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Susceptibility of Big Sagebrush and Green Rabbitbrush to 2,4-D as Related to Certain Environmental, Phenological, and Physiological Conditions[1]

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Abstract. Mixed stands of big sagebrush (*Artemisia tridentata* Nutt.) and green rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.) were sprayed with butyl ester of 2,4-dichlorophenoxyacetic acid (2,4-D) at 1, 2, 3, and 4 lb/A on six phenological dates in 1956, 1957, and 1958 at the Squaw Butte Experiment Station, Burns, Oregon. Data on soil moisture; soil temperature; growth development of herbaceous species; twig elongation of big sagebrush and green rabbitbrush; dry-matter, crude-protein, and total-carbohydrate contents of green rabbitbrush herbage; and crude-protein and total-carbohydrate contents of big sagebrush and green rabbitbrush roots were obtained at weekly to biweekly intervals in all 3 years to evaluate the ecological and physiological conditions that might indicate seasonal patterns of susceptibility to 2,4-D. Big sagebrush, a non-deciduous, non-sprouting plant, was easily killed with 2,4-D at 2 lb/A when soil temperatures and moisture contents were satisfactory for vigorous growth. The development of abundant leaf area on green rabbitbrush, a deciduous, sprouting plant, was important for spray interception and a photosynthetic rate sufficient to promote carbohydrate accumulation. Green rabbitbrush was controlled about 80% with a single application of 2,4-D butyl ester at 3 lb/A after the new twigs were 3 inches long and while soil moisture contents were sufficient for active growth. Differences in susceptibility between the two species are compared with morphological, phenological, and physiological differences, and seasonal patterns of susceptibility are further compared with environmental conditions.

DIFFERENCES among species in susceptibility to foliar herbicides can result from many causes. Those differences arising from conditions that may be observed readily in the field become valuable when information from spraying trials is applied on a practical basis. Considerable information about the chemical control of big sagebrush (*Artemisia tridentata* Nutt.) and of green rabbitbrush (*Chrysothamnus viscidiflorus* (Hook) Nutt.) is available (1, 2, 3, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18), but differences between the species in susceptibility by seasons and acid equivalent rates arouse curiosity and create difficulty in the field when the two species are found in mixed stands. These differences should be better understood to satisfy curiosity as well as to guide field personnel in judging when and how to spray.

This paper summarizes the data obtained in a three-year study relating the susceptibility of big sagebrush and green rabbitbrush to 2,4-dichlorophenoxyacetic acid (2,4-D) to certain environmental, phenological, and physiological conditions. The data substantiate previous reports about spraying these species with 2,4-D, explain in part the differences in susceptibility between the species, and suggest new indexes regarding proper seasons for spraying.

EXPERIMENTAL AREA

An area located near Squaw Butte Range of the Squaw Butte Experiment Station 40 miles west of Burns, Oregon was chosen for the experiments. This area lies at an elevation of about 4,600 feet on the Oregon high desert.

The average crop-year (September 1-June 30) precipitation at Squaw Butte Range for the 20-year period 1938–1957 is 11.3 inches, and precipitation in the crop-years 1956, 1957, and 1958, respectively, was 14.3, 13.1, and 16.2 inches. Crop-year precipitation amounts are identified by the year in which the 10-month crop-year periods terminated. Above normal precipitation in those three years provided relatively long effective spraying seasons.

The experimental area supported a mixed stand of green rabbitbrush and big sagebrush with an herbaceous understory including *Bromus tectorum* L. in abundance and a sparse occurrence of several native forbs and perennial grasses. This area, being in poor range condition, was unsuited for improvement by brush control but provided a mixed stand of brush suitable for the spraying trials.

The soil is a moderately developed Brown soil derived from sands deposited by water on a gently sloping alluvial fan. Table 1 presents a soil profile description.

Characteristics of the rabbitbrush-sagebrush association as determined from list-count data are summarized

Table 1. Soil profile description.[a]

Depth inches	Horizon	Description
0–4	A_1	Light brownish gray (10YR 6/2) dry, dark brown (10YR 3/3) moist, light fine sandy loam, soft when dry, non-plastic and slightly sticky when wet. Very weak thin platy structure, pH 6.8.
4–9	A_3	Grayish brown (10YR 5/2) dry, otherwise like the A_1.
9–12	B_1	Pale brown (10YR 6/3) dry, brown (10YR 4/3) moist, fine sandy clay loam, hard when dry, slightly plastic and sticky when wet, weak medium subangular blocky structure, very thin clay flows on the peds, pH 7.0.
12–20	B_2	Light gray (10YR 7/2) dry, brown (10YR 4/3) moist, light fine sandy clay, very hard when dry, plastic and very sticky when wet, moderate medium subangular blocky structure with the peds arranged roughly into plates, thin clay flows on the peds, pH 7.2.
20–25	B_3	Light gray (10YR 7/2) dry, brown (10YR 4/3) moist, fine sandy clay loam, hard when dry, slightly plastic and sticky when moist, moderate medium subangular blocky structure, very thin clay flows on the peds, pH 7.4.
25–32	Cm	Light gray (7/2) dry, brown (10YR 4/2–4/3) moist, extremely hard, cemented, massive, with small threads and veins of lime. The ground mass is not calcareous.

[a]The profile description was prepared by Dr. Ellis G. Knox, Soil Scientist, Oregon State University.

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as follows: (a) Mean densities were 51 and 142 per plot (8 by 80 feet), respectively, of big sagebrush and green rabbitbrush; (2) where sagebrush density varied from 50 to 80 per plot rabbitbrush density varied inversely (at a rate of about 2 rabbitbrush for a change of 1 in sagebrush density) in the range 90 to 150, but relations were indefinite at lower or higher densities; and (c) density fluctuations occurred in systematic patterns over the area and appeared to be related in part to changes in the structure of the surface soil.

High sagebrush densities were associated with the occurrence of a thin vesicular A_1, and high rabbitbrush densities were associated with a loose sandy soil surface. The growth form of rabbitbrush varied from broad-leafed forms typically *Chrysothamnus viscidiflorus* to narrow-leafed forms of *C. viscidiflorus* var. *stenophyllus* (A. Gray) Hall. The broad-leafed form was associated with the vesicular A_1, but the narrow-leafed form was essentially restricted to the loose sandy soil surface. Both of these forms are included in the common name green rabbitbrush used in this paper.

Procedure

Since green rabbitbrush and big sagebrush had been easy to kill in certain seasons with 2,4-D ester (15), attention was given to the timing of spray applications, rates of 2,4-D butyl ester, and the environmental and physiological factors related to seasonal patterns of susceptibility by the two brush species. Spraying experiments were conducted in 1956, 1957, and 1958. Each experiment was a 6 × 4 × 2 factorial arranged in split-plot randomized blocks. The 1956 experiment included 6 replications and the 1957 and 1958 experiments each included 2 replications for a total of 480 treatment plots.

Dates of spraying (the 6-level factor) were assigned randomly to whole plots, and were scheduled according to the phenological development of green rabbitbrush, as follows: (D_1) first new leaves about half as long as when mature—the half-leaf stage of development, (D_2) first new leaves at mature length—the full-leaf stage, (D_3) two weeks after full leaf, (D_4) three or four weeks after full leaf, (D_5) five or six weeks after full leaf, and (D_6) early flower. Calendar dates of spraying are given in Table 2.

Table 2. Phenological and calendar dates of spraying.

Year	Calendar dates by indicated phenological dates					
	D_1	D_2	D_3	D_4	D_5	D_6
1956........	April 24	May 14	May 26	June 7	June 22	July 18
1957........	April 30	May 26	June 4	June 18	July 3	July 17
1958........	April 29	May 13	May 28	June 13	June 23	July 10

The 4-level factor was 1, 2, 3, or 4 lb/A of 2,4-D butyl ester, and the 2-level factor was 5 or 10 gal/A of total spray volume. The herbicide was prepared in water emulsion including a spreader[3] at 0.2 gal/100 gal of spray. Spray emulsions were applied with a 4-nozzle (800067 tips), 4-foot, hand-held boom operated from a back-pack compressed-air sprayer at 35 psi. Plots were sprayed during the morning hours 5:00–8:00 a.m. while the air was calm and relatively cool and moist.

Two of the 6 replications treated in 1956 were retreated June 5, 1957, and 2 were retreated June 4, 1958. Retreatments involved a uniform rate of 2 lb/A of 2,4-D butyl ester emulsified in water at 10 gal/A to consider the effects of retreatment in one or two years if initial spraying gave poor brush control. The remaining 2 replications treated in 1956 were paired with 1957 and 1958 replications for a pooled analysis of variance including year differences and treatment by year interactions.

Individual 1/50 acre treatment plots were 9.9 by 88 feet. Live plants of big sagebrush and green rabbitbrush were counted on areas 8 by 80 feet centered within each treatment plot before spraying and one year after spraying. Decreases in plant density were expressed in percent of pre-spraying densities to evaluate plant mortality. Any plant whose stem originated in the list area and supported living crown above the area was counted as a live plant.

Soil thermistors and plaster of paris soil-moisture blocks were planted 6, 12, and 18 inches below the soil surface at eight locations distributed about the experimental area. Resistances in soil-moisture blocks were read directly as percent of available soil moisture and resistances in the thermistors were transformed to degrees Fahrenheit. Readings were obtained between 8:00 and 9:00 a.m. at weekly to biweekly intervals.

On each date of spraying, information was obtained concerning the growth development of herbaceous species and the twig elongation of brush species. In addition, samples of green rabbitbrush herbage and roots and big sagebrush roots were collected for laboratory determinations of herbage dry matter, herbage and root crude protein, and herbage and root total carbohydrates. To facilitate the measurement of twig growth on big sagebrush, several plants were sprayed with India ink before growth initiation. Herbage samples included only current season twigs and leaves, and root samples included only lateral roots. Untreated plants were sampled in all but one case. After spraying on June 18, 1957, treated rabbitbrush herbage was sampled at 1, 3, 6, 8, and 10 days to determine the effects of spraying on herbage dry matter, crude protein and total carbohydrates. Root samples were washed and all samples were dried in a forced-air electric oven at 90 C, ground to pass a 20-mesh screen, and preserved in glass jars for chemical determinations.

Crude-protein concentrations were determined by a standard Kjeldahl method in the Department of Agricultural Chemistry, Oregon State University, Corvallis. Total-carbohydrate concentrations were determined by the Shaffer and Hartmann modification of the Munson and Walker method (4:836). Two to four sub-samples were drawn, digested, filtered, clarified, and made to volume. Two aliquots were removed from each for determining glucose concentrations, and the results are reported as total carbohydrates in percentage glucose equivalent by oven dry weight. A preliminary identification of carbohydrate fractions was completed by chromotographic separations in 1957.

[3]The spreader used was X–77, Colloidal Products Corporation, Sausilito, California. The use of trade names does not constitute recommendation or preference over comparable products.

Results

Big sagebrush mortality.

Dates of spraying, rates of 2,4-D, solution volume, and the interaction of dates-by-rates were sources of significant variation in big sagebrush mortality after spraying in 1956. In the pooled analysis of data from 2 replications in each of 3 years those sources of variation were significant, and, in addition, the interactions of years-by-dates and years-by-dates-by-rates were significant. In each case, those sources of variation were significant at 1 percent. Consequently, the consideration of big sagebrush mortality is restricted to the data included in the pooled analysis.

Table 3. Mean mortalities of big sagebrush after spraying on the indicated phenological dates with 2,4-D butyl ester at 1, 2, 3, or 4 lb/A emulsified in water at 5 or 10 gal/A.[a]

Year	Sagebrush mortality (%) on indicated phenological dates[b]						
	D_1	D_2	D_3	D_4	D_5	D_6	Mean
1956	65 a	94 c	88 c	92 c	87 c	70 ab	83
1957	90 c	95 c	99 c	93 c	71 ab	67 ab	86
1958	76 b	87 c	91 c	77 b	68 ab	61 a	77
Mean	77 b	92 d	93 d	87 c	75 b	66 a	82

[a]The letters following the data denote multiple range groups of means significantly different at 5 percent. Border means are read for significance separately from the body of the table.
[b]The phenological dates enumerated 1 through 6 are defined in the text and listed by calendar dates in Table 2.

Table 3 includes mean mortalities of big sagebrush by phenological dates of spraying in each year. On the average, the phenological dates D_2, D_3, and D_4 were most favorable for killing big sagebrush. Spray effectiveness increased from D_1 to D_2 and decreased after D_4. The year-by-date interaction resulted from an early effective season in 1957 and a relatively short effective season in 1958. This interaction was, in part, the result of an inconsistent phenological timing device as well as of environmental differences among years.

Figure 1 includes mean mortalities of big sagebrush by rates of 2,4-D and phenological dates of spraying. A rate of 1 lb/A of 2,4-D was significantly less effective than higher rates throughout the seasons. Rates of 2, 3, and 4 lb/A killed 90 percent or more of the sagebrush when applied on dates D_2, D_3, and D_4, and differences among those three rates were not significant on these dates. Rates of 3 and 4 lb/A killed significantly more sagebrush than 2 lb/A only during relatively unfavorable seasons for spraying. Rates of 1.5 to 2.0 lb/A of a 2,4-D ester have been recommended for spraying big sagebrush (3, 7, 9, 11, 12, 16).

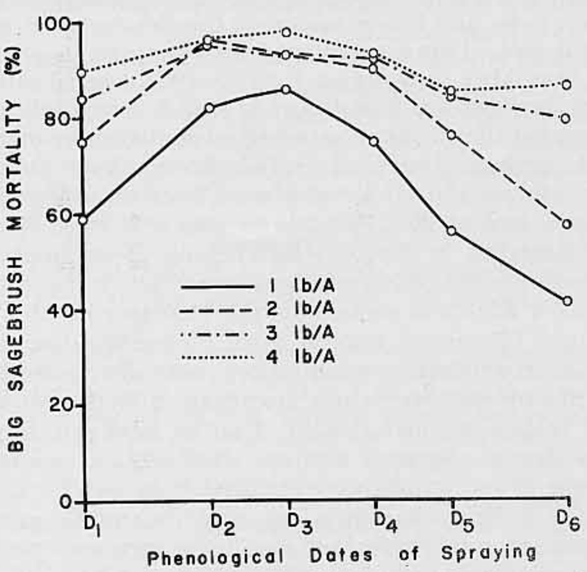

Figure 1. Big sagebrush mortality with indicated rates of 2,4-D butyl ester applied on indicated phenological dates (Table 2) in 1956, 1957, and 1958.

Spray emulsions of 5 gal/A killed an average of 80 percent of big sagebrush plants, and those diluted to 10 gal/A killed 83 percent. The difference due to spray volume was highly significant statistically, but is not of great practical importance. Optimum spray volumes were about 5 or 6 gal/A in previous trials (12).

Green rabbitbrush mortality.

The treatment factors causing significant variations in green rabbitbrush mortality after spraying in 1956 were dates, rates, volumes, and dates-by-rates interaction. In addition to those treatment factors, the interactions years-by-dates and years-by-dates-by-rates introduced significant variations when the data from all three years were considered in a pooled analysis. Thus, the factors important in big sagebrush mortality were also important in green rabbitbrush mortality. In each case, significant interactions involved changes in time of spraying; that is, treatment differences were variable from time to time.

Table 4. Mean mortalities of green rabbitbrush after spraying on the indicated phenological dates with 2,4-D butyl ester at 1, 2, 3, or 4 lb/A emulsified in water at 5 or 10 gal/A.[a]

Year	Rabbitbrush mortality (%) on indicated phenological dates[b]						
	D_1	D_2	D_3	D_4	D_5	D_6	Mean
1956	4 a	36 bc	60 cd	78 d	85 d	67 d	55
1957	44 bc	83 d	82 d	83 d	72 d	61 cd	71
1958	30 b	54 bc	72 d	64 d	64 d	63 d	58
Mean	26 a	58 b	71 bc	75 c	74 c	64 bc	61

[a]The letters following the data denote multiple range groups of means significantly different at 5 percent. Border means are read for significance separately from the body of the table.
[b]The phenological dates enumerated 1 through 6 are defined in the text and listed by calendar dates in Table 2.

Table 4 includes mean mortalities by years and phenological dates of spraying. Year-by-date interaction resulted from an early and relatively long effective season in 1957. Figure 2 includes mean mortalities by rates of 2,4-D and phenological dates of spraying. Overall means by rates of 1, 2, 3, and 4 lb/A, respectively, were 39, 60, 70, and 76 percent mortality. All comparisons among rate means are significant. Considered by individual phenological dates, no rate killed more than 89 percent of the green rabbitbrush plants, and only the 3 and 4 lb rates killed more than 80 percent. A rate of 3 lb/A of 2,4-D ester was needed to assure satisfactory control of green rabbitbrush.

Green rabbitbrush was more tolerant than big sagebrush of 2,4-D, except on dates D_5 and D_6 when mortalities of the two species were equal by rates of 2,4-D. Susceptibility in rabbitbrush increased more slowly during the spring than in big sagebrush, but also decreased

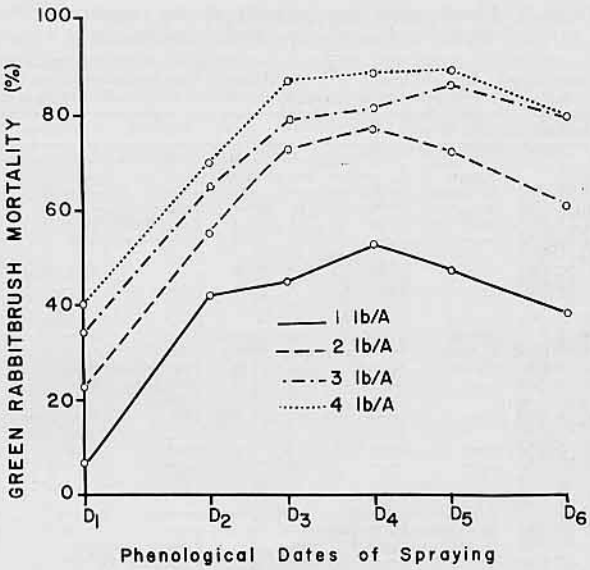

Figure 2. Green rabbitbrush mortality with indicated rates of 2,4-D butyl ester applied on indicated phenological dates (Table 2) in 1956, 1957, and 1958.

more slowly as soil moisture was depleted. Spraying on dates D_1 and D_2 was quite selective for big sagebrush. Spraying on dates D_3, D_4, and D_5 with 3 lb/A of 2,4-D killed 84 to 93 percent of big sagebrush and 78 to 86 percent of green rabbitbrush (Figure 3). This rate of

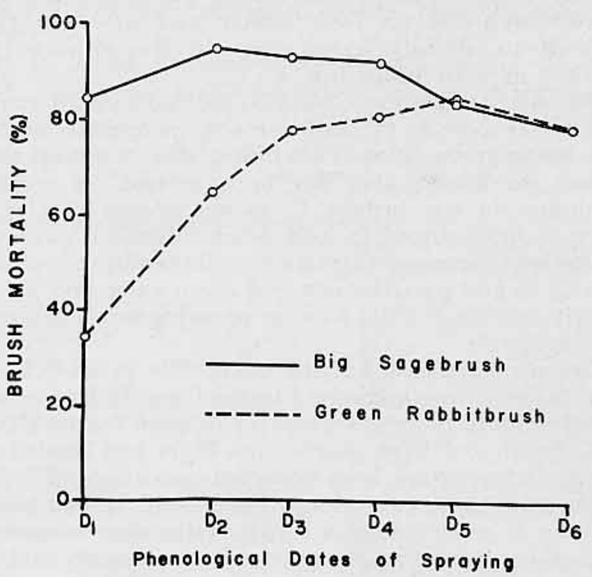

Figure 3. Average mortalities of big sagebrush and green rabbitbrush after spraying with 2,4-D butyl ester at 3 lb/A on indicated phenological dates (Table 2) in 1956, 1957, and 1958.

2,4-D is appropriate for the simultaneous control of the two species. Trends from D_4 to D_6 suggest that big sagebrush might become less sensitive than green rabbitbrush to 2,4-D in late summer.

Sprays diluted to 5 gal/A killed an average of 59 percent of green rabbitbrush and those diluted to 10 gal/A killed 63 percent. This difference is approximately equal in rabbitbrush mortality to ½ lb. of 2,4-D, but the cost of an additional ½ lb. of 2,4-D would be less than that of applying an additional 5 gallons of liquid by aerial spraying.

Spray retreatment.

Retreatment with 2 lb/A of 2,4-D butyl ester applied in early June either one or two years after the initial treatments in 1956 killed essentially all remaining big sagebrush and about 80 percent of remaining green rabbitbrush. Spray effectiveness was essentially the same as obtained with that rate of 2,4-D and timing of application in initial treatments. Emphasis should be placed upon proper timing and rates for optimum brush control in initial treatments, and when retreatments are needed the rate and timing requirements should be the same as for initial treatments.

Environmental conditions.

Big sagebrush susceptibility to 2,4-D was near a maximum as early as new growth activity became apparent. Since growth initiation coincides with seasonal temperature increases, soil temperatures might provide an index of the time to begin a spraying season on this species.

Table 5 includes soil temperatures and available-soil-moisture contents. The soil temperatures provide only

Table 5. Soil temperatures and available soil moisture contents on indicated dates and at indicated soil depths as recorded during the hour 8:00 to 9:00 a.m.

Calendar dates[a]	Soil temperatures, F, at depths indicated			Percent available soil moisture at depths indicated		
	6″	12″	18″	6″	12″	18″
1956						
April 4	44	42	42	67	71	71
April 23	55	50	49	77	80	78
May 1	53	50	50	76	79	79
May 8	50	48	49	79	80	80
May 14	55	48	48	80	80	78
May 21	69	58	56	86	87	85
May 28	58	53	54	78	81	83
June 4	53	54	55	73	82	84
June 11	64	57	56	65	76	84
June 18	61	57	56	52	69	80
June 24	61	58	58	39	61	76
July 2	64	61	60	24	48	74
July 9	77	68	63	12	41	65
July 16	69	65	64	12	34	54
1957						
April 9	48	44	44	73	72	73
April 29	56	49	48	78	76	77
May 6	54	48	48	78	77	77
May 13	54	49	50	79	78	79
May 20	49	48	49	76	77	80
May 27	62	54	53	82	80	82
June 3	70	60	57	77	82	84
June 10	64	56	56	44	74	83
June 17	63	55	55	40	66	81
June 24	71	61	59	21	44	76
July 1	70	63	61	10	28	49
July 8	73	65	63	6	20	34
July 15	72	64	63	4	15	25
1958						
April 11	45	44	44	71	70	73
April 28	49	45	45	71	71	74
May 5	59	52	50	78	76	79
May 12	53	49	50	70	76	80
May 19	65	55	54	60	75	82
May 26	64	59	56	23	60	83
June 2	63	56	56	8	32	67
June 9	59	55	55	10	50	72
June 16	76	70	57	12	43	68
June 30	68	59	59	14	37	56
July 7	72	64	61	14	36	53

[a]Dates italicized are those nearest the dates of spraying given in Table 2.

partial evidence of year differences, but at the beginning of the effective spraying seasons on big sagebrush soil temperatures at a depth of 6 inches varied from 53 to 56 F and at depths of 12 and 18 inches varied from 48 to 50 F. Since temperatures at a depth of 6 inches were erratic, they are less suitable as an index than temperatures at deeper levels in the soil. A soil temperature (recorded during the hour 8:00 to 9:00 a.m.) of 50 F at a depth of 18 inches could be used as a tentative index of big sagebrush susceptibility to 2,4-D. Spraying probably should not begin in the spring until this soil temperature prevails, but temperature fluctuations and lags in plant responses may preclude a more definite index with soil temperature.

Since the susceptibility of green rabbitbrush to 2,4-D developed more slowly in the spring than that of big sagebrush, it seems less likely to have been related to soil temperatures. The soil temperatures recorded at the times rabbitbrush susceptibility reached a near maximum were 58–64 F at a depth of 6 inches and 53–59 F at depths of 12 and 18 inches.

Soil moisture depletion is known to result in physiological changes and slower growth rates by the plants in that soil. Therefore, soil-moisture contents might provide an index to the conclusion of an effective spraying season. Table 5 includes available soil moisture contents. During the periods when spray effectiveness on big sagebrush dropped markedly, the available soil moisture contents at depths of 6, 12, and 18 inches, respectively, decreased in the ranges 40–10, 65–30, and 80–50 percent.

Big sagebrush growth activity (as indicated by decreasing susceptibility to 2,4-D) was influenced strongly by soil moisture contents at depths less than 12 inches. On the other hand, the slower decline in green rabbitbrush susceptibility suggests greater dependence on soil moisture at depths of 12 inches or more. There were no significant reductions in rabbitbrush susceptibility as the seasons progressed (Table 4). Excavations revealed a moderately dense, shallow, fibrous rooting system on big sagebrush, and a deeper, widely spreading system of thick lateral roots on green rabbitbrush. Both species have tap roots. This difference in rooting habits partially explains the seasonal differences in susceptibility to foliar herbicides, and (considered with variations in brush density and soil structure) suggests (a) competitive advantage by green rabbitbrush over big sagebrush on sandy soils and vice versa on heavier soils and (b) less competition with bunchgrasses by green rabbitbrush than by big sagebrush.

Phenological conditions.

Table 6 includes information on the phenological development of green rabbitbrush, big sagebrush, and associated bunchgrasses. Some developmental stages of growth were consistently related to periods of susceptibility to 2,4-D by the brush species.

Big sagebrush became susceptible to 2,4-D by the time (a) the first new leaves were as long as mature leaves retained over winter, (b) new twig growth was 1/4 inch long, and (c) *Poa secunda* Presl. had seedheads emerged from leaf sheaths. The latter index has been established previously (10, 12), and is more easily determined than the development of growth on big sagebrush. Big sagebrush retains leaves over winter and new growth is difficult to identify unless the old leaves have been marked as with India ink.

Table 6. Phenological development of big sagebrush, green rabbitbrush, and associated bunchgrasses.

Calendar dates & dates of spraying	Relative size of first new leaves		Ave age twig length–inches		Bunchgrass species by indicated developmental stages of growth[a]		
	Artr[a]	Chvi[a]	Artr	Chvi	Headed	Anthesis	Drying
1956							
April 17	minute	1/4 mature	none	none	——	——	——
April 24 (D_1)	1/4 mature	1/2 mature	none	none	——	——	——
May 14 (D_2)	mature	mature	1/4	1	Pose	——	——
May 26 (D_3)	——	——	1/2	3	Feid, Kocr	Pose	——
June 7 (D_4)	——	——	1	6	Stth, Sihy, Agsp	Stth	——
June 22 (D_5)	——	——	2	8	——	Sihy, Kocr	——
July 18 (D_6)	——	——	2	8	——	——	Pose
1957							
April 9	minute	minute	none	none	——	——	——
April 30 (D_1)	1/4 mature	1/2 mature	none	none	Pose	——	——
May 26 (D_2)	mature	mature	1/2	1 1/2	Feid, Kocr	Pose	——
June 4 (D_3)	——	——	1	3	Stth, Sihy, Agsp	Pose	——
June 18 (D_4)	——	——	3	5	Elci	Feid, Kocr, Sihy, Stth	——
July 3 (D_5)	——	——	4	6	——	Elci	Pose
July 17 (D_6)	——	——	5	7	——	——	——
1958							
April 11	minute	minute	none	none	——	——	——
April 29 (D_1)	1/4 mature	1/2 mature	none	none	——	——	——
May 13 (D_2)	1/2 mature	mature	none	1/2	Pose	——	——
May 28 (D_3)	——	——	1	3	Feid, Kocr, Sihy, Stth	Pose	——
June 13 (D_4)	——	——	3	5	Agsp, Elci	Feid, Kocr Sihy, Stth	Pose
June 23 (D_5)	——	——	4	6	——	——	——
July 10 (D_6)	——	——	4	6	——	——	——

[a]Species symbols are identified as follows:
Chvi, *Chrysothamnus viscidiflorus* (Hook.) Nutt.
Artr, *Artemisia tridentata* Nutt.
Pose, *Poa secunda* Presl
Feid, *Festuca idahoensis* Elmer
Kocr, *Koeleria cristata* (L.) Pres.
Stth, *Stipa thurberiana* Piper
Sihy, *Sitanion hystrix* (Nutt.) J. G. Smith
Agsp, *Agropyron spicatum* (Pursh) Scribn. & Smith
Elci, *Elymus cinereus* Scribn. & Merr.

Big sagebrush susceptibility to 2,4-D decreased rapidly when *Poa secunda* (a shallow-rooted perennial) herbage was losing green color. This index, also, has been established previously, and has been related to moisture depletion in the surface 12 inches of soil (12). Some irregularity occurred in 1958 when abundant June precipitation increased available soil moisture contents (Table 5) and partially restored green color and growth activity in *Poa secunda* without restoring susceptibility in big sagebrush.

Green rabbitbrush became susceptible to 2,4-D by the time (a) new twigs averaged 3 inches long, (b) *Poa secunda* had developed to anthesis, and (c) *Sitanion hystrix* (Nutt.) J. G. Smith and *Stipa thurberiana* Piper had headed out. These indexes have been reported previously (15). The index relating to twig elongation should be emphasized because it relates most directly to the development of foliage for increasing the interception of spray and sustaining photosynthetic production sufficient to promote an accumulation of carbohydrates.

The susceptibility of green rabbitbrush to 2,4-D decreased moderately as *Poa secunda* leaves lost green color, but this decreasing trend was slower than that of big sagebrush.

Physiological condition.

Table 7 includes data on the dry-matter, crude-protein, and total-carbohydrate contents of green rabbitbrush herbage (current season growth). Generally, the highest

Table 7. Dry matter, crude protein, and total carbohydrates in unsprayed green rabbitbrush herbage (current season growth).

Calendar date	Date of spraying	Percent dry matter	Crude protein, percent of dry matter	Total carbohydrates (percent glucose equivalent of dry matter)
1956				
April 24	D_1	22	34.2	13.8
May 14	D_2	22	26.3	19.8
May 26	D_3	22	21.2	16.4
June 7	D_4	28	15.5	21.3
June 22	D_5	29	14.8	17.9
July 18	D_6	39	9.9	19.0
July 30		48	7.8	17.7
1957				
April 30	D_1	28	23.3	16.0
May 26	D_2	25	17.5	22.7
June 4	D_3	24	17.2	24.3
June 18	D_4	29	13.7	21.7
July 3	D_5	33	11.4	20.3
July 17	D_6	35	11.5	18.3
1958				
April 29	D_1	28	24.6	20.2
May 12	D_2 (13th)	26	22.4	20.4
May 26	D_3 (28th)	27	19.0	16.5
June 9		29	16.0	20.6
June 16	D_4 (13th)	32	13.8	20.7
June 30	D_5 (23rd)	35	11.9	22.4
July 7	D_6 (10th)	36	12.4	20.5

mortalities of green rabbitbrush were obtained with spray applications coinciding with high carbohydrate contents (above 20 percent glucose equivalent) in the herbage. Robertson and Cords (17) also reported this relation, but more intensive sampling is needed to determine the dependence of susceptibility upon the carbohydrate contents of herbage. Otherwise, the physiological conditions of green rabbitbrush herbage seemed unrelated to susceptibility.

Data in Table 8 reveal decreases in moisture, crude protein, and total carbohydrates in green rabbitbrush

Table 8. Dry-matter, crude-protein, and total-carbohydrate concentrations in green rabbitbrush herbage after spraying with 2,4-D on June 18, 1957.

Calendar date	Percent dry matter	Crude protein percent of dry matter	Total carbohydrates (percent glucose equivalent of dry matter)
June 18	71	13.7	21.7
June 19	71	13.3	22.7
June 21	69	12.5	20.7
June 24	70	11.4	20.9
June 26	69	11.6	16.6
June 28	62	11.8	19.7

herbage after spraying with 2,4-D on June 18, 1957. These decreases were slightly advanced seasonally in comparison with those of untreated plants (Table 7).

Table 9 includes data on the crude protein contents of big sagebrush and green rabbitbrush roots. These data, in contrast to the strong seasonal decreases in the crude protein content of rabbitbrush herbage, reveal uniformly low and essentially constant concentrations of crude protein in the roots of each species.

Figure 4 includes data on the total carbohydrate contents of lateral roots of the two brush species. Big sagebrush contained an average of 13.7 percent carbohydrates as compared with an average of 19.4 percent in green rabbitbrush roots. Carbohydrate concentrations in rabbitbrush roots revealed seasonal increases in early June when

Table 9. Crude protein contents of lateral roots from untreated big sagebrush and green rabbitbrush.

Date	Crude protein content in percent of dry matter	
	Big sagebrush	Green rabbitbrush
1956		
April 24	3.5	4.0
May 14	3.2	4.6
May 26	2.8	3.9
June 7	3.2	3.8
June 22	3.2	3.6
July 18	3.4	3.4
July 30	3.7	4.6
Aug. 13	4.5	4.0
Aug. 27	3.1	3.6
1958		
April 9	5.1	5.8
April 29	6.2	6.4
May 6	5.8	6.4
May 12	4.0	4.9
May 19	3.0	4.0
May 26	4.5	5.0
June 2	4.1	3.6
June 9	4.8	4.2
June 16	4.6	4.2
June 30	4.1	4.2
July 7	4.9	5.2

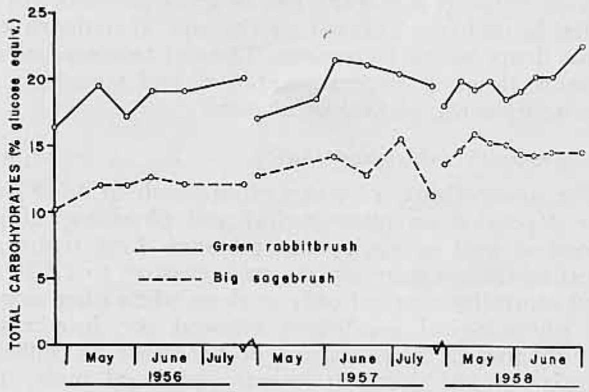

Figure 4. Total carbohydrates in the lateral roots of green rabbitbrush and big sagebrush.

the plants were most susceptible to 2,4-D. Seasonal patterns of carbohydrate accumulation in big sagebrush roots were indistinct. Rather, year differences and seasonal variability were revealed.

Chromatographic separations of carbohydrates established xylose as the principal sugar for both species. Thus, the principal storage-carbohydrate form is believed to be pentosan.

Discussion and Conclusions

Big sagebrush susceptibility.

Consideration of environmental, phenological, and physiological conditions related to seasonal patterns of 2,4-D effectiveness on big sagebrush indicates that susceptibility in this species depends essentially upon environmental conditions. Big sagebrush was killed readily with 2,4-D ester whenever soil temperatures and moisture contents were satisfactory for good growth activity. Phenological and physiological conditions failed to indicate limitations in susceptibility other than the requirement for vigorous growth activity.

Big sagebrush retained leaves over winter, and they appeared to become active in photosynthesis in the spring before the appearance of new leaves. This growth characteristic may serve as an adaptive alternative to higher carbohydrate concentrations in the roots and definite seasonal patterns of carbohydrate accumulation. Big sagebrush is a non-sprouting species that dies when the young wood, leaves, and apical meristems are destroyed. This characteristic was established by the clipping studies of Cook and Stoddart (5). Spraying before growth initiation caused defoliation without mortality, but, by inference, 2,4-D was lethal when sufficient amounts moved from intercepting leaf tissue through new wood and into apical meristems. Movement downward into underground parts is considered unnecessary to mortality except possibly in young mature plants. The effects of aging on big sagebrush susceptibility are not understood (1, 8, 10, 16).

Big sagebrush can be controlled with a single application of 2,4-D ester at 2 lb/A. Spraying can begin in the spring when (a) the first new leaves are as long as mature leaves held over winter, (b) *Poa secunda* exhibits heads, or (c) the soil at a depth of 18 inches has warmed to 50 F. Spraying should be stopped when (a) *Poa secunda* herbage exhibits a marked loss in green color or (b) the available moisture content of the soil at a depth of 6 inches drops below 40 percent. The soil temperature and moisture indexes are new, tentative, and seemingly less definite than the phenological ones.

Green rabbitbrush susceptibility.

The susceptibility of green rabbitbrush to 2,4-D butyl ester depended on phenological and physiological conditions as well as environmental ones. Leaf tissue and apical meristems were always very sensitive to 2,4-D, but plant mortality resulted only at times when phenological and physiological conditions allowed the interception and downward translocation of herbicide in sufficient quantity to kill dormant lateral and basal buds. This species sprouts prolifically from dormant buds when only the branches are killed.

Green rabbitbrush is deciduous and produces a completely new crop of leaves each spring. Spray interception increased in proportion to the amount of leaf tissue, and this phenological progress in growth coincided with physiological progress in photosynthesis and accumulation of carbohydrates. High concentrations of carbohydrates in the leaves, and a net downward movement of carbohydrates as indicated by accumulation in the roots, presumably promoted the translocation of the herbicide (17). The requirement for downward translocation of herbicides into lateral and basal buds probably explains, at least in part, the higher requirement in rate of 2,4-D to kill green rabbitbrush than to kill big sagebrush.

When phenological and physiological progress indicates high susceptibility to 2,4-D, one must then consider environmental conditions. Sustained susceptibility depended on a continuation of environmental conditions satisfactory to vigorous growth activity. The available moisture content of the soil at a depth of 12 inches apparently should be above 30 percent to assure vigorous growth.

Green rabbitbrush can be controlled about 80 percent with a single application of 2,4-D ester at 3 lb/A, if the spray is applied (a) after the new twigs have attained an average length of 3 inches and (b) while the soil moisture content remains above a minimum satisfactory level. The loss of green color in the herbage of *Poa secunda* or other relatively shallow-rooted plants may be used as an index of soil moisture depletion.

Mixed stands of big sagebrush and green rabbitbrush can be controlled with 2,4-D ester at 3 lb/A applied at an optimum time for the control of green rabbitbrush.

Summary

Environmental, phenological, and physiological conditions related to 2,4-D susceptibility by big sagebrush and green rabbitbrush were studied in 1956, 1957, and 1958 at the Squaw Butte Experiment Station, Burns, Oregon. Mixed stands of the two species were treated with 2,4-D ester at 1, 2, 3, or 4 lb/A on six phenological dates determined each year by the growth development of green rabbitbrush.

Data on soil moisture; soil temperature; growth development of herbaceous species; twig elongation on rabbitbrush and sagebrush; dry-matter, crude-protein and total-carbohydrates in rabbitbrush herbage; and crude-protein and total-carbohydrates in sagebrush and rabbitbrush roots were obtained at weekly to biweekly intervals in all three years.

Big sagebrush was easily killed with 2,4-D ester whenever soil temperatures and moisture contents were satisfactory for vigorous growth. Effective spraying can begin when (a) the first new leaves are as long as mature leaves held over winter, (b) *Poa secunda* exhibits heads, or (c) the soil at a depth of 18 inches has warmed to 50 F. Spraying should be stopped when (a) *Poa secunda* herbage exhibits a marked loss in green color or (b) the available moisture content of the soil at a depth of 6 inches drops below 40 percent. The indexes of soil temperature and moisture are new, tentative, and less definite than the phenological ones.

The development of abundant leaf area on green rabbitbrush was deemed important for spray interception and a photosynthetic rate sufficient to promote carbohydrate accumulation. Green rabbitbrush can be controlled about 80 percent with a single application of 2,4-D ester at 3 lb/A. Effective spraying (a) can begin after new twigs have attained an average length of 3 inches and (b) can continue while the soil moisture content remains above a minimum satisfactory level. The loss of green color in the herbage of *Poa secunda* indicates soil moisture depletion.

Mixed stands of big sagebrush and green rabbitbrush can be controlled with 2,4-D ester at 3 lb/A applied at an optimum time for the control of green rabbitbrush.

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