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Ecology of Aspen in Gunnison County, Colorado

M.D. Morgan

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M. D. MORGAN[1]
Department of Botany, University of Illinois, Urbana 61801

ABSTRACT: The ecology of quaking aspen was studied in Gunnison County, Colorado. In the study area, aspen stands often take the form of small islands surrounded by fescue grasslands. At its upper altitudinal limits, aspen generally abuts the spruce-fir forest. The greatest number of trees were 4- to 7-in DBH with only a few being greater than 10-in DBH. Aspen reproduction is evident, but many of the trees below 4-in DBH were dead. The aspen understory is very lush and is characterized by many tall herbaceous species. The disjunct distribution of several understory species does not seem related to soil or aspect conditions. Aspen soils are generally more fertile than adjacent spruce-fir or fescue grassland soils. All soils possessed several characteristics of immature soils: 1) little variation in silt and clay content throughout the profile, 2) little horizon and structural development, and 3) little variation in per cent base saturation throughout the profile. Aspen seed retained good viability after cool storage for 1½ years. The pattern of morphological characteristics, site conditions, and leafing times is much more complex than that reported in other areas in the central Rocky Mountains. Aspen appears to be successional to spruce-fir in the present study area, although in local sites that may be inaccessible to a spruce-fir seed source the present mosaic pattern of aspen groves within fescue grassland or sagebrush may persist.

INTRODUCTION

The physiognomy of the deciduous trembling aspen (*Populus tremuloides*)[2] contrasts markedly with that of the associated coniferous species *Abies lasiocarpa, Abies concolor, Picea engelmannii, Pseudotsuga taxifolia,* and *Pinus contorta latifolia.* Aspen is present in both the montane and subalpine zones of the central Rocky Mountains. In Utah, large areas of aspen forest which form an altitudinally defined belt (2,600-2,900 m) have been reported (Sampson, 1916, 1925; Fetherolf, 1917; Tidestrom, 1925; Cottam, 1929; Tanner and Hayward, 1934; Dixon, 1935; Graham, 1937; Lull and Ellison, 1950). Daubenmire (1943) considers the Great Basin area and vicinity to be the center of optimum development of trembling aspen in North America. He also cites an area in the Medicine Bow National Forest of Wyoming where aspen stands are present that are very similar to those of the Great Basin area. Aspen is less extensive in Wyoming and Colorado, although it occupies large areas of the western slopes in Colorado (Baker, 1921, 1925). Robbins (1910) stated that aspen is particularly common on the western slopes in Colorado, where it covers extensive areas and grows to considerable size. In southwestern Colorado the montane zone occurs between the altitudes of 2,750 and 3,200 m and is mainly aspen vegetated.

In Gunnison County, Colorado, aspen occupies a variety of sites

[1] Present address: University of Wisconsin-Green Bay, Green Bay, Wisconsin 54301.

[2] Nomenclature follows that of Harrington, 1954.

ranging from steep talus slopes to deep soils on gentle slopes near valley bottoms. The stands often take the form of small islands surrounded by *Festuca thurberi* (Fig. 1) or less frequently by *Artemisia tridentata* (Fig. 2). At its upper altitudinal limits, aspen generally abuts upon the spruce-fir forest. An important part of the ecology of aspen is its successional relationship to conifers.

Aspen stands have a characteristic luxuriant understory that readily differentiates the aspen community from the other communities present. Bark of some trees is chalkish-white whereas others have yellow-green boles. There are also differences in the degree of pruning that are not associated with stand density. The most dramatic difference between aspen trees can be observed in early spring and autumn. In spring, some trees break dormancy two weeks in advance of others. Autumn coloration in these same early-leafing trees occurs two weeks earlier than in the late-leafing trees.

With these many variable characteristics of aspen in mind, the ecology of aspen in the adjacent Anthracite and Crested Butte Quadrangles of Gunnison Co., Colorado, was investigated (Fig. 3). The most extensive study was conducted in the Gothic valley. For purposes of simplicity, the stands in Washington Gulch and Copper Creek valley are included in the Gothic valley area. Cement Creek valley and the Kebler Pass area were also studied to obtain an idea of the variability of aspen in adjacent areas. This study was undertaken to provide information on the following points: (1) a description of aspen communities including relationships of understory and soils,

Fig. 1.—Southeast-facing slope in Gothic valley showing aspen abutting spruce-fir above and fescue grassland below. Note that the aspen forest is not a continuous belt, but rather is present as "islands."

(2) relationships between bark color, pruning, and site conditions, (3) possible causes of the variation in leafing time, (4) the successional status of aspen in Gunnison County, and (5) the possible role of vegetation in soil development.

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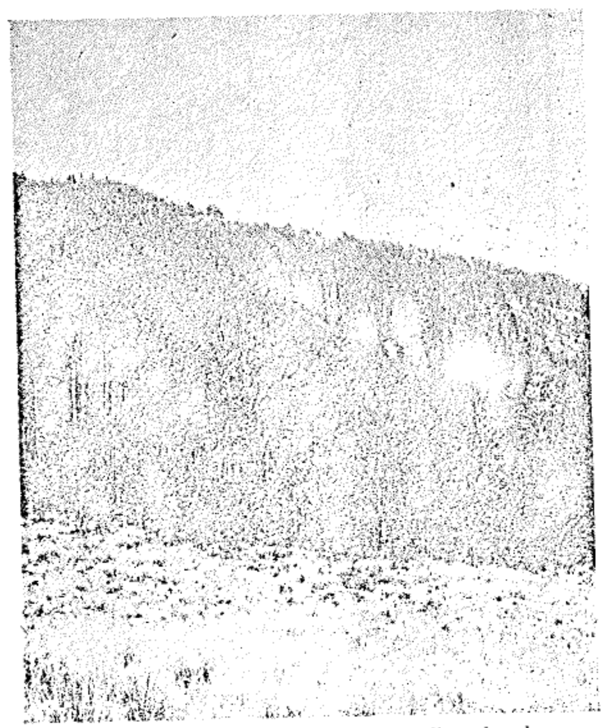

Fig. 2.—East-facing slope in Cement Creek valley showing aspen invasion of sagebrush. Note the presence of scattered subalpine fir trees within the aspen stand.

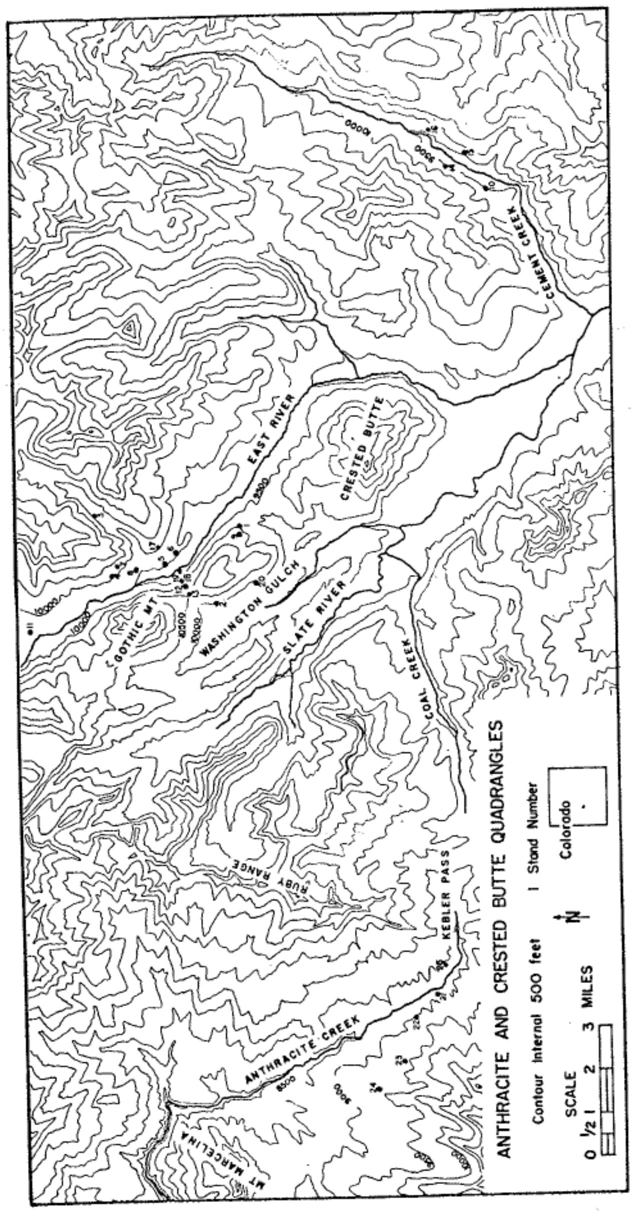

Fig. 3.—Topographic map of Anthracite and Crested Butte Quadrangles showing aspen stands that were studied (based upon U.S.G.S. Topographic Map).

DESCRIPTION OF AREA

CLIMATE

The nearest climatic data are available from the U. S. Weather Bureau station at Crested Butte (elevation 2,700 m), 1,300 m below the zone of optimum aspen development. The station is approximately 8 km from the study area. Therefore, climatic conditions within the aspen zone are unknown, but the data from the Crested Butte station give an idea of the general climate. Snowfall is heaviest in December, January, February, and March with an annual average of 424 cm (U. S. Weather Bureau, 1965). Rainfall is greatest in August (5.8 cm) and least in May (3.3 cm). The average annual precipitation for Crested Butte is 61 cm, but due to their higher elevation, aspen stands can be assumed to receive a greater amount of precipitation. The mean temperature during July is 14 C and during January —10 C. The average frost-free period extends from 2 July through 22 August (U. S. Dep. Agriculture Yearbook, 1941). It can be assumed that the frost-free period within the higher aspen zone is shorter.

GEOLOGY

The geology of the Crested Butte area is quite varied (Langenheim, 1962). Outcropping rocks are 90% sedimentary; the remaining 10% are mostly igneous, with minor amounts of metamorphic rock occurring in the contact zones around large igneous masses. Coarse clastic rocks, which include conglomerate and sandstone, are exposed over 60% of the area. Shale, mudstone, and siltstone cover 21% of the area with only approximately 6% of the outcroppings being calcareous. Glacial moraine and outwash are found in the valleys.

VEGETATION

The aspen community ranges from 2,700 to 3,350 m in the Crested Butte area (Langenheim, 1962), although it is most extensively developed in a zone between 2,750 and 3,200 m. The aspen community forms a relatively continuous forest belt below the spruce-fir or may be present as isolated groves invading the fescue grassland. Sagebrush may border on the aspen community below. Langenheim (1962) classified the aspen community in the Crested Butte region as a zonal climax community. She also recognized aspen as being successional within the spruce-fir zone.

GRAZING AND FIRE

Usage of the study area has been controlled since 1905 when the area was made a part of the Gunnison National Forest. Grazing in the Gothic and Cement Creek areas is limited; cattle usually avoid the dense aspen stands, perhaps due to the general scarcity of grasses in the aspen understory. While some sheep have been grazed in the aspen stands of the Kebler Pass area, grazing has not caused severe erosion.

Evidences of past fires are abundant, but exact fire dates are difficult to determine. Stahelin (1943) stated that portions of the Anthracite Quadrangle were burned in 1880 although he did not cite his source of information. Using increment borings of lodgepole pine, Langenheim (1962) suggested that fires in Cement Creek valley, which is one of the present study areas, occurred from 1885 to 1895, a period coinciding with the time of peak mining activity in this area.

METHODS

VEGETATION

Stands were selected in order that all aspect conditions on which aspen were growing in the study area were sampled. The vegetation was sampled using nested quadrats. Ten-meter-square quadrats were used for the trees, 4 × 4 m for the shrubs, and 2 × 2 m for the herbaceous understory. A compass bearing was used to set up the base lines, which were established well within the stands to avoid edge effect. Plots were placed every other 10 m along the base line and always to the left side of the line. Generally two base lines were set up with four quadrats on each line, thus making a total of eight nested plots per stand. The understory species were recorded and cover classes were determined using five cover classes (Braun-Blanquet, 1932). From the field data, frequency was determined. Basal area was determined for all trees larger than 1-in DBH.

Frequency and cover values were determined for each species for each stand. Since each stand was sampled with eight quadrats, except stand 3, constancy was determined for each species. Average cover per stand was found for each species by totaling cover per stand and dividing by the number of stands in which the species occurred. Average frequency was calculated similarly.

SOILS

The site of the soil pit in each stand was subjectively chosen to be the most typical in the stand relative to the vegetational composition. The border between the A and B horizons was generally evident. In many cases, however, very little development within the B horizon could be seen. If little development was found, a soil sample was collected from both the upper B and the lower part of the horizon. Laboratory analyses could then be used to determine if there were any significant differences between the upper and lower B. A profile description indicating horizon depth, rooting pattern, and other characteristics was prepared for each pit. For the comparative study of soils under different vegetation types, adjacent sites of aspen, spruce-fir, and fescue grassland were chosen.

Duplicate samples passed through a 2-mm sieve were used in the laboratory analyses. Soil texture was determined by the hydrometer method (Bouyoucus, 1951); per cent base saturation by the method of Brown (1943); *p*H on a 1:1 soil-water dilution; per cent organic matter using the Walkley-Black (1931) wet oxidation method; and soil color on laboratory-moistened samples with a Munsel Color Chart. Moisture tension data were determined using the pressure membrane for moisture contents at 3, 5, 8, and 15 atm, and the porous plate for 1/3 atm determinations (Richards, 1949). The soil nutrient analyses were performed at the Dixon Springs Agricultural Center, Simpson, Illinois. Ten grams of soil were leached with 250 ml of 1N ammonium acetate. The ammonium acetate was then evaporated and the elements were taken up with dilute hydrochloric acid. Potassium content was determined with a flame photometer, calcium and magnesium level by the EDTA method (Malmstadt and Hadjiioannou, 1959), and phosphorus by the phosphomolybdic acid method of Troug (1930).

SEED GERMINATION

Aspen seeds were collected from the only sites (4) in Gothic Valley where the trees had set seed (10 to 15 July 1964). After the catkins had air-dried for three days, the seeds were placed in glass jars and stored at 3.3 C. They were later shipped air express to the University of Illinois where they were immediately stored at 5.5 C.

For the germination tests, 20 full seeds were placed between Whatman No. 1 filter paper moistened with distilled water in each Petri dish and observed every 12 hours. On 12 December 1964 a preliminary test for germination was run at room temperature to determine if the seeds had retained viability after being stored and transported at several temperatures. On 12 March 1965 (240 days after collection) duplicate samples for each site were run in a cool room (oscillating between 2.2 and 3.9 C twice per hour) and at room temperature which fluctuated between 26.7 and 28.9 C. Additional germination tests were run using duplicate samples for each site at room temperature on 15 August 1965 (396 days after collection) and on 17 February 1966 (581 days after collection).

RESULTS AND DISCUSSION

VEGETATIONAL ANALYSIS

Aspen trees generally do not grow as large as associated conifers. Langenheim (1962) found few aspen trees greater than 10-in DBH; most were in the 1- to 5-in DBH range. Only 3% of the live trees sampled in the present study had a DBH greater than 10 in, with a majority in the 4- to 7-in DBH range (Table 1). There was much reproduction in aspen stands, with 27% of the living trees being less than 1-in DBH and 53% less than 4-in DBH. A marked exception were the stands in the Kebler Pass area, where only 30% of the living trees were less than 4-in DBH. Also in the Kebler area stands, there were not a large number of trees with a DBH greater than 4 in. These stands did contain, however, more trees with a DBH greater than 10 in than did stands in the other areas. The notable exceptions were stand 11 (Gothic valley) and 16 (Cement Creek valley). The stands in the Kebler Pass area also had the greatest basal area in the larger DBH classes. Of the trees sampled, 17% were dead and of these, 81% were less than 4-in DBH. Thus, even though there was good reproduction in most aspen stands, a high percentage of the trees died by the time they reached a DBH of 4 in. The mortality

TABLE 1.—DBH classes (inches) of live and dead aspen trees in 25 aspen stands in Gunnison Co., Colorado

Stand number	Stand location	Living trees 0-1 DBH	1-4 DBH	4-7 DBH	>7 DBH	Basal area per acre	Dead trees 0-4 DBH	>4 DBH	Percent[b] dead
1	Gothic valley	25	51	152	16	164.8	64	9	29.92
2	Washington Gulch	193	89	121	8	134.3	75	5	19.46
3[a]	Copper Creek valley	149	52	46	22	135.5	16	3	7.06
4[a]	Gothic valley	38	67	89	68	231.5	70	11	30.92
5	Gothic valley	26	13	111	64	238.7	61	56	54.67
6	Gothic valley	64	33	53	47	146.3	29	9	19.30
7[a]	Gothic valley	80	90	99	24	139.2	20	1	7.17
8[a]	Gothic valley	14	92	108	15	136.8	....	....	....
9	Gothic valley	103	128	113	27	164.6	29	....	7.82
10	Cement Creek valley	193	148	97	7	113.6	103	25	28.76
11[a]	Gothic valley	38	81	46	54	220.8	12	6	8.22
12[a]	Gothic valley	79	140	91	19	136.7	47	1	14.59
13[a]	Gothic valley	81	109	116	6	122.5	38	....	12.18
14[a]	Cement Creek valley	110	77	59	20	102.1	67	5	27.07
15[a]	Cement Creek valley	93	79	97	23	139.6	87	20	33.22
16	Cement Creek valley	68	97	79	33	189.8	92	6	35.38
17[a]	Gothic valley	7	35	39	66	191.8	19	3	14.97
18	Gothic valley	25	73	153	31	196.5	31	1	11.35
19	Gothic valley	165	122	91	71	238.1	61	2	14.03
20[a]	Washington Gulch	10	29	57	54	158.4	9	....	6.00
21[a]	Kebler Pass area	66	....	42	63	232.2	52	25	45.03
22[a]	Kebler Pass area	1	2	25	55	158.9	6	12	21.69
23[a]	Kebler Pass area	37	4	33	74	211.9	11	23	22.97
24[a]	Kebler Pass area	19	12	40	59	177.2	35	8	33.07
25[a]	Kebler Pass area	49	37	66	60	218.0	39	12	24.06

[a] Conifers present within or at edge of the stand.

[b] Per cent dead of total trees.

rate was lower in the larger size classes. Most stands, however, were probably not old enough to show much deterioration of the older trees. Increment borings of seven aspen trees in two stands showed an age range from 48 to 59 years for trees 7- to 9-in DBH.

Spruce and fir were sampled in only eight stands, although they were found in or at the edge of 16 of the 25 stands sampled. Due to unknown factors, fir was much more common than spruce in the aspen stands. The seedling stage was most prominent; very few conifers were present with a DBH greater than 5 in. The conifers thus did not contribute appreciably to the basal area of the stands. Aspen, spruce, and fir were the only tree species encountered in the aspen stands.

The aspen understory was generally very luxuriant in comparison with the understories of associated coniferous communities. Although only two species had a constancy of 100%, the 12 species with a constancy of 72% or greater form a very characteristic understory in aspen stands (Table 2). The presence of *Thalictrum fendleri*, *Senecio serra*, *Ligusticum porteri*, *Geranium richardsonii*, *Delphinium barbeyi*, and *Osmorhiza obtusa*, which formed the upper herb strata, gave the aspen stands their characteristic look of lushness. The legumes *Vicia americana* and particularly *Lathyrus leucanthus* formed thick entangled mats. *Carex geyeri*, *Fragaria ovalis*, and *Viola nuttallii* usually formed a lower layer while isolated culms of *Bromus ciliatus* were common.

TABLE 2.—Summary of understory vegetation in 25 aspen stands in Gunnison Co., Colorado

Species	Highest cover class	Ave. cover class	Highest freq. %	Ave. freq. %	Const.
Lathyrus leucanthus	2.37	1.49	100	85.9	100
Vicia americana	1.25	0.67	87.5	54.7	100
Thalictrum fendleri	2.25	1.61	100	82.8	96
Carex geyeri	2.50	1.19	100	75.0	92
Senecio serra	2.00	0.86	100	53.1	84
Bromus ciliatus	1.00	0.44	87.5	41.6	84
Ligusticum porteri	3.37	1.33	100	64.4	80
Geranium richardsonii	1.50	0.65	100	52.0	76
Fragaria ovalis	1.87	0.80	87.5	51.3	76
Viola nuttallii	1.75	0.81	100	61.1	72
Delphinium barbeyi	1.87	0.89	100	59.7	72
Osmorhiza obtusa	1.87	0.97	100	59.0	72
Galium boreale	1.37	0.69	100	52.2	68
Helianthella quinquenervis	1.67	0.40	87.5	29.4	68
Smilacina racemosa	1.80	0.58	100	37.5	64
Erigeron elatior	1.12	0.46	87.5	37.5	64
Heracleum lanatum	2.50	0.87	100	55.0	60
Taraxacum officinale	1.50	0.68	100	49.5	60
Epilobium angustifolium	2.00	0.71	100	49.2	60
Achillea lanulosa	1.37	0.62	87.5	46.7	60
Cirsium eatonii	1.37	0.55	87.5	38.4	56
Elymus glaucus	1.37	0.76	100	70.2	52

The shrub layer was not well developed in aspen stands, but *Symphoricarpos utahensis* was generally prominent when it was present. Other shrubby species such as *Rosa woodsii* and *Sambucus pubens* might be present, but usually did not form an important part of the shrub layer. Bare areas were defined as those areas where there was no living herbaceous or shrubby cover. Bare areas were not consistently present (constancy 48%), never occupied more than 25% of the area of a sample plot, and therefore were not prominent even in those stands where the herbaceous cover was not complete.

The species present in the understory that Langenheim (1962) classified as "mature" agree closely with the species that I had delimited as being characteristic of aspen stands. The only significant difference between the two studies concerns the species of *Carex* present. In this study, *Carex geyeri* had a constancy of 92% whereas Langenheim did not report this species. I found *C. siccata* with a constancy of only 10%; Langenheim reported a constancy of 60%.

Aspen understory composition has been described for the Front Range (Marr, 1961), Jackson Hole National Park (Reed, 1952), and Utah (Sampson, 1925; Dixon, 1935; Graham, 1937). Aspen understory for the Front Range was reduced and composed of several species which I found to be generally associated with drier sites in the present study areas. In Jackson Hole National Park, Reed found both open aspen stands on dry hillsides with poorly developed understories and closed stands on moist soils with lush herbaceous understories. The aspen understories described in Utah have many species in common with the present study area.

The stands used to determine coefficients of similarity (Table 3) were selected subjectively as being characteristic of the stands in the study areas. Coefficients of similarity based upon frequency were calculated using the formula $\frac{2w}{a+b} \times 100$ (Curtis, 1959). The stands in the Kebler Pass area consistently have a high coefficient of similarity among themselves and not as high with the stands of the other two areas. Of the 12 species with a constancy of 72% or greater for the entire study area, there are no significant differences between the Kebler Pass area and the other two areas. There are, however, a few important differences involving lesser species. The complete absence of *Taraxacum officinale* and the presence of *Pteridium aquilinum* var. *pubescens* only in the Kebler Pass area (Fig. 4) plus the much greater abundance of *Aster engelmannii* and *Symphoricarpos utahensis* make the aspen communities in the Kebler Pass area distinct from those in the other two areas. The reasons for the disjunct distribution of these four species remain to be found. There are no significant differences in aspect. The disjunct distribution does not appear to be related readily to soil properties. The soil analyses do not show any major differences between the Kebler Pass area soils and the soils in the other two areas. The explanation may lie with seed dispersal mechanisms and possibly the effects of man on species distribution.

Stand 13 shows little similarity with the other stands, probably because this stand is on a very steep slope and the soil is shallow, with a depth of only 22 cm to parent material. There are also many conifers present in the stand. These factors result in an understory that is very unlike the lush understory characteristic of stands on more gentle slopes with deeper soils.

SOILS

The work of Hoff (1957) comparing aspen and associated coniferous communities and soils in northern Colorado and southern Wyoming appears to be the only source of quantitative data dealing with aspen and coniferous soils. Without exception all soils were sandy loams and there were no significant differences in texture be-

Fig. 4.—Lush *Pteridium* understory in Stand 23 in Kebler Pass area. Note the relative scarcity of aspen reproduction within the stand. These trees are gray-barked and self-pruning.

tween the aspen and coniferous stands. As a general rule, soil moisture, *p*H, and organic matter were greater in the aspen stands than in the coniferous stands. The *p*H of the coniferous communities ranged from 6.6 to 7.1 and in the aspen groves from 6.6 to 7.4. Organic matter content varied from 0.88% to more than 17.00% under aspen whereas in the coniferous stands it ranged from 0.90% to 6.12%.

In the present study, the border between the A and B horizons was relatively evident due to differences in organic matter content. Delimiting within the B, however, was very difficult because there were few color or textural differences (Table 4) that could be determined in the field. Structural development was so weak that it was considered nonexistent. The lack of horizon and structural development suggests that the soils are immature.

Many of the soils had a sandy loam texture throughout the entire profile. This lack of variation in silt and clay content throughout the profile is additional evidence that the soils are immature. Due to the above characteristics, the soils were classified as inceptisols (U. S. Dep. Agr., 1960). Generally there is a greater percentage of available water (Table 4) in the A than in the B and C horizons. This is associated with the greater organic matter content in the A than in the lower horizons.

The organic matter values (Table 5) concur with those of Hoff (1957) except the values for aspen soils in the present study were not quite as high. Because of the low clay content in these soils, organic matter plays a relatively more important role in soil moisture rela-

TABLE 3.—Coefficient of similarity values for selected aspen stands in Gunnison Co., Colorado (values based upon frequency for the species sampled in each stand)

Location and stand number	Gothic, Stand 4	Gothic, Stand 13	Cement Creek, Stand 16
Gothic, Stand 1	60.88	27.81	42.34
Gothic, Stand 4	....	27.03	55.05
Gothic, Stand 13	....	....	36.07
Cement Creek, Stand 16	....	....	....
Kebler Pass, Stand 21	....	....	....
Kebler Pass, Stand 23	....	....	....
	Kebler Pass, Stand 21	**Kebler Pass, Stand 23**	**Kebler Pass, Stand 24**
Gothic, Stand 1	51.90	38.07	43.89
Gothic, Stand 4	51.82	41.41	54.76
Gothic, Stand 13	37.84	37.10	24.88
Cement Creek, Stand 16	50.46	42.52	39.20
Kebler Pass, Stand 21	....	60.70	65.87
Kebler Pass, Stand 23	....	....	64.14

TABLE 4.—Physical properties of selected aspen, spruce-fir, and grassland soils in Gunnison Co., Colorado

Stand	Horizon	Depth (cm)	Color	Texture	Soil moisture % ovendry weight 1/3	15	Available
Washington Gulch	A_0	1-0					
Aspen	A_1	0-6	10 YR 2/2	Sandy loam	32.02	12.89	19.13
	B_{21}	6-25	10 YR 3/3	Sandy loam	24.25	13.59	10.66
	B_{22}	25-58	10 YR 4/3	Sandy loam	22.80	12.53	10.27
	C	58+	10 YR 5/6	Loam	19.42	10.51	8.91
Washington Gulch	A_0	1-0					
Spruce-fir	A_1	0-10	10 YR 3/3	Sandy loam	27.83	12.89	14.94
	B_{21}	10-25	10 YR 4/3	Sandy loam	22.10	10.50	11.60
	B_{22}	25-51	10 YR 4/4	Sandy loam	20.61	9.81	10.80
	C	51+	10 YR 5/6	Sandy loam	17.64	9.39	8.25
Washington Gulch	A_0	5-0					
Fescue	A_{11}	0-15	10 YR 3/2	Sandy loam	25.73	12.86	12.87
	A_{12}	15-86	10 YR 3/3	Sandy loam	23.67	12.15	11.52
	C	86+	10 YR 5/3	Loam	16.94	8.07	7.87
Crested Butte	A_0	3-0					
Aspen	A_1	0-7	10 YR 3/3	Loam	23.40	10.38	13.02
	B_2	7-36	10 YR 4/3	Sandy loam	21.57	9.55	12.02
	C	36+	10 YR 5/4	Loam	18.81	7.49	11.32

TABLE 4.—(continued)

Stand	Horizon	Depth (cm)	Color	Texture	Soil moisture % ovendry weight 1/3	15	Available
Crested Butte	A_0	2-0					
Spruce-fir	A_1	0-10	10 YR 3/3	Sandy loam	25.73	13.29	12.44
	B_2	10-25	10 YR 4/3	Sandy loam	25.63	13.66	11.97
	C	25+	10 YR 5/3	Sandy loam	17.81	3.94	8.87
Gothic valley	A_0	10-0					
Stand 4 Aspen	A_1	0-25	5 YR 3/2	Sandy loam	25.01	18.23	6.78
	B_2	25-142	5 YR 3/3	Sandy loam	18.09	9.12	8.97
	C	142+	5 YR 3/4	Sandy loam	16.15	6.45	9.70
Gothic valley	A_0	1-0					
Stand 4 Fescue	A_1	0-15	5 YR 3/2	Sandy loam	22.60	11.54	11.06
	B_{21}	15-64	5 YR 3/3	Sandy loam	19.19	10.92	8.27
	B_{22}	64-112	5 YR 3/4	Sandy loam	18.99	10.38	8.61
	C	112+	5 YR 4/4	Sandy loam	15.20	8.69	6.51
Kebler Pass	A_0	5-0					
Stand 21 Aspen	A_1	0-15	10 YR 2/2	Loamy sand	20.80	16.63	4.17
	B_{21}	15-58	10 YR 3/2	Sandy loam	17.57	11.64	5.93
	B_{22}	58-109	10 YR 3/4	Sandy loam	14.87	7.36	7.51
	C	109+	10 YR 4/3	Sandy loam	13.77	5.79	7.98

tionships and in total base exchange capacity. The decrease in total base exchange capacity with depth can be correlated with a corresponding decrease in organic matter. Because per cent base saturation does not vary greatly throughout the profile, it is assumed that these soils are relatively young and leaching of the minerals has not progressed to a great degree. Except for aspen stand 4, the *p*H values for both aspen and coniferous soils were generally well below the values found by Hoff (1957). The nutrient level of the soils in the present study is generally very high, but nutrient content varies considerably within a stand and between stands. A profile that has a high content of one certain element may be very low in other nutrients. Aspen stand 4 was very high in Ca and Mg but low in P and K, a relationship particularly evident in the C horizon. The C horizon was generally the poorest in nutrient content.

A comparative study of the relative effects of aspen, spruce-fir, and fescue grassland on soil properties was made by digging a soil pit in each of the different communities where they were in close contact. It was assumed that the adjacent stands were on the same parent material. This assumption was qualitatively verified by the observation that there were no noticeable differences in the rocks and parent material present in the adjacent soil pits. Because time, climate, and topography should be constant for a small area, the principal soil formation variable would be vegetation.

Aspen soils are generally more fertile than spruce-fir or grassland soils. Aspen soils usually have a greater organic matter content, higher *p*H, larger cation exchange capacity with associated greater per cent base saturation, and larger amounts of nutrients present (Table 5). These characteristics make aspen soils very productive.

Aspen has been called a soil-improving species (Lutz and Chandler, 1946). Daubenmire (1953), working in the northern Rocky Mountains, found that the leaf litter of aspen was definitely superior in nutrient content to coniferous litter. Aspen is apparently very effective in nutrient recycling. This would account in part for the high nutrient content in the upper portion of the aspen soil profile. The lush herbaceous understory probably also aids in maintaining a high nutrient content. Aspen leaf litter is also more basic than that of the associated conifers (Lutz and Chandler, 1946). Thus, one would expect soils developed under aspen to be less acidic than those developed under conifers. The aspen soil in Washington Gulch is higher in every criterion than the adjacent spruce-fir soil. On Crested Butte Mountain, however, the spruce-fir soil has greater values than the aspen soil. At the present time, no supportable explanation can be given for these data.

Fescue grassland soils have higher chemical property levels than aspen soils only in the organic matter of the lower B horizon (Table 5). In aspen stands, the numerous small aspen feeder roots and the extensive root systems of the luxuriant herbaceous understory give the soil a higher organic matter content in the A horizon than in the A of the fescue soil. The fescue grassland plants, especially the grasses, are deeper rooting than the herbaceous plants in the aspen stands. This probably explains the greater organic matter content in the lower horizons in the grassland soils.

In the only comparison of adjacent spruce-fir and grassland soils, the spruce-fir soil has a higher organic matter content in the A horizon with organic matter in the fescue soil becoming greater than that of the coniferous soil at lower depths (Table 5). As in the case of the aspen stands, the A horizon of the spruce-fir soil has numerous roots, but the herbaceous understory of the spruce-fir stand is very reduced compared with that of aspen stands. The soil is covered, however, with a large quantity of needles in various stages of decomposition and incorporation. The cation exchange capacity in the spruce-fir soil is greater than that of the fescue soil in the upper horizons probably as a result of the higher organic matter content. The per cent base saturation is much greater, however, in the fescue soil, which reflects the higher *p*H and greater concentration of nutrients in the grassland soil.

REPRODUCTION

The marked capacity of aspen to reproduce vegetatively by root suckers is well documented (Baker, 1918, 1925; Day, 1944; Cottam, 1954; Buell and Buell, 1959). All papers concerned with the successional status of aspen state that aspen generally occupies burned areas by root suckers, derived usually from a few remnant aspen trees present in the coniferous forest. The importance of sexual reproduction is more controversial. The findings of aspen seedlings in Utah by Ellison (1943) and Larson (1944) appear to be the only citations of natural seedlings in the western United States. Cottam (1954) states that aspen does occasionally produce viable seed, but because of droughts in early June, germination and establishment of seedlings in Utah are nonexistent. He attributed the present extensive aspen stands to a past period of more intensive and evenly distributed precipitation.

Laboratory studies of aspen seed germination have been performed by Faust (1936) and Moss (1938) in the eastern United States and by Montgomery (1957) and Strain (personal communication) in the western United States. Moss (1938) and Montgomery (1957) found that dried seeds stored at room temperatures decrease greatly in viability after several months. Faust (1936) and Strain found that air drying at room temperatures for three days followed by cold storage greatly increased the viability period. Under greenhouse conditions, aspen seedlings grew successfully and thus Strain demonstrated that the establishment of aspen seedlings is possible if certain conditions of high soil moisture, moderate air temperature and relative humidity, and sufficient light intensity are available.

Seed germination tests were made to determine if aspen trees in the study area produce viable seed, and secondarily to determine the effects of prolonged cold storage on seed viability.

TABLE 5.—Chemical properties of selected aspen, spruce-fir, and grassland soils in Gunnison Co., Colorado

Stand	Horizon	Organic matter %	*p*H	Total base exchange cap. me/100 g soil	Base saturation %	Ca	Mg	K	P ppm
						me/100 g soil			
Washington Gulch	A	8.49	5.8	16.5	70.9	13.99	14.95	....	13
Aspen	B_{21}	6.10	5.6	13.3	63.9	8.65	10.86	....	7
	B_{22}	4.21	5.5	12.0	55.8	7.74	10.08	....	9
	C	0.94	5.2	7.5	58.7	5.91	7.76	....	27
Washington Gulch	A	6.70	4.9	14.7	47.6	6.34	8.24	....	11
Spruce-fir	B_{21}	3.49	4.7	12.3	39.8	3.96	5.64	....	14
	B_{22}	2.48	4.9	10.0	40.0	4.13	5.27	....	11
	C	0.91	5.3	7.2	48.6	4.42	5.62	....	14
Washington Gulch	A_{11}	5.42	5.5	13.0	57.7	7.62	9.10	....	16
Fescue	A_{12}	4.09	5.5	11.7	57.3	6.71	8.26	....	12
	C	0.67	5.6	5.7	61.4	4.67	6.01	....	50
Crested Butte	A_1	3.55	5.4	12.1	52.1	7.03	8.26	....	50
Aspen	B_2	2.52	5.5	11.2	52.7	6.45	7.58	....	34
	C	0.67	5.6	7.2	48.6	3.96	4.76	....	65

TABLE 5.—(continued)

Stand	Horizon	Organic matter %	pH	Total base exchange cap. me/100 g soil	Base saturation %	Ca	Mg	K	P ppm
						me/100 g soil			
Crested Butte	A_1	4.56	5.2	13.2	54.6	7.36	8.97	....	23
Spruce-fir	B_2	3.58	5.4	12.7	56.7	8.84	10.18	....	21
	C	0.91	5.5	6.1	60.7	5.06	6.47	....	34
Gothic Valley	A_1	7.30	6.5	16.3	88.3	16.30	18.33	3.59	26
Stand 4 Aspen	B_2	2.88	7.4	20.1	100	13.90	15.00	2.31	61
	C	1.81	7.4	20.1+	100	32.10	32.92	1.67	4
Gothic Valley	A_1	5.36	6.2	12.7	66.9	9.85	10.80	....	39
Stand 4 Fescue	B_{21}	3.95	6.0	11.4	63.2	9.06	9.90	....	38
	B_{22}	2.95	6.4	9.6	75.0	9.25	9.76	....	56
	C	1.11	7.4	8.2	97.6	9.98	10.65	....	111
Kebler Pass	A_1	5.85	5.6	19.5	83.1	10.55	13.08	7.18	24
Stand 21 Aspen	B_{21}	4.02	5.8	17.2	86.0	9.50	11.33	5.26	20
	B_{22}	2.01	5.8	14.3	81.8	6.90	8.67	2.82	26
	C	0.94	5.5	14.4	78.4	5.85	7.17	1.54	34

The germination tests were made at room temperature (25 to 29 C). The average germination of 160 seeds in the first tests on 12 December 1964 was 88%. The result of the last date of germination tests on 17 February 1966 (583 days after collection) was 79%. The germination percentages of 160 seeds for the intermediate dates of 12 March 1965 and 15 August 1965 were 83% and 81%, respectively. A t-test (3 df and .95 significance level) showed that there was no significant decrease in viability after 1½ years of cold storage.

Although there was a high percentage of germination in seeds from three of the four sites, many of the germinating seeds did not develop properly. The percentage of the total germinated seeds showing good subsequent development is as follows: 12 March 1965, 58%; 15 August 1965, 62%; and 17 February 1966, 65%. In most cases, the hypocotyl turned brown 24 hours after germination and apparently died. There was little subsequent development of the young seedlings. Since there was good seedling development in many cases, the lack of development by some seedlings can be assumed to be due to conditions within the embryo and not to the experimental method. It can thus be said that even if there is good germination under natural conditions, many of these probably would not develop into healthy seedlings regardless of environmental conditions.

Those seeds that were placed in the cool room at 2.2 to 3.9 C showed little germination. Seeds which did germinate demonstrated little further elongation of the hypocotyl and epicotyl and the cotyledons did not turn green. Faust (1936), however, found that germination took place in the range of 0 to 35 C. Germination at 5 C occurred after five days. In the present study, there was little germination after seven days. The cold-room seeds were then removed to the laboratory and left at room temperature. After six days at room temperature, there was little difference in germination percentage between the seeds which had been at 2.2 to 3.9 C for a week and then placed at room temperature and those which were started initially at room temperature.

VARIATION IN LEAFING TIME

The most dramatic difference among aspen stands can be seen in the early spring and late fall. Trees in some stands break dormancy and leaf two to three weeks earlier than trees in nearby stands. These same early-leafing trees will also turn color earlier in the fall than the late-leafing forms.

In Utah, early-leafing stands generally dominate at upper and middle altitudes with the late-leafing variety at the lower altitudes (Baker, 1921; Cottam, 1954). Trees of each leafing time have been found to be associated with yellow boles and poor pruning as well as white bark and self-pruning characteristics (Cottam, 1954). Contiguous aspen colonies have been found in Utah with the same morphological characteristics but differing in leafing time by two or three weeks. In one case, due to differences in topography at the same elevation, the late-leafing stand had a temperature regime corresponding to an increase in elevation of approximately 300 m above the late-leafing stand. No transplant experiments were performed, however, to determine leafing time when trees from each stand were exposed to the temperature regime opposite to that present in the field. In another instance, transplanting experiments showed that leafing time was not environmentally controlled and, therefore, races of aspen with different leafing times must exist (Cottam, 1954).

Egeberg (1963) working on the Front Range of Colorado found a wide variation in the degree of frost damage in aspen. He attributed the variation to differences in time that the buds broke dormancy, these differences in time being attributed in turn to hybridization. The apparent high degree of hybridization conflicts with the two-race hypothesis of Baker (1921). Marr (1947), also working in Colorado, found that yellowish-white barked trees averaged 15% frost killing as compared with 80% killed in grayish-barked trees. Montgomery (1957) working on the eastern slope of the Snowy Range found no correlation of bark color with the early-leafing trees.

In the Gothic valley, the earliest date of leafing was 31 May, when one small stand broke dormancy (R. Willey — personal communication). By 5 June, many stands were in leaf and leafing continued until 21 June, when the last stand under observation broke dormancy. These observations of several leafing times agree with those of Egeberg (1963) in the Front Range.

Both gray-barked and yellow-barked trees are present in the Gothic area. Each bark characteristic is associated with both poor and self-pruning. Each of the four combinations of bark color and pruning is in turn associated with both late and early leafing times. There are, thus, eight combinations of bark color, pruning characteristics, and leafing time in the Gothic area. There are no apparent relationships of any combination of characteristics with slope direction or altitude. Both early- and late-leafing clones were growing side by side and many times intermingled throughout the range of aspen. Also a few late-leafing clones were found above some early-leafing clones. Due to little topographic effect and complex patterns of leafing times within many stands, it is difficult to believe that the environment plays a major role. The correlation of external morphology and altitude found in Utah cannot be applied to this area.

Leafing time possibly may be correlated with the sex of the trees. Female trees in the study area were always found to be early-leafing, but no early-leafing male trees were found. Unfortunately only a few aspen clones flowered in 1964, thus the relationship between leafing time and the sex of the clones cannot be fully elucidated for all stands within the study area. Maini (personal communication) working in the prairie groves of Saskatchewan found that generally most female clones leaf earlier in the spring and shed leaves earlier in the fall than some male clones. There was a slight overlap in the leafing times of both sexes.

SUCCESSIONAL STATUS

The successional status of aspen in the central Rocky Mountains has received considerable attention (Sampson, 1916; Fetherolf, 1917; Bates, 1917; Baker, 1921, 1925; Graham, 1937; Stahelin, 1943; Daubenmire, 1943; Lull and Ellison, 1950; Langenheim, 1962). All previous workers agree that where aspen is present in the original coniferous stand, it will tend, after a burn, to take over suitable areas vegetatively. The question then arises as to whether the conifers will replace the aspen. In its area of optimum development in western Colorado and central Utah, aspen occupies very large areas and the rate of coniferous invasion is slow because of the relative lack of coniferous seed trees. In these areas, aspen has been considered as climax relative to forest management (Baker, 1925). In areas outside its optimum development, aspen is less extensive and the rate of coniferous invasion is greater. In these areas, aspen has generally been considered successional.

There is much evidence that aspen stands in the present study area have invaded following fire. Several soil pits showed deeply buried charcoal indicating a series of past fires. Charcoal was lacking in only three pits, one on a recently stabilized talus slope and two in aspen stands of Cement Creek valley. The lack of charcoal cannot be taken as conclusive proof that fire has not taken place in these stands, especially since charcoal was found in soil pits of other stands in Cement Creek valley. Many stands take the form of "islands" surrounded by fescue grassland. This pattern suggests that isolated trees which have survived the conifer-destroying fires have subsequently colonized an area by root suckers in a centrifugal pattern. This observation supports the hypothesis of Stahelin (1943).

The question remains whether the present-day aspen stands are successional or climax. To be considered climax, a species must be able to reproduce within the community. The following indicates that the aspen stands in the Kebler Pass area may be regarded as the oldest stands of the three study areas. They have maximum tree size and basal area in the higher DBH classes. Coefficients of similarity are consistently higher in these stands.

Because the trees were widely spaced, aspen suckering should have been abundant but very few trees with a DBH of 1 to 5 in were present in the stands and many saplings 0 to 1 in had a leaf spot disease that greatly reduced their photosynthetic area. A pathological rotation of 80 to 90 years has been suggested for aspen trees in Utah (Meinecke, 1929). It appears that most aspen stands in the Kebler Pass area are not capable of maintaining a closed, well developed forest even without coniferous invasion and coniferous invasion is more advanced in the Kebler Pass area than in the other two study sites (Fig. 5). Both fir trees and seedlings were present in all five stands sampled. Whether this degree of invasion is the result of the gradual opening of the aspen stands or merely reflects an apparent longer fire-free period remains unanswered.

Graham *et al.* (1963) stated that aspen stands on good sites in the Great Lakes region may deteriorate any time after the stand reaches the age of 35 years. Unless the trees are cut, few root suckers will develop and the stand reverts to an open condition. It is probably untenable to apply the deterioration ages of aspen from the Great Lakes region, where aspen is clearly successional, to the Rocky Mountains, where the successional status is questionable. It would appear that if there is a deterioration age in Gunnison County, it is older than in the Great Lakes region. There is a real need to determine if a deterioration cycle is present in aspen stands in the central Rockies.

Another characteristic of a climax species is that it provides an environment unfavorable for the successful invasion of a potentially climax species. It is assumed that the potential climax species can enter the community. If there is no seed source and the species does not reproduce vegetatively, then the species cannot invade. Conifers were present in all three study areas, but they were found within or at the edge of only 16 of the 25 stands sampled (Table 1). There were few coniferous seedlings beneath the scattered parent trees although these trees had been of seed-bearing age for several years. All seedlings appeared to be growing well.

The question, therefore, arises as to why coniferous reproduction has been so limited within the aspen stands. Both spruce and fir are good seed producers (Le Barron and Jemison, 1953), but with only a few seed trees present, the seed crops will not be large. Birds and small animals may be responsible for destruction of many of the seeds. The favorableness of the aspen seedbed for the germination and early

Fig. 5.—Several size classes of fir present in Stand 13 in Gothic valley. The stand is open with a relatively sparse understory.

establishment of the conifers is another variable. A bare mineral soil is superior to a natural forest floor for spruce and fir seed germination (Le Barron and Jemison, 1953). Comparatively heavy shade is also desirable for the initial establishment of both species. Thus, even though aspen excludes the presence of a heavy grass sod, the luxuriant understory will not provide a seedbed as favorable as bare mineral soil. Shading in aspen stands is generally not a critical factor. The smallness of the seed source plus the lack of a bare mineral soil may account for the slow invasion of conifers.

If conifer invasion of aspen stands is slow with conifers present in the same stand or in the same valley, then in those areas of Utah, Wyoming, and western Colorado where pure stands cover many square miles, a very long period will obviously be required for conifer dominance. In areas of extensive aspen it may be of academic interest whether the species is successional or climax. The author agrees with Baker (1921, 1925) that, concerning forest and watershed management, aspen should be considered climax in Utah and western Colorado. As previously stated, aspen in Gunnison County is less extensive than in more western areas. Since conifers are reproducing in many stands, I believe that conifers will replace most of the aspen. However, the continued presence of aspen stands within fescue grassland, isolated from conifers, seems assured.

REFERENCES

BAKER, F. S. 1918. Aspen reproduction in relation to management. *J. Forest.*, **16**:389-398.

———. 1921. Two races of aspen. *Ibid.*, **19**:412-413.

———. 1925. Aspen in the central Rocky Mountain region. *U. S. Dep. Agr. Bull.* 1291. 46 p.

BATES, C. G. 1917. Forest succession in the central Rocky Mountains. *J. Forest.*, **15**:587-592.

BOUYOUCOS, G. J. 1951. A recalibration of the hydrometer method for making mechanical analyses of soils. *Agron. J.*, **43**:434-438.

BRAUN-BLANQUET, J. 1932. Plant sociology (translated by Fuller and Conrad). McGraw-Hill Book Co., New York. 439 p.

BROWN, I. C. 1943. A rapid method of determining exchangeable bases. *Soil Sci.*, **56**:353-357.

BUELL, M. F. AND H. F. BUELL. 1959. Aspen invasion of prairie. *Bull. Torrey Bot. Club*, **86**:264-265.

COTTAM, W. P. 1929. Some phytogeographic features of Utah. *Proc. Utah Acad. Sci.*, **6**:6-7.

———. 1954. Prevernal leafing of aspen in the Utah Mountains. *J. Arnold Arb.*, **35**:239-248.

CURTIS, J. T. 1959. The vegetation of Wisconsin: an ordination of plant communities. Univ. Wisconsin Press, Madison. 657 p.

DAUBENMIRE, R. F. 1943. Vegetational zonation in the Rocky Mountains. *Bot. Rev.*, **9**:236-393.

———. 1953. Nutrient content of leaf litter of trees in the northern Rocky Mountains. *Ecology*, **34**:786-793.

DAY, M. W. 1944. The root system of aspen. *Amer. Midl. Natur.*, **32**:502-509.

DIXON, H. 1935. Ecological studies on the high plateaus of Utah. *Bot. Gaz.*, **97**:153-156.

EGEBERG, R., JR. 1963. Inherent variation in the response of aspen to frost damage. *Ecology*, **44**:153-156.

ELLISON, L. 1943. A natural seedling of western aspen. *J. Forest.*, **41**:767-768.

FAUST, M. E. 1936. Germination of *Populus grandidentata* and *P. tremuloides*, with particular reference to oxygen consumption. *Bot. Gaz.*, **97**:808-821.

FETHEROLF, J. M. 1917. Aspen as a permanent forest type. *J. Forest.*, **15**: 757-760.

GRAHAM, E. H. 1937. Botanical studies in the Uinta Basin of Utah and Colorado. *Ann. Carnegie Mus.*, **26**. 432 p.

GRAHAM, S. A., J. R. HARRISON AND C. E. WESTELL, JR. 1963. Aspens. Phoenix trees of the Great Lakes Region. Univ. of Michigan Press, Ann Arbor. 272 p.

HARRINGTON, H. D. 1954. Manual of the plants of Colorado. Alan Swallow, Denver. 666 p.

HOFF, C. C. 1957. A comparison of soils, climate, and biota of conifer and aspen communities in the central Rocky Mountains. *Amer. Midl. Natur.*, **58**:115-140.

LANGENHEIM, J. H. 1962. Vegetation and environmental patterns in the Crested Butte area, Gunnison County, Colorado. *Ecol. Monogr.*, **32**:249-285.

LARSON, G. C. 1944. More on seedlings of western aspen. *J. Forest.*, **42**:452.

LE BARRON, R. K. AND G. M. JEMISON. 1953. Ecology and silviculture of the Engelmann Spruce-Alpine Fir type. *Ibid.*, **51**:349-355.

LULL, H. AND L. ELLISON. 1950. Precipitation in relation to altitude in central Utah. *Ecology*, **31**:479-484.

LUTZ, H. J. AND R. F. CHANDLER. 1946. Forest soils. John Wiley & Sons, New York. 514 p.

MALMSTADT, H. V. AND T. P. HADJIIOANNOU. 1959. Rapid and accurate automatic titration method for determination of calcium and magnesium in plant material with EDTA titrant. *J. Agr. Food Chem.*, **7**:418-420.

MARR, J. W. 1947. Frost injury to aspen in Colorado. *Bull. Ecol. Soc. Amer.*, **28**:60.

———. 1961. Ecosystems of the east slope of the Front Range in Colorado. *Univ. Colorado Stud.*, No. 8. 134 p.

MEINECKE, E. P. 1929. Quaking aspen: a study in applied forest pathology. *U.S. Dep. Agr. Tech. Bull.*, 155. 34 p.

MONTGOMERY, D. H. 1957. A phenological study of aspen in the Medicine Bow Mountains. Unpublished B Paper. Univ. Wyoming Library. 25 p.

MOSS, E. H. 1938. Longevity of seeds and establishment of seedlings in species of *Populus*. *Bot. Gaz.*, **99**:529-542.

REED, J. F. 1952. The vegetation of the Jackson Hole Wildlife Park, Wyoming. *Amer. Midl. Natur.*, **48**:700-729.

RICHARDS, L. A. 1949. Methods of measuring soil moisture. *Soil Sci.*, **68**:95-112.

ROBBINS, W. W. 1910. Climatology and vegetation in Colorado. *Bot. Gaz.*, **49**:256-280.

SAMPSON, A. W. 1916. The stability of aspen as a type. *Proc. Soc. Amer. Foresters*, **11**:86-87.

———. 1925. The foothill-montane-alpine flora and its environment. In Tidestrom pp. 24-31.

STAHELIN, R. 1943. Factors influencing the natural restocking of high altitude burns of coniferous trees in the central Rocky Mountains. *Ecology*, **24**:19-30.

TANNER, V. M. AND C. L. HAYWARD. 1934. A biological study of the La Sal Mountains, Utah, Report no. 1. *Proc. Utah Acad. Sci.*, **9**:209-235.

TIDESTROM, I. 1925. Flora of Utah and Nevada. *Contrib. U. S. Nat. Herb.*, **25**. 665 p.

TROUG, E. 1930. The determination of readily available phosphorus of soil. *Amer. Soc. Agron. J.*, **22**:874-882.

U.S. DEPARTMENT OF AGRICULTURE 1941 Yearbook. Climate and Man: Colorado, pp. 789-808.

U.S. DEPARTMENT OF AGRICULTURE SOIL CONSERVATION SERVICE, SOIL SURVEY STAFF. 1960. Soil classification, a comprehensive system. 7th Approximation. 265 p.

U.S. WEATHER BUREAU. 1965. Annual Summary, Colorado. 1964. **69**: (13). U.S. Dept. Comm., Weather Bur., Asheville.

WALKLEY, A. AND I. A. BLACK. 1931. An examination of the Degtkareff method for determining soil organic matter, and a modification of the chromic acid titration method. *Soil Sci.*, **31**:29-37.

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