore arctique?: 9th Intern. Bot. Congr.: Toronto, Univ. Toronto Press, v. 2, p. 399
- 1959b, Der autochtone Grundstock der arktischen Flora und ihre Beziehungen zu den Hochgebirgsfloren Nord- und Zentralasiens: 9th Intern. Bot. Congr.: Toronto, Univ. Toronto Press, v. 2, p. 400
- Trelease, S. F., and Beath, O. A., 1949, Selenium, its geological occurrence and its biological effects in relation to botany, chemistry, agriculture, nutrition, and medicine: New York, authors, 292 p.
- Wallace, A. R., 1900, Studies, scientific and social: New York, Macmillan, v. 1, 526 p.
- 1905, My life, a record of events and opinions, v. 2: New York, Dodd, Mead & Co., 464 p.
- Watson, Sereno, 1890, Relation of Mexican flora to that of the United States: Amer. Assoc. Adv. Sci., 39th Meeting Proc., p. 291-292
- Weber, W. A., 1955, Additions to the flora of Colorado, II: Univ. Colorado Stud., Ser. Biol., v. 3, p. 65-108
- 1961, Additions to the flora of Colorado, III: Univ. Colorado Stud., Ser. Biol., v. 7, p. 1-26.
- Wolfe, J. A., and Barghoorn, E. S., 1960, Generic change in Tertiary floras in relation to age: Amer. J. Sci., v. 258A, p. 388-399
- Wright, C. W., 1952, An ecological description of an isolated piñon pine grove: Univ. Colorado M.S. thesis, 43 p.

SUMMARY

The Southern Rocky Mountain flora contains the following elements and sub-elements: (1) Circumpolar, which includes Boreal-Asiatic, Boreal-American, Central Rocky Mountain-Pacific Northwest, and Northern Rocky Mountain sub-elements; (2) Madro-Tertiary, which includes Tertiary-relict, Chihuahuan, Sonoran-Great Basin, and alpine-desert disjunct sub-elements; and (3) Eastern Woodland-Prairie elements.

In a broad sense the Cordilleran elements display contracting ranges and the Madro-Tertiary elements expanding ones. Several alpine species that impart a special character to the flora are clearly related to vicariads in the desert steppe. The unique association of Cordilleran, Boreal, and eastern elements in the Black Hills extends sporadically along the east slope of the Rockies through New Mexico to southeast Arizona. Several supposedly ancient species, endemics, and monotypes also occupy this area. Present alpine floras of North American mountain systems probably antedate in part the present arctic flora and demonstrate strong connections with the alpine flora of central-Asiatic mountain systems.

Temperate-asiatic, eastern woodland and Madro-Tertiary genera were well represented in the woody flora of Colorado during the Oligocene and Miocene, but many of these were eliminated regionally during the Pliocene.

Optimum sites for alpine rarities or disjuncts are those east-west trending mountain ranges where the highly xeric continental climate is modified by local conditions favoring a higher and more stable moisture level.

Eastern Woodland-Prairie element

(accidentally omitted from the paper as published)

- Agastache foeniculum Kuntze
 Agrimonia striata Michx.
 Amorpha nana Nutt.
 Andropogon gerardii Vitman
 Andropogon scoparius Michx.
 Anemone canadensis L.
 A. cylindrica A. Gray
 Antennaria neglecta Greene
 Apios americana Medic
 Aralia nudicaulis L.
 Aralia racemosa L.
 Aristida basiramea Engelm.
 Aster ptarmicoides (Nees) T. & G.
 Athyrium angustum (Willd.) Presl
 Betula papyrifera Marsh
 Bromus purgans L.
 Campanula aparinoides Pursh
 Carex brevior (Dewey) Mack.
 Carex deweyana Schwein.
 Carex sprengei Dewey
 Carex stipata Muhl.
 Carex torreyi Tuck.
 Carex vulpinoidea Michx.
 Ceanothus herbaceus Raf.
 Claytonia rosea Rydb. (aff. C. virginica)
 Corylus cornuta Marsh
 Cyperus schweinitzii Torr.
 Cypripedium calceolus L. var. pubescens (Willd.) Correll
 Cystopteris bulbifera (L.) Bernh.
 Danthonia spicata (L.) Beauv. var. pinetorum Piper
 Desmodium rigidum (Ell.) DC.
 Erigeron philadelphicus L.
 Eupatorium maculatum L.
 Galium triflorum Michx.
 Gaura neomexicana Woot. (aff. G. biennis)
 Gentiana andrewsii Griseb.
 Geum aleppicum Jacq. ssp. strictum (Ait) R. T. Clausen
 Helianthemum bicknellii Fernald
 Humulus lupulus L. var. neomexicanus A. Nels. and Ckll.
 Hypericum majus (A. Gray) Britt.
 Hypoxis hirsuta (L.) Coville
 Impatiens capensis Meerb.
 Juncus acuminatus Michx.
 Juncus brachycephalus (Engelm.) Buchenau
 Krigia biflora (Walt.) Blake
 Leersia oryzoides (L.) Swartz
 Lilium philadelphicum L.
 Lobelia siphilitica L. var. ludoviciana A. DC.
 Lysimachia ciliata L.
 Mimulus ringens L.
 Monotropa hypopitys L. var. latisquama (Rydb.) Kearney & Peebles
 Onoclea sensibilis L.
 Oryzopsis asperifolia Michx.
 Osmorhiza longistylis (Torr.) DC.
 Oxalis violacea L.
 Panicum perlongum Nash
 Parthenocissus vitacea (Knerr) Hitchc.
 Pedicularis canadensis L.
 Physocarpus opulifolius (L.) Maxim.
 Polygonum sagittatum L.
 Prenanthes racemosa Michx.
 Prunus pennsylvanica L.
 Ranunculus abortivus L.
 Ranunculus pennsylvanicus L. f.
 Rhus glabra L.
 Ribes americanum Mill.
 Rubus pubescens Raf.
 Rudbeckia laciniata L. var. ampla (A. Nels.) Cronq.
 Salix petiolaris J. E. Sm.
 Salix serissima (Bailey) Fernald
 Sanicula marilandica L.
 Senecio plattensis Nutt.
 Silphium integrifolium Michx.
 Silphium laciniatum Michx.
 Smilax herbacea L. var. lasioneura (Hook.) A. DC.
 Solidago speciosa var. pallida Porter
 Sphenopholis obtusata (Michx.) Scribn.
 Sporobolus heterolepis (A. Gray) A. Gray
 Stipa spartea Trin.
 Teucrium canadense L. var. occidentalis (Gray) McClintock & Epling
 Thalictrum dasycarpum Fisch. & Lall.
 Trautvetteria carolinensis (Walt.) Vail
 Verbena hastata L.
 Viburnum edule (Michx.) Raf.
 Viola pedatifida Don
 Vitis vulpina L.
 Zizia aptera (Gray) Fernald

PART II: BIOGEOGRAPHY

PHYTOGEOGRAPHY AND PALYNOLOGY

- Phytogeography and Palynology of Northeastern United States DAVIS
Problems in the Quaternary Phytogeography of the Great Lakes Region CUSHING
Palynology and Pleistocene Phytogeography of Unglaciated Eastern North America WHITE-
HEAD
Pleistocene Pollen Analysis and Biogeography of the Southwest MARTIN, MEHRINGER
Plant Geography in the Southern Rocky Mountains WEBER
A Pleistocene Phytogeographical Sketch of the Pacific Northwest and Alaska HEUSSER
The Boreal Bryophyte Flora as Affected by Quaternary Glaciation STEERE
Polyploidy, Distribution, and Environment JOHNSON, PACKER, REESE

ZOOGEOGRAPHY AND EVOLUTION

- Quaternary Mammals of North America HIBBARD, RAY, SAVAGE, TAYLOR, GUILDAY
Avian Speciation in the Quaternary SELANDER
Amphibian Speciation BLAIR
Reptiles in the Quaternary of North America AUFFENBERG, MILSTEAD
Quaternary Freshwater Fishes of North America MILLER
Pleistocene Events and Insects ROSS
The Study of Pleistocene Nonmarine Mollusks in North America TAYLOR
Other Invertebrates—An Essay in Biogeography FREY
Recent Adjustments in Animal Ranges SMITH

GENERAL

- Pleistocene Nonmarine Environments DEEVEY

PART III: ARCHAEOLOGY

- Late Quaternary Prehistory in the Northeastern Woodlands GRIFFIN
An Outline of Southeastern United States Prehistory with Particular Emphasis on the Paleo-
Indian Era WILLIAMS, STOLTMAN
Quaternary Human Occupation of the Plains STEPHENSON
Postglacial Climate and Archaeology in the Desert West BAUMHOFF, HEIZER
Pacific Coast Archaeology MEIGHAN

PART IV: MISCELLANEOUS STUDIES

- Late Quaternary History, Continental Shelves of the United States CURRAY
Isotope Geochemistry and the Pleistocene Climatic Record BROECKER
Quaternary Paleopedology RUHE
Geochemistry of Some Quaternary Lake Sediments of North America SWAIN
Quaternary Paleohydrology SCHUMM
Glaciers and Climate MEIER
Volcanic-Ash Chronology WILCOX
Quaternary Paleomagnetic Stratigraphy COX, DOELL, DALRYMPLE
Tectonics of Quaternary Time in Middle North America KING
Dendrochronology FRITTS
Theoretical Paleoclimatology MITCHELL



Colorado State University
Fort Collins, Colorado
80523

Colorado State Forest Service

December 5, 1978

TO: Dick Wood Liz Morris
 Gil Fechner Frank Hawksworth
 Ralph Dix Howard Alden
 Wayne Brewer

FROM: Terry Beeson

SUBJECT: December 14 Meeting

I am enclosing a draft outline of the management plan for comment
at the meeting which will be in:

Room 218
Old Forestry Building

at 1 PM
December 14.

Looking forward to seeing you.

A handwritten signature in cursive script, appearing to read 'Terry'.

RTBmk
Enc.

Draft Outline

next mtg → Jan 18 afternoon

Ron Ryder

MANAGEMENT AND ADMINISTRATION PLAN
OWL CANON PINON GROVE NATURAL AREA

Objectives of mgmt (from lease agreement)

I. Summary

- A. Name and location of area
- B. Present owner state (land Bd)
- C. Leasing arrangement and provisions
- D. Natural Areas authority and provisions - Not assessed
- E. Period for which the plan is prepared and period of revision 5 yrs of the plan
- F. Special sites, reserves, and general condition of the area ?
- G. Cooperators, credits and working relationships

Characteristics of area
II. Data Presentation and Analysis

- A. History of the area - mine lease, interest in prohibiting
- B. Archeological data - Liz
- C. Biotic data - Wayne Brewer gave some
- D. Abiotic data - 2 land bd, geology
- E. Climatological data
- F. Land use data - land board
- G. Ecological, interrelationships and analysis of data

III. Management and Administration

- A. Objectives of management (ed) & (research)
- B. Alternatives available to achieve objectives
- C. Alternatives analysis and selection
- D. Management recommendations (1) ed, (2) research, (3)
- E. Schedule of implementation of recommendations

Nondestructive

ed

Dickward - has info.

- F. Organization of management and administration
- G. Authority, responsibilities of implementing and maintaining recommendations

IV. Conclusions

- A. Summary of recommendations
- B. Budget and funding sources
- C. Areas of possible expansion *Catherine Roberts, Evans*

V. Appendix

- A. Maps - *Aerials*
- B. Photographs
- C. Other data as needed

II-C

OWL CANYON - INSECT RESEARCH

Owl Canyon, located northwest of Fort Collins, constitutes an extremely valuable area for insect research. In part, this is because it is the northern-most native stand of pinyon on this side of the Rockies in the United States. In addition, it has been isolated for many years by approximately 150 miles from the next nearest native stand. This probably means that the pinyon specific insects present in the Owl Canyon area have been isolated from other pinyon areas for a considerable amount of time. Studies on the kinds and numbers of pinyon specific insects in this area should reveal some information about the origin and existence of the stand, questions which have been debated for a considerable period of time.

My students and I are presently spending a considerable amount of time working on pinyon insects at Owl Canyon. One of our projects involves a ~~tip~~ tip moth in the genus Dioryctria. This new, and presently undescribed, species of moth has also been found at low populations in southern Colorado. Since the Owl Canyon populations are confined to the area by the lack of surrounding pinyons (which would normally allow dispersion), they may have built up to population levels not found in other areas. The result is heavy damage such that nearly all new growth on the trees is pruned back every year by the high populations of this moth. My students and I have been working on the life history of the moth for the past year and a half. Although the life cycle is very complex, it appears that we will be able to complete this work within the next year.

Another interesting research problem involves a complex of needle gall midges that occur in many pinyon areas of the state. In some cases, for example near Salida, Colorado, we are able to find five different species commonly occurring on the needles at relatively high levels. In the Owl Canyon area, however, we have been able to find only one species at very low population levels. We are interested in learning something about the ecology of this gall forming midge since it appears to exist at Owl Canyon in the absence of its competitors. We feel that by comparing the Owl Canyon area and other pinyon growing areas in the state we will be able to answer some important ecological questions about inter-specific and intraspecific competition of gall midges on this tree. In addition, complete studies on the gall midges should help us answer some questions as to the origin and development of the stand.

Other pinyon insects that would be of interest to us from a research standpoint include several moths and a species of beetle that attack cones. It is possible that these insects are responsible for the tremendous variation in seed production that we see in many pinyon areas and in particular at the Owl Canyon site. A ^bdark beetle specific to pinyon and a needle miner that has previously been undescribed are also found in the Owl Canyon area.

Obviously, the Owl Canyon pinyon site offers a productive area for insect research for many years to come. Because of the close proximity of this area to Colorado State University, it is ideal for research by students and faculty in this department. I

feel that we could solve numerous insect problems and answer many questions about growth and population development of this increasingly important Colorado tree if we can use the Owl Canyon site for our research program.

Tom - Jerry B.

thought CSFS

should pay this

56.50 but this

letter sounds $4/18$

like CSU is

going to pay it.

do you agree or
know more?

El. 4/17



Office of Vice President for Finance

Colorado State University
Fort Collins, Colorado
80523

April 13, 1979

RECEIVED

APR 1 11

CSFS-80

TO: J. R. Hehn
FROM: D. L. McClintock
SUBJECT: Owl Canyon Lease Payment

Attached is a copy of the lease of the Owl Canyon Pinon Grove. You will note that a payment of \$56.50 is due the STATE BOARD OF LAND COMMISSIONERS with reference in the transmittal documents to be made to Application No. 78/226, Lease No. S-36778. It seems to me that payment from the Land Suspense Account would be appropriate if other funds are not available.

DLM:es

Attachment

cc: T. B. Borden ✓
R. F. Conard
E. G. Goss

RECEIVED

APR 17 1979

CSFS-80

Commissioners

ROWENA ROGERS
ROBERT D. McPHEE
TOMMY NEAL



BOARD OF LAND COMMISSIONERS
Department of Natural Resources
620 Centennial Building
1313 Sherman St., Denver, Colorado 80203
(303) 839-3454

April 11, 1979

ANTHONY SABATINI
Administrator

THOMAS E. BRETZ
Minerals Director

ROBERT L. HAPGOOD
Chief Accountant

STATE BOARD OF LAND COMMISSIONERS
DEPARTMENT OF NATURAL RESOURCES
620 Centennial Building
1313 Sherman Street
Denver, Colorado 80203

Application No. 78/226
Lease No. S-36778

State of Colorado
Board of Agriculture



The following charges are due in connection with the renewal of your lease and must be remitted along with the enclosed documents.

Rental	\$ <u>50.00</u>
Lease Fee	\$ <u>1.00</u>
Service & Filing Fee	\$ <u>5.50</u>
Bond Premium	\$ _____
TOTAL FIRST YEAR'S CHARGES	\$ <u>56.50</u>

Remit by check payable to this Board. Make reference to the above application number.

STATE BOARD OF LAND COMMISSIONERS

SLB #251 (Rev. 10/76)

Mr. Eugene T. Petrone
Executive Secretary
State Board of Agriculture
Colorado State University
Fort Collins, Colorado 80523

Dear Mr. Petrone: *Eugene*

Re Lease S-36778

We are sending to copies of your Lease S-36778 covering the Owl Canyon Pinon Grove Natural Area.

Also enclosed is a statement for \$56.50 to cover the rental and related fees as per the attached statement. This amount covers the rental to November 3, 1979.

As per your request a copy of this lease is being sent to Mr. Tom Borden.

It has been a long time working out this agreement, but as you know we had numerous individuals and agencies involved and it was really a matter of cooradinating all the needs of the different agencies and it was held up for many months in the office of the Attorney General.

In any event the agreement is completed and we are looking forward to a meaningful relationship with you.

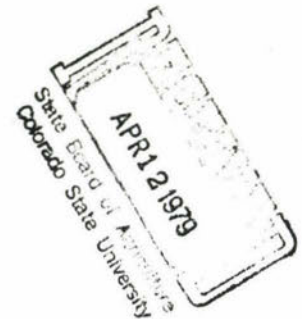
Very truly yours,

STATE BOARD OF LAND COMMISSIONERS

Anthony Sabatini
Anthony Sabatini
Administrator

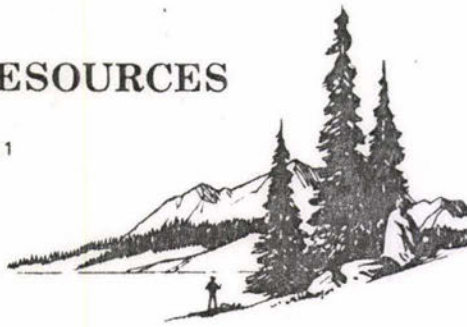
AS/mc
Enclosures 2
cc Tom Borden
State Forester

Dr. Carol "Carse" Pustmueller



DEPARTMENT OF NATURAL RESOURCES

HARRIS D. SHERMAN, Executive Director
1313 Sherman St., Room 718, Denver, Colorado 80203 839-3311



*Terry Beeson H205
old Forestry Bldg.*

Board of Land Commissioners
Division of Administration
Division of Mines
Division of Parks & Outdoor Recreation
Division of Water Resources
Division of Wildlife
Geological Survey
Oil and Gas Conservation Commission
Soil Conservation Board
Water Conservation Board
Mined Land Reclamation

February 1, 1979

Mr. and Mrs. J. Evan Roberts
Livermore, Colorado 80536

Dear Mr. and Mrs. Roberts:

It was good to talk to you on January 29 about the possibility of expanding the recently designated Owl Canyon Pinyon Grove Natural Area by including some of your land which harbors Pinyon Pines and is adjacent to the north boundary of the area. Since our conversation, I have spoken with both the Natural Areas Council and Terry Beeson of the Colorado State Forest Service at CSU, who is in charge of developing a management plan for the natural area.

At this point, I would briefly like to outline the necessary procedure for designating some of your acreage to the natural area, assuming you may wish to do so. Some pertinent information on the Natural Areas Program is enclosed for your convenience and describes both the objectives of and the procedures for the designation of natural areas. Please note that designation of areas can only occur when there is a willing owner; i.e., designation of your property is voluntary. As soon as your cooperation is apparent and you have determined the boundaries, I will draft the articles of designation for your area which no doubt will be very similar to the enclosed copy of articles of designation for the Owl Canyon Pinyon Grove Natural Area, a legal agreement between the State Board of Land Commissioners and the Colorado Department of Natural Resources. In the case of your property, the articles would establish an agreement between you (as the landowner), and the State of Colorado, Department of Natural Resources (administrator of the Natural Areas Program). This legal document can be as strong as you prefer.

The State Board of Land Commissioners, through its Lessee (Colorado State Forest Service, Colorado State University) will maintain the state property solely as a natural area (see Owl Canyon Articles of Designation, page 3 of 5, item number 4). Since the State Forest Service is currently drafting a management plan (which calls for admission by permission and pre-arranged appointment only) and has a lease agreement with the State Board of Land Commissioners

Roberts
2/1/79

Two

as the managers of the existing natural area, and since you have commented that your property adjacent to the natural area is currently willed to CSU, it might be wise for you to consider State Forest Service management of your part of the natural area. However, it is also your option to manage your part of the natural area yourselves. If you wish to work with the State Forest Service, then a separate legal agreement between you and the Forest Service should exist. Terry Beeson (482-8185) will contact you soon to discuss management aspects.

I mentioned to Terry and to the Council your dissatisfaction with the fact that one of your favorite trees was not included within the existing natural area. Possibly you should mention it again to Terry (with more detail on where the tree is) to determine its potential threat.

The Natural Areas Council and staff are excited about the possibility of increasing the size of the Owl Canyon Pinyon Grove Natural Area in order to protect as large a grove as possible. The larger the area, the more feasible it will be to perpetuate the existence of this pinyon pine ecosystem, hopefully for all time. I look forward to hearing from you soon. Thank you.

Sincerely,

Carse Pustmueller

Carse Pustmueller, Ph. D.
Director/Natural Areas Program

for COLORADO NATIVE PLANT
SOCIETY NEWSLETTER

DRAFT 1-12-79 (bjm)

PINYON IN THE COLORADO FRONT RANGE

The outlier of *Pinus edulis* at Owl Canyon, about 25 km north of Fort Collins, is well known. In 1961, W. A. Weber (Univ. Colo. Studies, Ser. Biol. No. 7) reported 2 pinyons in Rist Canyon, some 19 km south of Owl Canyon (T. 8 N., R. 70 W., Sections 28 and 29). Since then, five other pinyon localities have been found in Larimer County: two additional areas in Rist Canyon (T. 8 N., R. 70 W., Sections 30 and 32), north fork of the Poudre River (T. 9 N., R. 70 W., Sec. 15), Hewlett Gulch (T. 9 N., R. 71 W., Sec. 27), and Poudre Canyon near Fort Collins Mountain Park (T. 9 N., R. 72 W., Sec. 4). The latter area is about 26 km WSW of the Owl Canyon Grove. In all these localities, only one or a few trees are present and they probably are a result of spread by jays from the main Owl Canyon Grove.

The northernmost locality of the main population of pinyon along the Front Range seems to be in southern Douglas County. Pinyon was recently collected on the west side of the Rampart Range in Missouri Gulch (T. 10 S., R. 69 W., Sec. 35), about 16 km north of Woodland Park (F. G. Hawksworth 1869, October 1978, CS).

The northernmost locality on the east side of the Rampart Range seems to be Douglas Creek, 5 km north of Garden-of-the-Gods, El Paso County (D. G. Steward, W. Boyd, and J. W. Marr, Colorado-Wyoming Acad. Sci. J. 8:50, 1976). E. L. Little (Atlas of United States trees. Vol I. Conifers and Important Hardwoods, U.S. Dep. Agric., 1971) shows a location in southern Douglas County on the east side of the Rampart Range, but this has not been confirmed.

Pinyon has also been collected in Boulder County: Boulder Canyon, 14 miles west of Boulder (W. A. Weber 12979, 1966, COLO.) Dr. Weber says that only a single tree was found (which has been subsequently removed) and it was probably not native. Little (1971 op cit) shows a pinyon location in central Jefferson County, but I have not been able to confirm this report.

Any further information on the natural distribution of pinyon in the Colorado Front Range would be appreciated. Frank Hawksworth, U.S. Forest Service, Rocky Mountain Station, 240 W. Prospect St., Fort Collins, Colorado 80526.

STATE OF COLORADO

COLORADO NATURAL AREAS PROGRAM

Department of Natural Resources
1313 Sherman Street, Room 718
Denver, Colorado 80203

Phone (303) 866-3311

July 20, 1984


Mr. Tom Owens
State Forest Service
Colorado State University
Fort Collins, Colorado 80526

Dear Tom:

Enclosed is a copy of the Management Plan for the Owl Canyon Pinyon Grove and Natural Area, including its numerous appendices. Also, I have enclosed a copy of my letter to Steve Leavitt.

Please keep in touch re: the Owl Canyon Pinyon Grove. I will give you a call when I expect to be in the area.

Sincerely,

Carse Pustmueller 

Carse Pustmueller, Ph.D.
Director,
Colorado Natural Areas Program

CJP:bck

Enclosure

P.S. I have misplaced the exact boundaries of Brackenberry property donated to the Colorado Division of Wildlife. On Appendix A map, I have drawn in pencil the approximate area.



Richard D. Lamm
Governor

David H. Getches
Executive Director

Carol J. Pustmueller, Ph.D.
Program Director

Colorado Natural
Areas Council

Theodora Colborn
Chair

Olin Webb
Vice-Chair

Richard G. Beidleman
Colorado Board of
Parks and Outdoor
Recreation

Wallace Hansen
Member

Wm H. Claire
State Board of
Land Commissioners

Jean Tool
Colorado Wildlife
Commission

David R. Sturges
Member

STATE OF COLORADO

COLORADO NATURAL AREAS PROGRAM

Department of Natural Resources
1313 Sherman Street, Room 718
Denver, Colorado 80203

Phone (303) 866-3311



July 17, 1984

Mr. Steve Leavitt
Lab. of Isotope Geochemistry
Department of Geosciences
University of Arizona
Tucson, Arizona 85721

Dear Steve:

Enclosed is the complete copy of the management plan for the Owl Canyon Pinyon Grove Natural Area and its appendices. The permits are the last two pages of the plan.

Tom Owens, Colorado State Forest Service, Colorado State University, Fort Collins, Colorado 80523, 303-491-6303, is the contact for the Owl Pinyon Grove. He has replaced Terry Beeson. I have contacted Tom, and he will look out for your permit. He has no problem with four cores from each of eight trees on state land if you plug the resulting holes adequately from potential infestations, and if data obtained from the area is supplied to the State Forest Service.

I hope you have a successful trip to Owl Canyon State Natural Area. Please call me if you have any problems.

Sincerely,

Carse Pustmueller, Ph.D.
Director,
Colorado Natural Areas Program

Richard D. Lamm
Governor

David H. Getches
Executive Director

Carol J. Pustmueller, Ph.D.
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State Board of
Land Commissioners

Jean Tool
Colorado Wildlife
Commission

David R. Sturges
Member

CJP:bck

Enclosures

RECEIVED

FEB 23 1979

6878-80

20 years ago today

November 7, 1951

Decision to ask Governor Thornton and the Colorado State Land board to set aside a half-section containing the best timbered part of the Owl canyon grove of giant pinon pine trees was the outcome of a "field day" held in the area under auspices of the Livermore pinon grove committee.

The group decided to ask that the north half of section 36, township 10 north, range 70 west be set aside as a public preserve, in order to save the best portion of the pinon forest, farthest-north stand of the species in North America. Some of its oldest trees are estimated to be 700 to 800 years old.

Fort Collins' board of education decided to proceed with construction of a new gymnasium addition at Fort Collins High School.

The motion of approval included authorization to ask a federal allocation for the needed building steel, with the prospect that it can be obtained in the third quarter of 1952.

W. F. Bugas, secretary of the Eddie Hanna Athletic Award association, announced the adoption of a constitution by the association.

The purpose of the association is to collect funds to assist outstanding athletes enrolled at Colorado A and M College. The awards will be made in memory of Eddie Hanna, student at Colorado A and M who died shortly after playing a football game at Colorado Springs, Sept. 17, 1949.

Two local women's organizations are assisting in service projects of the Larimer County Red Cross Chapter, according to Mrs. Glenn C. Whittle, chapter volunteer special services chairman.

With funds provided by the Red Cross, the Quota Club will select and pack articles for 50 gift boxes to be sent to soldiers who will be at sea at Christmas time. Mrs. Adelia Davis is Quota Chairman for the project.

Members of the Blue Triangle club will make 50 dresser and table scarves for the Fort Lyons hospital.

Jerry, this old clipping may be of interest
to you.

Wayne Brewer

Jerry Beeson
Colorado State Forest
Foresty ^{Service} Rd
Campus

11/9
TERRY
6

November 8, 1978

Mr. Harris D. Sherman, Executive Director
Colorado Dept. of Natural Resources
1313 Sherman, Room 718
DENVER, Colorado, 80203

Dear Harris:

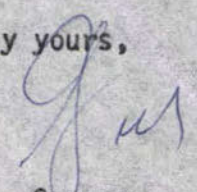
Congratulations on getting the Owl Canyon Pinon Pine Natural Area established. The ceremony at CSU last Friday was very appropriate, and a great many of us were much pleased to see this happen.

I have two specific suggestions to make as a result of the accomplishment and the ceremony designating it. The J. Evan Roberts family of Livermore own a ranch which includes some pinon which I am quite sure adjoins the state school section from which the 101 acres were designated as a natural area. Mr. Roberts, and especially his wife Catherine, have spoken for years to us when we have met and visited with them, about the desirability of preserving some of that state land, and they were, no doubt, among those persons writing to Jim Lloyd "irate" letters, as he put it, asking why the state couldn't do something. On at least a couple of occasions in our presence the Roberts have said that if the state would take appropriate action to preserve the pinon grove they would be willing to add some of their adjoining land, which also contains pinon, to it. Clearly someone ought to follow up on this. I am sure the Roberts would have been at the ceremony except that they had left the state a week earlier for an extended visit to relatives in the east.

The other suggestion relates to the information which was reported to us last Friday by those several speakers. I was much impressed with the fact that a number of items were completely new to me, although I have lived here for twelve years and have been much interested in the area all this time. It seems to me it would be a shame if immediate action was not taken to assemble the information presented there into the form of a nice brochure on the new natural area. It would have been easiest if someone had used a tape recorder to record all of the comments made, and it seemed to me that most of the speakers had fairly detailed notes and each of them ought to be glad to supply either his notes or a few paragraphs which could be used to prepare such a brochure.

I am sending a copy of this^{to} Tom Borden, and to Reed Kelley, but I especially hope that you as the ultimate authority for the Natural Area System will see fit to follow up on both of these suggestions. With congratulations again on the accomplishment which was celebrated last week, I am,

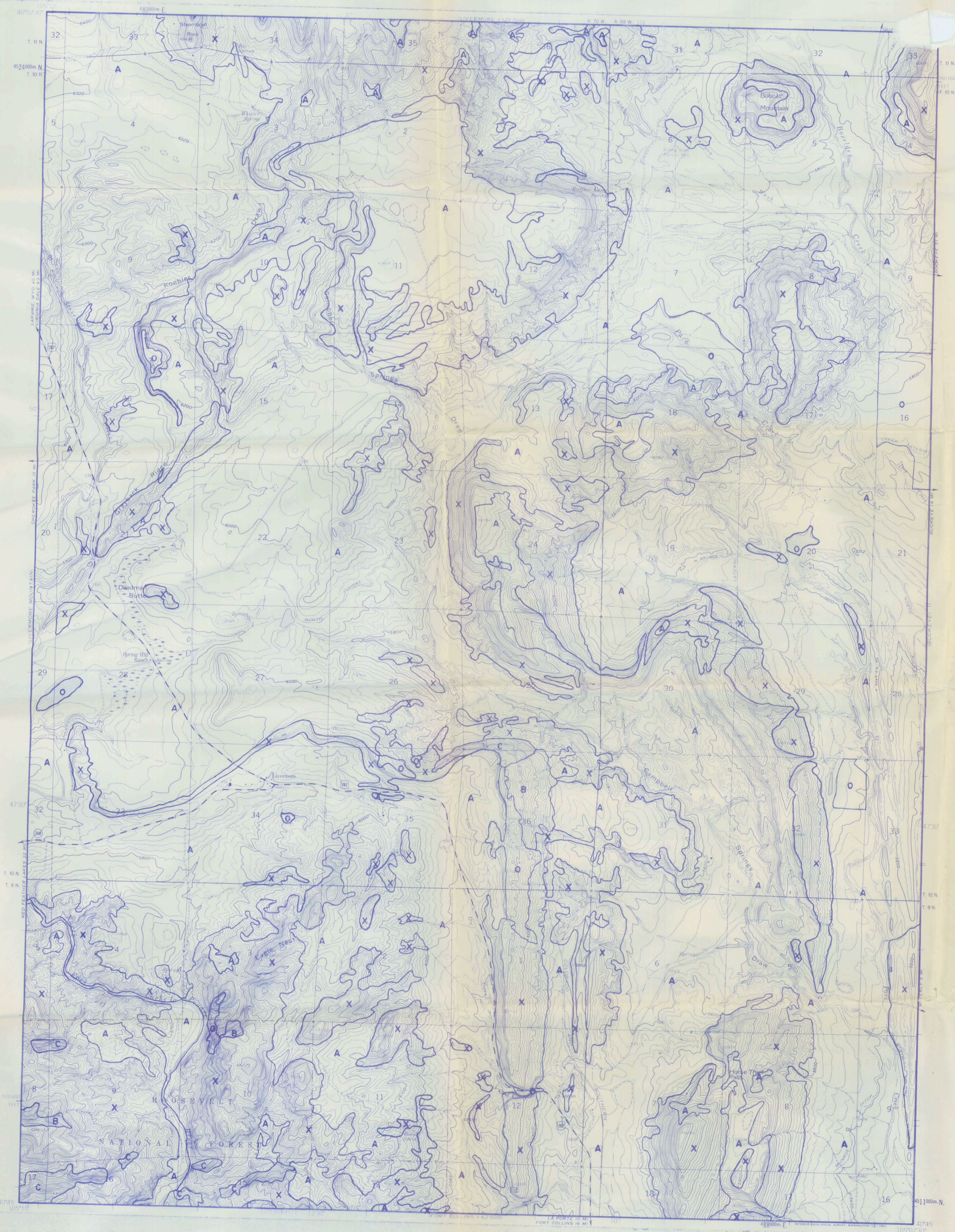
Sincerely yours,


Gustav A. Swanson,
Emeritus Professor and Department Head.

cc. Reed Kelley and Tom Borden

WILDFIRE HAZARD AREA MAP

FUEL TYPE



Specific areas on all maps require more detailed analysis and diagnosis from your State District Forester.

Basemap is a 7 1/2' topographic quadrangle from U.S.G.S., 1960

Wildfire hazard information was compiled by optical transfer methods. Aerial photography flight 752-H-1 1975. Scale 1:24,000. Field check 1976.

SCALE 1:24,000
CONTOUR INTERVAL 20 FEET



**LIVERMORE, COLO.
LARIMER CO.**

Prepared by Colorado State Forest Service, Fort Collins, Colo.

WILDFIRE HAZARD CLASSES

- O - No hazard
- A - Low hazard
- B - Medium hazard
- X - Severe hazard - brush
- C - Severe hazard