Site Factor Relationships with Volatile Oils in Big Sagebrush[1]

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Highlight

The volatile oil content in big sagebrush leaves varied greatly on different sites, ranging form 3.5% of the air-dry weight in short plants on poor sites to 6.0% in tall plants on favorable sites. A regression equation using selected site factors accounted for 91% of the variation in oil content. Oil content was most highly correlated with sagebrush size and the amounts of magnesium and phosphorus in the A horizon. Short big sagebrush plants on poor sites should be maintained as forage plants, but tall big sagebrush plants on favorable sites should be replaced with other more palatable species. Chemicals which can reduce or retard volatile oil production should be studied.

The range of big sagebrush (*Artemisia tridentata*) extends from British Columbia to northern Mexico, and from the western Dakotas and central Colorado to Washington, Oregon, and southwestern California. The total area distribution of the big sagebrush type is about 211 million acres in 11 western states (Beetle, 1960).

By virtue of its wide range and ecological amplitude, big sagebrush has a significant influence on rangeland. Within its range, big sagebrush is certainly a competitor for sunlight, soil moisture, and soil nutrients; and is sometimes valuable as forage for livestock and game.

Reports concerning the forage value of big sagebrush are somewhat conflicting because of the different conditions under which the various studies were conducted. However, the literature does indicate that the forage value of sagebrush changes seasonally and varies among sites. Variability in forage value is influenced partially by the volatile oil content of the leaves because these volatile oils kill rumen microorganisms, decrease appetite (Nagy, Steinhoff, and Ward, 1964), and digestibility of forage (Nagy et al., 1964, Smith et al., 1966), and increase plant toxicity (Cook, Stoddart, and Harris, 1954) and apparent energy values (Cook, Stoddart, and Harris, 1952). Volatile oils are complex substances consisting largely of terpene-base esters, aldehydes, alcohols, and ketones (Guenther, 1948).

This study was conducted in northwestern Colorado to gain information about the relations between the volatile oil contents of big sagebrush and site factors. The primary objectives were: (1) to determine if there is a difference in oil content in big sagebrush on different sites, and, if so, (2) to determine the relationships between oil content in big sagebrush and different site factors.

The possibility that site factors do affect oil content has been indicated by some previous work on sagebrush and on volatile oils in other plants. In general, the more vigorously a plant grows, the larger the quantity of volatile oil formed (Guenther, 1948). In North Park, Colorado, low-growing forms of big sagebrush on shallow, ridgetop soils contained less volatile oils than tall-growing forms on adjacent, deeper slope soils (Nagy, 1966). Sage-grouse (*Centrocerus urophasianus*), in this area, spent more time feeding on the low-growing forms of big sagebrush than on the tall-growing forms (Gill, 1965).

Cook et al. (1954) noted that "big sagebrush plants of lower stature on poor sites or on heavily grazed areas were more readily eaten than robust ones on favorable sites." In speaking of a rabbitbrush species (*Chrysothamnus stenophyllus*), which also contains volatile oils, they stated, "The use of yellowbush appeared to be determined by site. On gentle alluvial slopes or plateaus, use was generally light or negligible; however, on rocky foothills it was frequently heavy and sometimes destructively so." Green et al. (1951) stated also that ". . . where yellowbush was grazed, it appeared to be the same plants that had been grazed year after year."

Study Area and Methods

The study area is located near Craig in northwestern Colorado. The soils were formed on sedimentary material and are primarily of the Brown, Lithosol, and Sierozem Great Soil Groups. The elevation of the study area ranges from about 6000 to 8500 feet. Topography varies from gently rolling to rough and broken. Annual precipitation for the area is about 13 to 17 inches; most of which falls between September and April. Annual snowfall varies from 40 to 60 inches with an annual number of days with snow cover between 60 and 80 days. Prevailing winds are from the west, and deep snow drifts often pile up on the east and northeast slopes.

Site Factors

During the summers of 1966 and 1967, 39 locations were selected in the study area to give a wide range of vegetative, physiographic, and soil factors. Each location consisted of a plot 100 by 100 ft with maximum uniformity of soil and vegetation. The soil profile for each plot was described using procedures described by the Soil Survey Staff (1951).

Physical and chemical soil factors were expressed as the concentration of a factor in the A horizon and in the 0- to 6-, 6- to 12-, and 12- to 24-inch soil layers. Major emphasis was placed on the A horizon and upper foot of soil because big sagebrush roots are most abundant in the surface foot

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of soil. Chemical analyses of soil samples included pH, phosphate (P_2O_5), potash (K_2O), lime ($CaCO_3$), organic matter, electrical conductivity, nitrogen, and water soluble sodium, potassium, calcium, and magnesium.

Soil depth factors included depth to lime accumulation, depth of roots common, depths of roots few, depth to C horizon, and effective rooting depth. Effective rooting depth was determined by subtracting the net depth of rocks and gravel from the depth of roots few. Other soil factors included surface stoniness, percent sand, and percent clay in each soil layer. Physiographic factors included elevation, percent slope, slope length, slope position, and aspect.

Vegetative factors included crown diameter of the five largest sagebrush plants per transect, height of the five tallest sagebrush plants per transect, percent shrub cover, percent sagebrush cover, and density of sagebrush plants per transect. Crown cover and maximum plant height were determined for each shrub on five 100-ft line transects (Canfield, 1941). Density of big sagebrush plants was determined by counting the number of plants rooted in five 100- by 1-ft belt transects (Weaver and Clements, 1938).

Leaf samples

Two samples of leaves were collected on each plot from two groups of 50 to 75 big sagebrush plants in early September, 1967. One to two grams of leaves were picked from the outer edge of the crown of each plant. Plants of all age classes and degrees of vigor were sampled, if such a plant was the nearest to the toe at every third step.

Leaf samples were packed in an insulated box containing dry ice and transported to the laboratory. The oil content in each sample was determined by steam distillation (Nagy, 1966). At the time of distillation, a portion of each sample was placed in a paper bag and air dried to a constant weight. Oil content was then expressed in percent of air dry weight. Differences in oil content in big sagebrush leaves from different plots were tested by analysis of variance (Snedecor, 1956).

Correlation and Regression Analysis

The relationships between oil content and different site factors were defined by multiple regression analysis. Oil content was used as the dependent variable, and vegetative, physiographic, and soil factors were used as independent variables. An initial screening process was carried out to determine which variables were singularly important in predicting oil content and which variables showed interaction with other variables. Scatter diagrams were prepared to indicate whether the relationship between the X-variable and oil content was linear or curvilinear. When a scatter diagram indicated curvilinearity, the appropriate transform was made. All variables and transforms used in this study have been described by Powell (1968).

Simple linear correlation coefficients were calculated among the X-variables and between each X-variable and oil content. When the correlation coefficient between two X-variables was greater than 0.9, the variable having the higher correlation with oil content was retained.

A program called "Furnival's Variable Screen" (Furnival, 1964) was also used in the initial screening process to indicate positive interaction between two or more X-variables. Basically, the program is written so that all possible regressions for any two or more X-variables and the Y-variable can be determined. Interaction was indicated when the amount of variation in Y accounted for by two or three X-variables together in the same regression was greater than the sum of the variation in Y accounted for by the same two or three X-variables in separate regressions. When interaction was indicated, scatter diagrams for the X-variables in question were studied to determine what transform should be used in the analysis.

The initial screening process indicated that 24 X-variables were relatively unimportant in comparison with the remaining 49 X-variables. These 49 variables, including 10 transforms, were then studied using Stepwise Linear Regression Analysis (Geist, 1965; Smith, 1966). Through the process of elimination by stepwise regression, the final regression equation obtained a "best fit" for this set of data. In this equation, each of the X-variables used had to account for a significant ($P < .05$) amount of the variation in oil content.

Both simple linear and highest order partial correlation coefficients were used to study the relationships among site factors and between each site factor and oil content. Partial correlation coefficients were determined using a program called "Regress" (Van Dyne, 1965).

Results and Discussion

Oil Content in Plants on Different Sites

Big sagebrush was the dominant shrub on 30 plots and subdominant on 9 other plots. Dominant shrubs on the 9 other plots included alkali sagebrush (*A. longiloba*), black sagebrush (*A. nova*), and bitterbrush (*Purshia tridentata*).

The difference in oil content in big sagebrush leaves between plots was significantly ($P < .01$) greater than that within plots. The average difference in oil content for the two samples from each plot was 0.2%. Oil content averaged 4.7% for the 39 plots sampled and ranged from 3.5 to 6.0%.

Plots with plants having low oil content are characterized by short sagebrush plants on shallow, highly calcareous, rocky soil. Plots with plants having high oil content are characterized by tall, vigorous plants having an abundance of seed heads on deep, sandy loam soils with a low line content.

Volatile Oil Regression Equation

In an attempt to develop a regression equation that would be applicable under a wide range of conditions, data from all 39 plots were used. The regression equation used to predict the volatile oil content in big sagebrush leaves accounted for 90.7% of the total variation (Table 1). The confidence interval about the mean oil content of 4.7% at the 5% probability level was ±.42. The regression equation is as follows:

$$Y = 3.84 + 0.012X_1 - 0.043X_2 + 0.046X_3 + 0.539X_4 + 0.012X_5 - 0.001X_6 - 0.021X_7 + 0.310X_8 - 0.040X_8^2$$

In this equation, Y is percent oil content, X_1 is effective rooting depth, X_2 is percent clay in the

Table 1. Analysis of variance for regression equation used to predict percent volatile oil in big sagebrush leaves on different sites in northwestern Colorado.

Partial regression coefficient	X_i	Source of variation	Mean square	Percent of total variation
3.84	X_0			
0.012	X_1	Effective rooting depth (in)	0.511**	3.8
−0.043	X_2	Clay in eff. root. depth (%)	0.744**	5.6
0.046	X_3	Clay 0–6 inches (%)	0.861**	6.5
0.539	X_4	Nitrogen 6–12 inches (%)	0.589**	4.4
0.012	X_5	P_2O_5 A horizon (lb/acre)	1.802**	13.5
−0.001	X_6	K_2O A horizon (lb/acre)	0.371**	2.8
−0.021	X_7	Mg (meq/100 gm) × A horizon (in)	3.419**	25.6
0.310	X_8	Sagebrush size (ft^2)	1.261**	9.5
−0.040	X_9	(Sagebrush size)^2((ft^2)^2)	2.449**	18.4
		Regression	1.334**	90.7
		Residual	0.042	9.3

** Significant at 1% level.

effective rooting depth, X_3 is percent clay in the 0- to 6-inch layer, X_4 is percent nitrogen in the 6- to 12-inch layer, X_5 is phosphate in the A horizon, X_6 is potash in the A horizon, X_7 is magnesium content times thickness of the A horizon, and X_8 is sagebrush size.

The amount of total variation accounted for by each of the site factors in the equation was highly significant ($P < .01$). The most important variables in this equation were sagebrush size, magnesium, and phosphorus. Respectively, each accounted for 28, 26, and 14% of the total variation in oil content.

Volatile Oil–Site Factor Relationships

The discussion of the relationships between oil content and various site factors is based on the highest order partial correlation coefficients (Table 2). In effect, highest order partial correlations show the relationship between any two variables after the variation due to all the other variables considered has been removed.

Table 2. Highest order partial correlation coefficients between volatile oil content and site factors used in prediction equation.

Factor	Partial correlation coefficient
Effective rooting depth	.52**
Clay in eff. root. depth	−.59**
Clay 0–6 inches	.62**
Nitrogen 6–12 inches	.55**
P_2O_5 A horizon	.75**
K_2O A horizon	−.46**
Mg × thickness A horizon	−.84**
Sagebrush size	.69**
(Sagebrush size)^2	−.80**

** Significant at 1% level.

Oil content in big sagebrush plants on different plots was positively and highly correlated with effective rooting depth, phosphate in the A horizon, nitrogen in the 6- to 12-inch layer, clay in the 0- to 6-inch layer, and sagebrush size. Each of these factors reflects an increase in oil content with an increase in the favorableness of growing conditions for big sagebrush. Although big sagebrush growth can be retarded on heavy clay soils (Thatcher, 1959), the average percent clay in the 0- to 6-inch layer for these plots was only 16%. Oil content was negatively correlated with clay content in the effective rooting depth (sagebrush size)^2, and potash and magnesium in the A horizon.

Sagebrush Size (Crown Diameter × Height)

Sagebrush size was the only important factor which showed a curvilinear relationship with oil content. Volatile oil content increased linearly as the sagebrush size increased up to 7 ft^2 (Fig. 1).

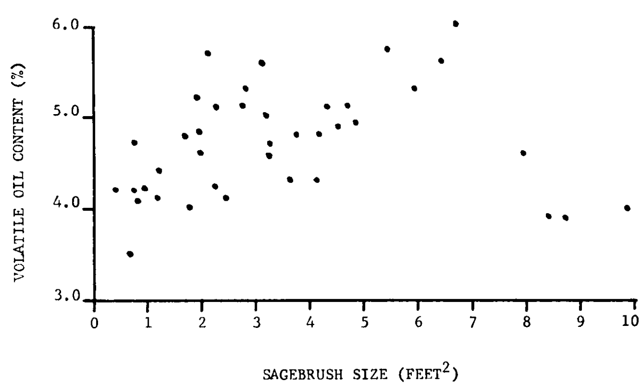

FIG. 1. Relationship between volatile oil content in big sagebrush leaves and sagebrush size (crown diameter × height) in northwestern Colorado.

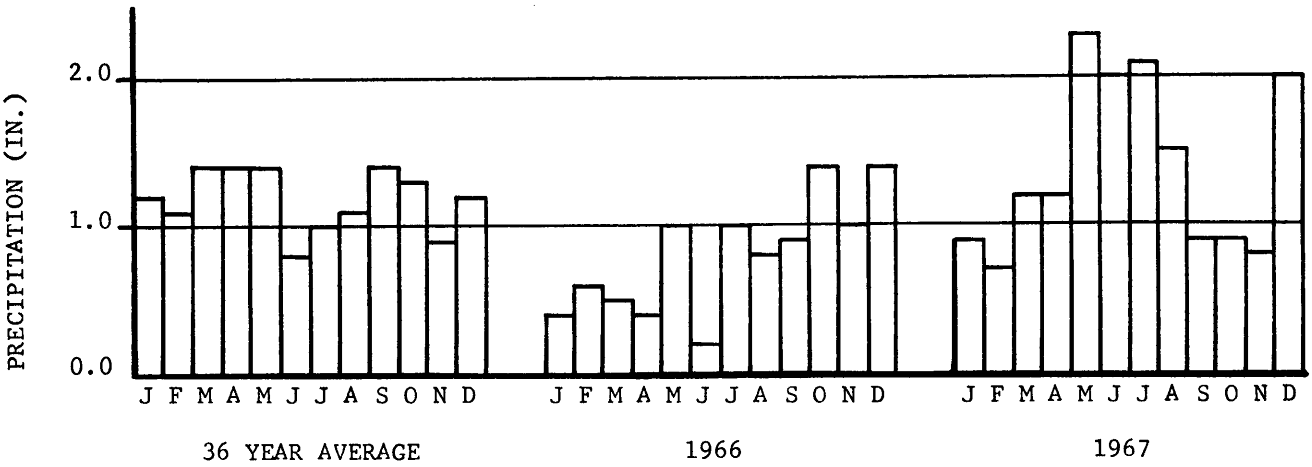

FIG. 2. Monthly precipitation at Lay, Colorado.

Beyond this point, oil content decreased with increasing sagebrush size. The highest order partial correlation coefficients between oil content and sagebrush size and between oil content and (sagebrush size)^2 were .69 and –.80, respectively.

A possible explanation of why there was a curvilinear relationship between oil content and sagebrush concerns a midsummer soil moisture stress on some plots, but not on others. The formation by plants of differentiation products, such as rubber, volatile oils, and alkaloids, is favored by conditions under which the precursors accumulate in the plant and are not used for other purposes. Since moisture stress limits growth relatively more than it limits photosynthesis, more carbohydrate is available for purposes other than growth under conditions of moisture stress than when moisture is not limited (Black, 1957).

This situation may have been the case in this study. The large, low-oil producing plants were located on finer textured soils and on sites with better "moisture economy" than the large, high-oil producing plants. Moisture economy refers to the net effect of those factors, such as deep soil, higher elevation, and steep north or east facing slopes, which maximize moisture supply and minimize moisture loss. Since most of the annual precipitation occurs as snow in this area, available soil moisture after about July 1 is closely related to soil depth and moisture retention. It is possible that, with above average precipitation in 1967, the large, low oil producing plants remained in a high state of vegetative activity and were not subjected to the moisture stress that occurred on sandier soils. Precipitation from September 1, 1966 to September 1, 1967, was 20% greater than the long term average for this period and 170% greater than that for the same period in 1966 (Fig. 2).

The plots which had large, low oil producing plants represented the most mesic sites and most productive soil conditions. These soils provided the greatest effective rooting depth and the greatest amounts of nitrogen, phosphate, and soil moisture. The more favorable moisture economy of these sites was also indicated by the presence of serviceberry (*Amelanchier alnifolia*), mountain snowberry (*Symphoricarpos oreophilus*), lupines (*Lupinus* spp.), barberry (*Berberis repens*), arrowleaf balsamroot (*Balsamorhiza sagittata*), and other species normally found on the more mesic sites in big sagebrush areas. Lupine and balsamroot plants were still succulent in September on these sites, although they had dried by this time on all other sites.

If a midsummer soil moisture stress on vigorously growing plants does cause an increase in oil content, then the large plants with a relatively low oil content in 1967 may have a much higher oil content during years of average or below average precipitation. Oil content in sagebrush plants should be determined on the same sites under different climatic conditions to determine whether oil content remains relatively constant during both "wet" and "dry" years.

Magnesium

Of all the variables considered, magnesium in the A horizon showed the strongest correlation with volatile oil content. Extractable magnesium ranged from 0.8 to 4.6 meq/100 gm of soil and was not significantly correlated with any aspect of sagebrush size. The partial correlation coefficient between magnesium and oil content was –.84 ($P < .01$ (Fig. 3).

Magnesium affects plant physiology in the following three ways: (1) it is important in photosynthesis because of its presence in the chlorophyll molecule; (2) it plays a role in the phosphate metabolism of plants and indirectly, therefore, in the respiratory mechanism; and (3) magnesium

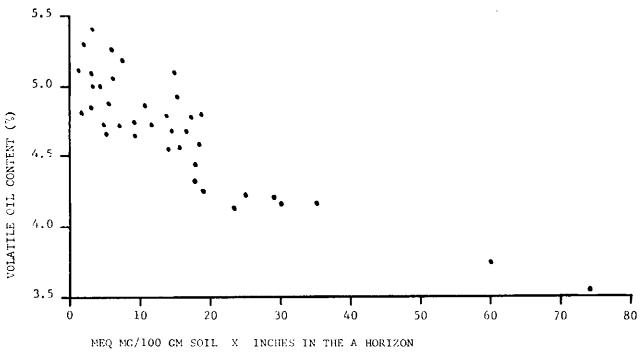

FIG. 3. Highest order partial correlation between magnesium content in the A horizon and volatile oil content adjusted for all other factors in the regression equation.

ions appear to be specific activators for a number of enzymes, including certain transphosphorylases, dehydrogenases, and carboxylases (Meyer, Anderson, and Bohning, 1960). In general, these physiological processes affect either energy transfer or carbohydrate synthesis and conversion. Since volatile oils are considered to be metabolic by-products (Meyer et al., 1960), increased magnesium content in the plant may retard volatile oil production by increasing respiration or by increasing the efficiency of carbohydrate conversion into plant compounds other than volatile oils.

Additional research is needed to determine: (1) if there is a cause-and-effect relation between magnesium and volatile oils, (2) the biochemical nature of such a relation, and (3) how this relationship could be manipulated to reduce oil content in plants and, therefore, increase forage quality. The effect of different levels of magnesium, nitrogen, phosphorus, and potassium on oil production should be studied under controlled field conditions in order to hold constant the other interacting factors. Both foliar and soil applications of these nutrients should be studied.

If the relationships indicated in this study are verified and more precisely defined through additional research, then research concerning the artificial manipulation of the chemical composition of sagebrush is surely warranted. We have about 211 million acres of sagebrush. Economically speaking, we should either destroy it or use it. I think we should seriously consider the prospects of making sagebrush more useful.

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