A STUDY OF THE ROLE OF <u>RHUS</u> <u>COPALLINA</u> IN THE COMMUNITY DYNAMICS OF THE FOREST-PRAIRIE ECOTONE IN NORTH-CENTRAL OKLAHOMA

by

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CHAPTER I

INTRODUCTION

Winged sumac, *Rhus copallina*, is a rhizomatous, perennial shrub or small tree which attains a maximum height of 9-10 m and a diameter-at-breast height of 2.0-2.5 dm (Sargent 1926). In the eastern United States this species is typically found on dry, gravelly or sandy upland areas and is able to thrive in soils which are low in both nutrients and soil moisture (Van Dersal 1938, Hough 1947). Near the western limits of the eastern deciduous forest *R. copallina* occupies more level soils and often forms large clones in open areas.

R. copallina occurs throughout eastern and central Oklahoma as a shrub, or very infrequently as a tree, and forms large clones in open, unforested areas. Clone formation is initiated by the production of offshoots from shallow rhizomes of the parent plant. These rhizomes generally radiate outward from the parent plant so that after several years of growth a clone often acquires an oblong shape with the older and taller stems at the center and younger and smaller stems toward the periphery of the clone.

In the cross-timbers region of north-central Oklahoma clones of this species occupy a variety of habitats from dry, rocky upland sites with shallow soils, to areas adjacent to bottomland forests where soils are deeper and soil moisture relations are much better. *R. copallina* is somewhat weedy in nature and often becomes established along fence rows, in overgrazed fields, and in situations in which soil disturbance is evident. In less disturbed sites it frequently occupies ecotonal areas between hardwood forests and adjacent tall grass prairies. Occasionally, the simultaneous establishment of several adjacent clones forms a belt of R. copallina parallel to the forest edge which may extend for 40-50 m in length and appear to be rapidly encroaching on adjacent prairie.

I have observed many situations in which saplings and small trees of the surrounding hardwood forests were present in or near the oldest portions of a clone. The interpretation of these observations was difficult. In certain instances, it appeared as if R. copallina became established around a few young saplings and young trees and spread outward from these. At other times, it appeared that the establishment of these saplings and young trees occurred sometime after the establishment of the clone.

Earlier workers who have described the forest-prairie ecotone have reported similar findings. Weaver and Thiel (1917), Pool, Weaver, and Jean (1918), and Aikman (1927) noted extensive areas in the tension zone between bottomland forest and prairie in eastern Nebraska where shrubs predominated and recorded their encroachment on adjacent prairie. Aikman (1927) reported R. glabra, Corylus americana, and Symphoricarpos spp. as the dominant shrubs in this zone. Fitch and McGregor (1956) have reported similar descriptions of bottomland forest borders in Kansas. All of these accounts were descriptive and observations were not quantified.

In north-central Oklahoma R. copallina, R. glabra, Cornus drummondii, and Prunus angustifolia are the most prominant shrub invaders of tall grass prairie. Of these four, R. copallina appears to be the most abundant as well as the most aggressive invader.

The mechanisms that allow R. copallina to invade and replace established tall grass prairie are unknown. Aikman (1927) suggested that Rhus sp. and other shrubs outcompete prairie species for both light and nutrients, however, little quantitative data was presented concerning the second factor. Rice (1965) has found R. copallina to produce toxins which inhibit the growth of some nitrogen-fixing bacteria and reduce nodulation on legumes, but the potential effects of these toxins on non-leguminous higher plants has not been investigated.

The major goals of this research were to determine the role of R. copallina in initiating the invasion of climax tall grass prairie by both upland and bottomland forest, and to study the mechanisms, particularly the role of allelopathy, by which clones of R. copallina are able to replace members of the tall-grass prairie which they are often associated with.

CHAPTER II

SITE DESCRIPTION

All field research was conducted approximately 8 miles west of Stillwater, Oklahoma on the Oklahoma State University Ecology Preserve and on adjacent land to the north which surrounds Lake Carl Blackwell (Payne Co: T19N-R1W-Sec 16-21,29).

This region is located in the Central Redbed Plains geomorphic province. The topography consists of gently rolling hills which are composed predominantly of red sandstones and shales formed when shallow Permian seas covered the area (Johnson et al. 1972). The soils are predominantly residual loams and sandy loams of the Vernon series (Gray and Galloway 1959).

Three important vegetational communities are found in the region. Bottomland forests occur along intermittent and permanent streams and in areas immediately adjacent to Lake Carl Blackwell. These forests are composed of mesic components of the eastern deciduous forest and extend westward across Oklahoma along watercourses. The dominant trees which compose the bottomland forests of the study area are american elm (_Ulmus americana_)* and hackberry (_Celtis_ spp.). Several other species are found less frequently such as bur oak (_Quercus macrocarpa_), Shumard's oak (_Q. shumardii_), black walnut (_Juglans nigra_), green ash (_Fraxinus pennsylvanicus_) and redbud (_Cercis canadensis_). A large

*Nomenclature follows Waterfall, 1969.

variety of herbs and several shrubs and vines are associated with these forests.

The drier, shallow soiled hill crests are usually occupied by upland forests dominated by post oak (Q. stellata) and blackjack oak (Q. marilandica) and to a lesser extent by eastern red cedar (Juniperus virginiana). Both american elm and hackberry are found in small numbers in these forests, particularly near the lower limits where they merge with tall grass prairie.

In undisturbed areas tall grass prairie generally occupies an area intermediate between these two forest communities. The dominants of this community are little bluestem (Andropogon scoparius), indiangrass (Sorghastrum nutans), and Scribner's panicum (Panicum oligosanthes var. scribnerianum). A variety of other grasses and forbs are present, particularly members of the Compositae and Leguminosae.

The study area has been used in the past predominantly for pasture and hay production, but at present, no cattle are being grazed. Most of the prairie sites have reverted back to climax or near climax vegetation as described by Booth (1941) since grazing was eliminated.

The climate is temperate (Table I) and is characterized by substantial variation in temperature and precipitation both seasonally and annually (Myers 1976). Temperatures generally rise above $38^{\circ}C$ in the summer and drop below $-18^{\circ}C$ in the winter. The annual precipitation averages 81.74 cm and occurs predominantly during the growing season from thunderstorm activity. The average freeze free period occurs from April 10 through October 17 (192 days).

TABLE I

AVERAGE MONTHLY PRECIPITATION, EVAPORATION, AND MINIMUM AND MAXIMUM AIR TEMPERATURES FOR 1893-1975 AND 1976

	Average Precipitation(cm)			Average Evaporation	Average Air Temperature(C^{o})	
					1893-1975	
Month	1893-1975*	1976**	Deviation(cm)	1893-1975	Maximum	Minimum
January	2.97	0	-2.97	---***	9.00	- 3.66
February	3.46	1.87	-1.59	---	12.68	- 2.00
March	4.76	4.76	.00	---	17.14	2.75
April	7.32	9.73	+2.41	20.02	22.42	9.37
May	11.83	8.73	-3.10	21.50	26.24	13.91
June	10.86	1.33	-9.53	26.14	31.02	17.65
July	9.04	4.86	-4.18	28.77	33.89	21.23
August	8.22	4.63	-3.59	26.14	33.94	20.47
September	8.65	6.68	-1.97	20.43	29.74	16.02
October	7.11	4.28	-2.83	15.23	23.92	8.49
November	4.74	1.23	-3.51	---	16.32	2.80
December	3.43	.46	-2.97	---	9.20	- 2.34
Yearly Total	82.39	48.56	-33.83	---		

*All data from 1893-1975 recorded at the OSU Agricultural Experiment Station, Stillwater, Oklahoma.

**1976 Precipitation values recorded at Lack Carl Blackwell USDA Hydraulic Laboratory.

***Insufficient monthly data available.

CHAPTER III

VEGETATIONAL CHANGES WITH THE ENCROACHMENT OF *RHUS COPALLINA*

Woody Vegetation

Fifteen clones of *R. copallina* were sampled during September and October, 1976, to determine if woody components of surrounding hardwood forests were becoming established within these clones, and to determine what changes occur in the herbaceous vegetation as a clone invades climax prairie. Clones were selected which were well established (center height $\geq$ 2.0 m) with moderate to relatively high stem densities. Small, poorly established clones with low densities or stunted growth were avoided.

Five clones were selected from each of three different topographic types. One group of clones occurred directly adjacent to upland forests. A second group occurred in open, climax prairie and was isolated from surrounding forests by at least 30 m of prairie. The third group occurred directly adjacent to bottomland forests. All of the clones selected appeared to be actively invading climax or near-climax prairie and exhibited no obvious signs of hardwood establishment (e.g., saplings protruding from the canopy of the clone).

At each clone three parallel transects were established. One transect was placed directly in the center of the clone (avg. stem height > 2.0 m), a second was placed near the edge of the clone (avg. stem height .7 m - 1.2 m), while a third transect was placed in the adjacent prairie in close proximity to the clone. Transects at the forest edge sites were placed perpendicular to the forest margin. Along each transect 6 points were established at 1 m intervals from which the point-center quarter method was used to sample the density, frequency, and composition of the herbs, woody seedlings, and shrubs present. In addition, the density and diameter (5 cm above ground) of stems of R. copallina were determined. In using the point-center quarter method, the stem closest to the point was recorded. Distance measurements were taken from the base of the stem to the point. Visual counts were employed when densities were very low. Measurements and counts were limited to a zone within 2 m of either side of the transect line.

Results and Discussion

Tables II and III summarize the data collected for woody species found in the clones. Tree seedlings were found in all 15 clones (avg. density = $.99/m^2$), while shrubs were found in 14 of the clones sampled. Both seedling and shrub densities were substantially higher in the centers of clones and decreased toward the peripheries. In the adjacent prairie, seedlings were found in only 5 of the 15 sites and occurred in very low densities (avg. density = $.025/m^2$). This represents a reduction of approximately 98% from the seedling densities in the center of the clones. Shrubs with forest affinities were absent from all prairie sites.

TABLE II

DENSITIES AND RELATIVE DENSITIES (AS PERCENTAGE) OF SHRUBS WITHIN AND ADJACENT TO CLONES OF RHUS COPALLINA

	Density (#/M^2)									Relative Density (%)								
	Center of Clone			Edge of Clone			Prairie			Center of Clone			Edge of Clone			Prairie		
Species	UF*	CP	BF	UF	CP	BF	UF	CP	BF	UF	CP	BF	UF	CP	BF	UF	CP	BF
Symphoricarpos orbiculatus	.219	16.25	2.97	.010	.100	.108	--	--	--	34.27	87.94	77.96	6.49	21.55	19.01	--	--	--
Cornus drummondii	.412	--	.84	.050	.348	.460	--	--	--	64.48	12.06	22.04	32.47	75.00	80.99	--	--	--
Prunus angustifolia	.008	2.23	--	.090	--	--	--	--	--	1.25	--	--	61.04	3.45	--	--	--	--
Amorpha canescens	--	--	--	--	.016	--	--	--	.016	--	--	--	--	--	--	--	--	100
Ave. Site Density	.639**	18.253**	3.81**	.150**	.464**	.568**	--	--	.016									
Total Density		7.56			.394			.005										

*UF = in R. copallina clones adjacent to upland forest
CP = in R. copallina clones in climax prairie
BF = in R. copallina clones adjacent to bottomland forest
**Significant differences ($p < .01$) were found between the shrub densities at the center and edge of clones for all three topographic types (UF, CP, BF).

TABLE III

DENSITIES AND RELATIVE DENSITIES (AS PERCENTAGE) OF SEEDLINGS WITHIN AND ADJACENT TO CLONES OF <u>RHUS COPALLINA</u>

	Density ($\#/M^2$)									Relative Density								
	Center of Clone			Edge of Clone			Prairie			Center of Clone			Edge of Clone			Prairie		
Species	UF*	CP	BF	UF	CP	BF	UF	CP	BF	UF	CP	BF	UF	CP	BF	UF	CP	BF
<u>Quercus</u> <u>stellata</u>	.203	.012	.166	--	--	.036	--	--	.02	54.42	1.50	4.44	--	--	7.75	--	--	100
<u>Quercus</u> <u>marilandica</u>	.020	.060	.022	--	--	--	--	--	--	5.13	36.90	2.19	--	1.30	6.90	--	--	--
<u>Celtis</u> sp.	.030	.296	.082	.002	.002	.032	--	--	--	8.04	7.48	.58	1.24	--	--	--	--	--
<u>Ulmus</u> <u>americana</u>	.090	.354	3.318	.145	.145	.380	--	--	.03	24.13	44.14	88.87	90.06	94.77	81.90	--	--	100
<u>Juniperus</u> <u>virginiana</u>	.020	.080	.032	.006	.006	.016	--	--	--	5.36	9.98	.85	3.76	3.93	3.44	--	--	--
<u>Cercis</u> <u>canadensis</u>	.010	--	.012	.008	--	--	--	--	--	2.68	--	.32	4.96	--	--	--	--	--
<u>Juglans</u> <u>nigra</u>	--	--	.098	--	--	--	--	--	--	--	--	2.61	--	--	--	--	--	--
<u>Bumelia</u> <u>lanuginosa</u>	--	--	.012	--	--	--	--	--	--	--	--	.32	--	--	--	--	--	--
<u>Diospyros</u> <u>virginiana</u>	--	--	--	--	--	--	--	.02	--	--	--	--	--	--	--	--	100	--
Ave. Site Density	.384	.865	3.85	.189	.162	.464	.025	.020	.031									
Total Density		1.700			.272			.025										

*UF = in <u>R</u>. <u>copallina</u> clones adjacent to upland forest.
CP = in <u>R</u>. <u>copallina</u> clones in climax prairie.
BF = in <u>R</u>. <u>copallina</u> clones adjacent to bottomland forest.

**Significant differences ($p < .01$) were found between the seedling densities at the center and edge of clones for all three topographic types (UF, CP, BF).

The composition of the seedlings within a clone appeared to be highly influenced by the proximity of seed sources. In clones adjacent to upland forests seedlings of Q. stellata were most abundant while near bottomland sites U. americana predominated. Clones in open prairie sites were dominated by U. americana and Q. marilandica and appeared intermediate in composition between upland and bottomland sites. Overall, seedlings of 8 tree species were found in the centers of clones, 5 in the edges of clones and only 3 in the adjacent prairies.

Importance values for R. copallina were calculated based on the relative density and relative diameters of the stems in each clone. No correlation was evident between the importance value and the density of seedlings of tree species found within a clone. This suggests that the number of seedlings found within a clone is most strongly related to the proximity and abundance of seed sources, the vagility of the species, and other dispersal-related phenomena rather than the density or age of the Rhus clone. However, within a given clone seedling densities almost always increased from the periphery toward the older, center portions of the clone (Figure 1). As with seedlings, shrub stem density decreased markedly toward the periphery of the clone.

Two shrubs, Symphoricarpos orbiculatus and Cornus drummondii, were common at all three sites. S. orbiculatus was most abundant in bottomland sites while C. drummondii predominated in upland sites.

Evidence from the data and from field observations indicate that most species of trees are unable to successfully invade climax prairie without the initial invasion of R. copallina or other shrubs. Although Quercus stellata, Q. marilandica, and J. virginiana are able to become established in climax prairie without initial shrub invasion, the

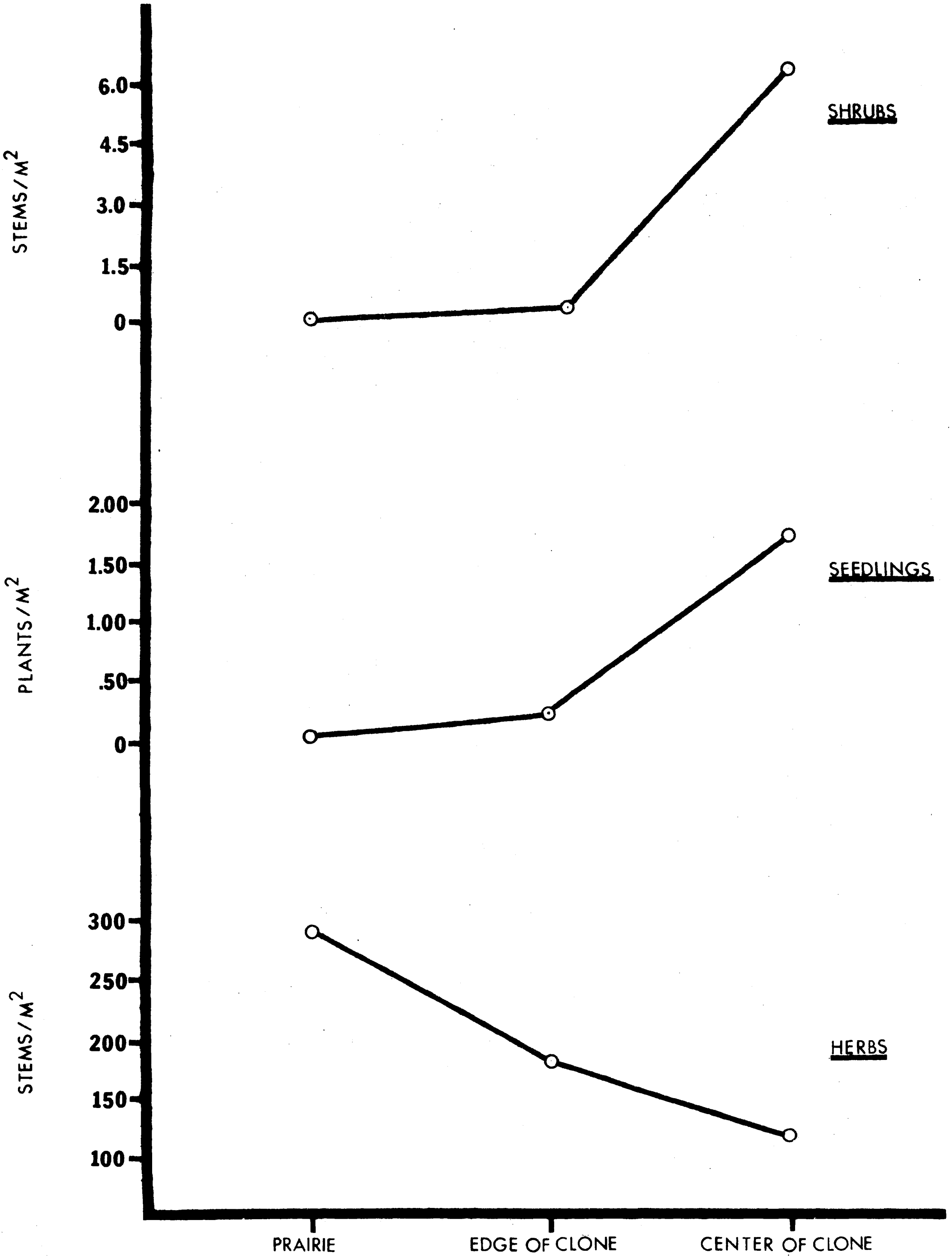


Figure 1. Changes in the Densities of Tree Seedlings. Shrubs, and Herbs when Sampled at the Center of Clones, at the Edge of Clones, and in Adjacent Climax Prairie

presence of such shrubs appears to considerably enhance the establishment of seedlings of these species.

Rate of Encroachment

The border between forest and prairie has long been known to be a product of the dynamic interaction of several environmental factors. Fire, which occurred every few years in primeval times (Jackson, 1965), has played an important role in determining the position of the forest-prairie edge, particularly in areas such as the prairie peninsula of the mid-west where conditions are suitable for tree establishment (Kozlowski and Ahlgreen 1974). The reestablishment of forest on what was previously prairie in conjunction with man's general reduction in the frequency of prairie fires has been noted by several authors.

Ring counts of _Rhus_ stems from 10 selected clones from the study site indicated an average fire occurrence of 18-20 years at any particular locality. This great reduction in the frequency of fire has led to the reinvasion of _R. copallina_ in many areas. Nine clones of _R. copallina_ were subsequently selected to determine the rate of encroachment into climax prairie. In each clone a transect was established from the center of the clone to the edge. Points were established at 1 m intervals and at each point the first two _Rhus_ stems which were within 20 cm of a line running perpendicular to the transect and through the point were selected. The vertical height of each stem was measured with a stadium rod and the stem was aged by counting growth rings of stems which were severed approximately 5 cm above ground level. The average height and age of the stems in each transect interval was determined and the rate of vertical and horizontal growth of the clone per year was calculated. Dead and frequently charred stems found at the base of living stems in four of the clones indicated past fires.

The average rate of advancement of the 9 sampled clones was 1.25 m/year and occurred at a fairly constant rate from year to year for any particular clone. The data also indicates that the occasional fires which now occur in the area act to stimulate the vertical growth and horizontal spread of these clones, therefore enhancing the reinvasion process. Resprouts from rhizomes following a fire grew on the average 232% faster than those of unburned clones while the horizontal spread of clones increased only slightly. Energy and nutrients stored in the rather bulky rhizome system may largely account for this burst of growth following a fire, however, new stems which had formed from the lateral spread of runners several years after a fire still exhibited substantially higher vertical growth (176%) than non-burned clones. These findings are significant since the increased fire frequencies which characterized primeval prairies generally acted to halt the invasion of almost all woody taxa (Kozlowski and Ahlgren 1974).

Herbaceous Vegetation

The sampling of the herbaceous and woody vegetation occurred during the autumn at a time when most plants had nearly completed their seasonal growth and were nearing dormancy. During this period, Japanese brome (Bromus japonicus), a common winter annual throughout the state, was germinating. Some clones supported extremely high densities of plants, particularly towards the center of the clones, because of the high densities of seedlings of B. japonicus. These seedlings have a very high mortality rate, very few surviving to maturity. The presence of such high seedling densities not only tended to overemphasize the importance of *B. japonicus*, but also served to underestimate the relative importance of other prairie species present. For this reason, a modified average has been included in Table IV based on the omission of data from 4 clones which supported high densities of *B. japonicus*. It is believed that these modified averages offer a much more realistic representation of the vegetation densities of most of the species present. The following discussion will be based on these modified values.

An analysis of the data indicates that a significant reduction in stem density as well as a substantial compositional change occurs in the herbaceous vegetation as a clone invades a prairie (Table IV). An average reduction of 37.8% in the density of herbaceous vegetation was found at the edge of the clones and 59.8% at the center of the clones. All but two of the clones sampled exhibited reduced understory densities. The variability in percent reduction was quite high and ranged from only slight reduction to over 99% reduction. Almost all of the climax prairie species were reduced substantially (avg. > 70%) in the center of the clones. Increases in herbaceous species which comprise the understory of the surrounding bottomland and upland forests were slight. The major increasers with hardwood forest affinities were *Geum canadensis*, *Smilax bona-nox* and *Muhlenbergia schreberi*. Other species such as *Vitis* sp., *Sanicula canadensis*, and *Leersia virginica* were present only rarely.

TABLE IV

STEM DENSITIES (M^2) OF HERBACEOUS VEGETATION FOUND WITHIN OR ADJACENT TO CLONES OF *RHUS COPALLINA*

	Bottomland Forest			Prairie			Upland Forest			Total for All Clones		
	C*	E	P	C	E	P	C	E	P	C	E	P
	4	485	625	448***	189	400	2	209	293	117	181	291
	469***	117	176	132	117	336	44	105	346			
	9	27	216	836***	219	346	878***	236	503			
	243	407	144	229	176	222	24	131	375			
	2	181	450	87	98	150	161	204	242			
Total	727	1217	1611	1732	824	1454	1109	885	1759			
Average	145	243	322	346	160	291	221	177	352			
Modified Average**	65	275	359	149	138	236	58	162	314			

*C = Center of clone
E = Edge of clone
P = Climax Prairie

**omitting *Bromus japonicus* from the calculations.

***clones omitted in modified average.

Summary

Evidence from the vegetational analysis of the clones sampled indicates that R. copallina is able to successfully invade climax prairie by vegetative means. These invasions are in many instances characterized by a reduction in the density of the prairie vegetation and a concomitant increase in seedlings, shrubs, and to a minor extent, herbaceous vegetation which comprises the surrounding hardwood forests. In most instances bottomland forests appear to be unable to effectively invade climax prairie without the prior invasion of shrubs. On the other hand, Q. stellata, Q. marilandica, and J. virginiana, are able to invade climax prairie in the absence of shrubs, but these invasions are enhanced when R. copallina and other shrubs acted as initial invaders. Field observations indicate that the successful establishment of hardwood seedlings is generally restircted to older and larger clones with moderate to high densities. Poorly formed or underdeveloped clones generally show little reduction in prairie vegetation and little or no hardwood seedling establishment. Field observations indicate that clones which form in open prairie are most susceptible to fire damage so that the chance of successful hardwood establishment is reduced. Hardwood establishment in clones appears to be most successful along forest ecotones.

CHAPTER IV

MECHANISMS OF REINVASION

Methods of Study

Field and laboratory experiments were initiated to investigate the factors which result in the partial or almost total exclusion of many prairie species from _R. copallina_ clones. Three factors were selected for study which were thought likely to be of major significance in producing this phenomenon. These factors were; a reduction in light intensity, an increase in water stress, and the production of chemical inhibitors by _R. copallina_.

The literature is replete with works stressing the importance of light intensity in regulating species occurrence and abundance. Most prairie species thrive in direct sunlight so that a substantial reduction in light intensity could be limiting to them. Seedlings are particularly susceptible since overhanging foliage of herbs may further reduce light intensities.

Rhus copallina produces a shallow root and rhizome system which might act to deplete surface soil moisture and to increase water-stress to a critical point for many herbaceous species. _R. copallina_ is drought-tolerant (sensu lato) and can readily withstand water-stress in soils which might preclude the establishment of some prairie plants. Although many prairie grasses and forbs are deep-rooting and may be tolerant of such stress, seedlings of these plants could be susceptible to water-stress, particularly in late summer when precipitation is generally scant.

Tannins are a group of rather poorly identified, organic compounds which are produced in copious amounts by the leaves and flowers of R. copallina and are readily leached from the plant into the soil (Sargent 1926, Sievers and Clark 1944, Clark and Rogers 1949). Clark and Rogers (1949) have found tannin content in leaves of R. copallina to compose as much as 36.6% of the dry weight leaf biomass. Both tannic and gallic acids have been found under stands of R. copallina in sufficient concentrations to cause inhibition of nodulation and hemoglobin formation in the nodules of bean plants (Blum and Rice 1967), however, the inhibition of vascular plants by R. copallina has not been explored.

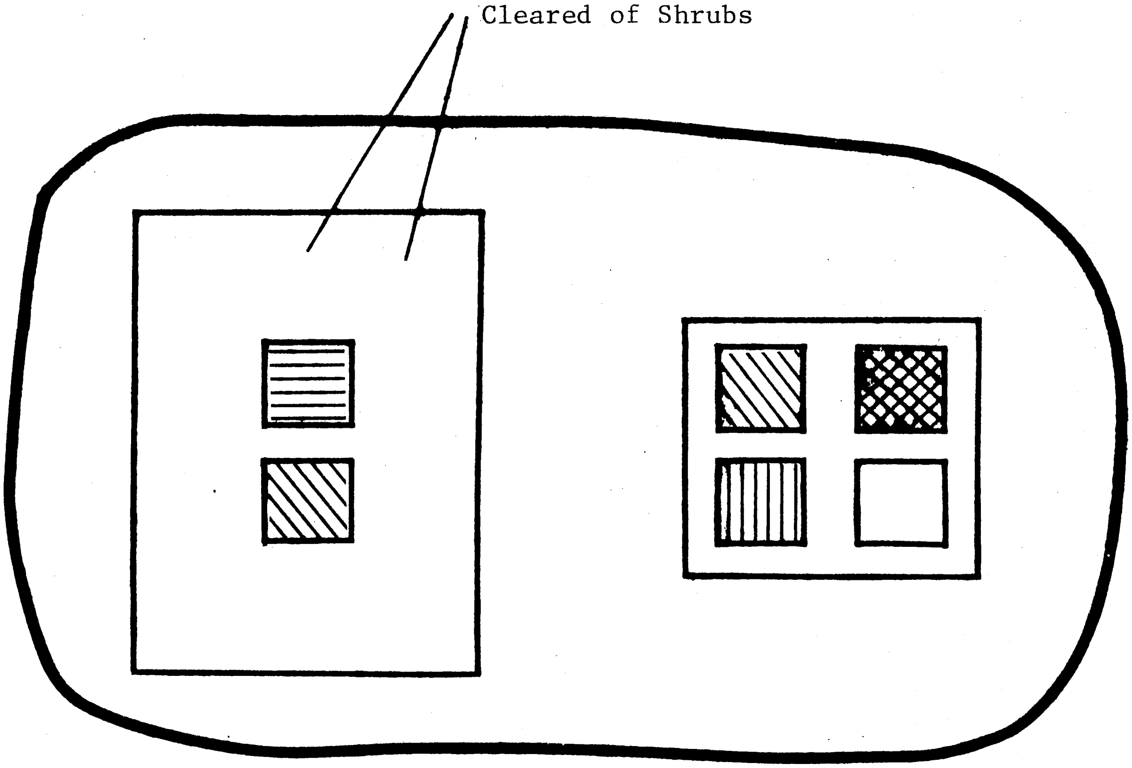
A final factor which is often important in limiting the occurrence of species is soil fertility. Macronutrient analysis of soils collected from the top 5 cm of soil of 8 different clones and in adjacent prairie showed that soils inside of stands of R. copallina contained slightly higher amounts of nitrogen, almost twice the amount of phosphorus, and approximately 25% more potassium than the surrounding vegetation while the pH was almost identical. Other factors which were considered, but after careful field observation are thought not to be significant, include grazing, litter accumulation, and the influence of rodents.

Eight clones of R. copallina were selected for experimentation. Seven of these clones were located in areas adjacent to Lake Carl Blackwell while the remaining clone was located on the Ecology Preserve.

All of these sites have been used for pasture or hay in the past, but at present no cattle are being grazed. Mowing for hay is still practiced at several of the sites but the areas adjacent to clones have not been mowed and remain relatively undisturbed. All of the selected sites are composed of climax or early climax vegetation as described by Booth (1941).

Clark and Rogers (1949) have shown that tannin production in R. copallina is decreased by shading and is inversely related to the height of the plant. In order to reduce these variables, 4 clones which were growing in full sunlight were selected for each of two height classes. Class I clones contained stems averaging 1.8 m or less in height, while Class II clones contained stems averaging 2.3 m or more in height.

In each clone 6 one m^2 plots were established and 4 different treatments were applied (Figure 2). In plots which received treatment I soil moisture was monitored by thermocouple psychrometers placed in the soil at a depth of 5 cm and water was applied to these plots when soil moisture stress became evident. In plots which received treatment II, the inhibitory effects of tannins were alleviated by cutting the stems of R. copallina at ground level and applying the systemic herbicide, 2,4,5-T, to the freshly cut stumps in order to assure root kill. Rhizomes passing outside of these plots were severed to prevent translocation of the herbicide to adjacent individuals. A frame was then erected over each plot and layers of window screen were lain on the frame until the light intensity of the plot approximated that of the control. In plots which received treatment III the exact procedure for treatment II was used, but the shade frame was not erected. All shrubs



▤ Shrubs removed, 2,4,5-T applied to the stumps, Leachate applied.

▧ Shrubs removed and 2,4,5-T applied to the stumps.

▦ Water applied in times of stress.

▥ Shrubs removed, 2,4,5-T applied to the stumps, and artificial shade applied.

□ Control

Figure 2. Diagram of Treatments Applied to one m^2 Plots of Eight Study Clones

within 2 meters of these plots were cleared to prevent any shading of the plots by the surrounding vegetation. Treatment IV was similar to treatment III, but in addition, a leachate was applied after soaking leaves and stems from the clone for 3 hours in the equivalent of 1.2 cm of rainfall. The amount of foliage soaked was derived by counting the number of growing tips found in a 10 m^2 area of the clone. The average number of stem tips per m^2 was then harvested each period following a rain and the leachate prepared and applied to the plots. A final plot was unmodified and served as a control. Figure 2 illustrates the distribution and treatment of plots for each clone. The number of seedlings which appeared in each plot were counted at 6-week intervals from April 1976 - January 1977.

Laboratory tests were also initiated to investigate the potential inhibitory effects of _R_. _copallina_ on seeds and seedlings of climax prairie species and on several weedy test species.

Results

Throughout the summer growing season seed germination in the experimental plots was extremely low so that field bioassays to determine the significance of shading and water stress proved futile. Even plots which were manipulated to alleviate the effects of toxins and in which ample amounts of sunlight and water were applied showed practically no response. The reasons for this lack of response remain unclear, however, indirect evidence suggests that an unusually prolonged breakdown time of soil toxins produced by _R_. _copallina_ may have greatly retarded seed germination.

Toxins which are produced by other allelopathic species of higher plants are usually biodegraded rather rapidly by soil microorganisms upon entering the soil. One of the assumptions when the plots were established was that toxins produced by *R. copallina* from the previous growing season would decompose either before or shortly after the onset of the next growing season. Laboratory bioassays of leachates prepared from leaf litter of *R. copallina* collected at intervals throughout the winter months through January 28 significantly inhibited the growth and germination of most test species. Blum and Rice (1969) have detected tannic acids in soils under clones of *R. copallina* during the growing season as deep as 70 cm and found a definite zone of accumulation at the 45-55 cm level. Since the rhizome and root system of *R. copallina* lies so close to the surface of the soil it is doubtful that exudates from roots would be substantial at these depths. Apparently these toxins have leached down from the surface, a process which would require considerable time and imply a very long breakdown period. If soil toxins were released from leaf litter into the soil and retained in a toxic form for the first few months of the growing season, little seedling response would be expected.

Secondly, weather conditions prior to and during the spring germination period were generally suboptimal. Rainfall for the first 6 months of the year was only 64% of the average for this period. This decrease in precipitation along with the reduced humidities and increased temperatures may have retarded seed germination to some extent.

Thirdly, the rather high density of prairie vegetation in the younger (class I) clones may have precluded the establishment of many seedlings. All four of the control plots in these clones showed less than a 20% reduction in cover of prairie vegetation. However, the older clones (class II) generally showed much higher reductions in cover so that substantial areas of bare soil were present in most of these plots.

A final possibility is that seeds of prairie species simply were not present in the plots. However, this seems unlikely since an abundant seed source was available for dispersal both in the adjacent prairie and from plants found within the clones.

Seedling response increased dramatically in December due to the germination of several winter annuals, but occurred at a time when neither light or soil moisture were limiting. The data from winter seedling response did illustrate significant inhibition of germination of seeds by _R_. _copallina_. Evidence of the significance of all three factors from laboratory tests, measurements, and the literature are presented in the next chapter.

CHAPTER V

ENVIRONMENTAL FACTORS OF SIGNIFICANCE

Laboratory Evidence of Allelopathy

Methods and Materials

Laboratory bioassays for toxin production by the rhizomes, leaves, seeds, flowers, and leaf litter of R. copallina were run at various times throughout the study period. Seeds of the test species were placed in 100 x 15 mm petri dishes containing 70 g of washed and dried commercial sand which had previously been sifted through a No. 10 (2.00 mm) U.S. Standard Sieve to remove any bulky particles. Seeds of Panicum virgatum were germinated between two pieces of filter paper rather than in sand. Each dish was then irrigated with either 10 ml of distilled water (control) or with 10 ml of leachate prepared by soaking the test material in distilled water for approximately 3 hours.

The amount of leaf, litter, and root material to be leached were determined from actual measurements of biomass/m^2 present in selected clones, while the amount of water these were leached in was equivalent to .63 cm (¼ in) of rainfall. Leachates of seeds and flowers were prepared in an arbitrary 10 ml water/1 g plant material ratio. After watering, each dish was sealed with plastic wrap to retard water loss and placed under a photobank set for 12 hours of light per day and incubated at $25^\circ \pm 1.5^\circ$ C. After allowing sufficient time for germination and early growth, the radicle length of each seedling and the percent germination of the test species were recorded. Appendices A and B list the test species and all pertinent information concerning the germination procedures used for these experiments.

Results

Green Foliage

Freshly cut foliage of R. copallina which is submerged and agitated in distilled water for only a few seconds will produce a light tea-colored solution. This very rapid discoloration of the water suggests that tannins may be secreted onto the surface of the leaves during the growing season, since any substantial leaching of tannins from within the leaves would probably require considerably more time. Leachate prepared from this foliage caused no significant reduction ($p = .05$) in either the percent germination or the rate of seedling growth from that of the control (Table V). It is quite probable that the tannins which leach from the leaves during the growing season are biodegraded to form toxic substances by soil organisms. Tannins in general are easily hydrolysed by enzymatic degradation to form sugars and phenol carboxylic acids (Haslam 1966). The various tannins in Rhus generally form gallic and tannic acids upon hydrolysis. Both of these compounds have been reported to inhibit nitrification in legumes (Rice 1965) and have been implicated as inhibitors of higher plants (Varga and Koves 1959). In addition, Blum and Rice (1969) have found substantial concentrations of tannic and gallic acids under clones of R. copallina throughout the growing season. All of these facts

TABLE V

THE EFFECTS OF LEACHATE FROM LIVING FOLIAGE OF *RHUS COPALLINA* ON THE PERCENT GERMINATION AND RADICLE GROWTH OF EIGHT TEST SPECIES

Test Species	N of Control	Germination (% of Control)	Radicle Length (% of Control)
Andropogon scoparius	47	85	98
Sorghastrum nutans	55	93	99
Psoralea tenuiflora	18	144	125
Lespedeza capitata	48	100	103
Achillea lanulosa	23	126	113
Plantago purshii	54	152	107
Bromus japonicus	36	111	86
Haplopappus ciliatus	56	79	97

suggest that biodegradation of tannins occur after tannins enter the soil.

Test of Leaves at Various Stages of Ecdysis

Beginning in mid-July the lower canopy leaves of many clones of *R. copallina* begin to yellow and soon drop to the ground. This process continues throughout the summer until the major leaf-fall occurs with the onset of colder weather and results in a slow accumulation of litter during this period. A leachate (49 ml H_2O/1 g leaves) prepared from recently yellowed leaves which were collected from a 1 m^2 area of foliage inhibited the growth or germination of *Andropogon scoparius* and *Psoralea tenuifolia* while the remaining 4 test species were unaffected (Table VI). This experiment was repeated 21 September at a time when many clones were undergoing autumnal leaf-fall. Leaves which had just recently begun to change colors, as well as leaves which were very close to abscission were collected from a 1 m^2 frame placed over the foliage and separately bioassayed for toxin production (Tables VII and VIII). Leachate prepared from leaves collected 21 September which had only recently changed colors significantly inhibited the germination or radicle growth of 3 of the 9 test species, *A. scoparius*, *P. purshii*, and *B. japonicus*. These results are very similar to those obtained for recently yellowed leaves collected on 29 July. Leachate prepared from leaves collected just prior to abscission significantly inhibited the germination or radicle growth of all but one of seven test species. Climax and weedy species were affected about equally.

These test results indicate that leaves become increasingly toxic prior to abscission. The source of these toxins has not been

TABLE VI

THE EFFECTS OF LEACHATE FROM RECENTLY YELLOWED LEAVES OF <u>RHUS COPALLINA</u> COLLECTED JULY 29 ON THE GERMINATION AND RADICLE GROWTH OF SIX TEST SPECIES

Test Species	N of Control	Germination (% of Control)	Radicle Length (% of Control)
<u>Andropogon scoparius</u>	175	93	84**
<u>Psoralea tenuiflora</u>	20	60**	57**
<u>Lespedeza capitata</u>	36	105	91
<u>Achillea lanulosa</u>	42	100	92
<u>Bromus japonicus</u>	76	104	96
<u>Plantago purshii</u>	37	102	92

**Significant at $p < .01$

TABLE VII

THE EFFECTS OF LEACHATE FROM LEAVES COLLECTED SEPTEMBER 21 SHORTLY AFTER AUTUMNAL COLOR CHANGE ON THE GERMINATION AND RADICLE GROWTH OF NINE TEST SPECIES

Test Species	N of Control	Germination (% of Control)	Radicle Length (% of Control)
Andropogon scoparius	105	83**	81**
Panicum virgatum	59	96	90
Desmodium sessilifolium	20	125	97
Lespedeza capitata	50	106	94
Lespedeza striata	36	86	117
Achillea lanulosa	53	87	96
Plantago purshii	49	112	70**
Bromus japonicus	50	110	84*
Haplopappus ciliatus	39	112	112

*Significant at $p < .05$
**Significant at $p < .01$

TABLE VIII

THE EFFECT OF LEACHATE FROM LEAVES COLLECTED SEPTEMBER 21 JUST PRIOR TO ABSCISSION OF THE GERMINATION AND RADICLE GROWTH ON SEVEN TEST SPECIES

Test Species	N of Control	Germination (% of Control)	Radicle Length (% of Control)
Andropogon scoparius	101	104	75**
Bouteloua curtipendula	47	53**	80**
Lespedeza capitata	46	93	199
Lespedeza striata	68	75**	158
Achillea lanulosa	73	89	65**
Plantago purshii	56	102	58**
Bromus japonicus	40	118	27**
Haplopappus ciliatus	46	59**	80**

**Significant at $p < .01$

determined but most logically they accumulate for one of two reasons. Tannins are generally stored by plants in vacuoles or vesicles and are isolated from oxidizing enzymes present in the cell sap (Swain 1965). The release of tannins into the cell sap through membrane degradation and the subsequent enzymatic oxidation of these compounds to form gallic and tannic acids prior to leaf abscission seems probable. Alternatively, the leaves might act as a sink for toxins produced in other areas of the plant (e.g. the rhizomes) prior to leaf-fall.

Tests of Leaf Litter

Leaf litter of R. copallina undergoes relatively slow decomposition throughout the winter months. Leaf litter was collected from underneath clones on 5 September, 17 December, and 28 January for bioassaying. Nine test species were used for the bioassays of litter collected on 5 September, while 3 test species were used for litter collected on 17 December and 28 January. Leachate prepared from leaf litter collected 5 September was very inhibitory to the germination or radicle growth of almost all test species (Table IX). Leachates prepared from litter collected on 17 December and 28 January produced significant inhibition of all three test species (Figure 3). Leaf litter showed a peak toxicity at the time of deposition in the fall and a subsequent decrease in toxicity as the winter progressed. This is most logically due to the leaching of tannins from the leaves during periods of rainfall or snowmelt. In any case, leaf litter contained significant concentration of toxins well into the winter months.

The release of toxins from nearly abscised leaves during the end of the summer growing season probably has very little immediate effect

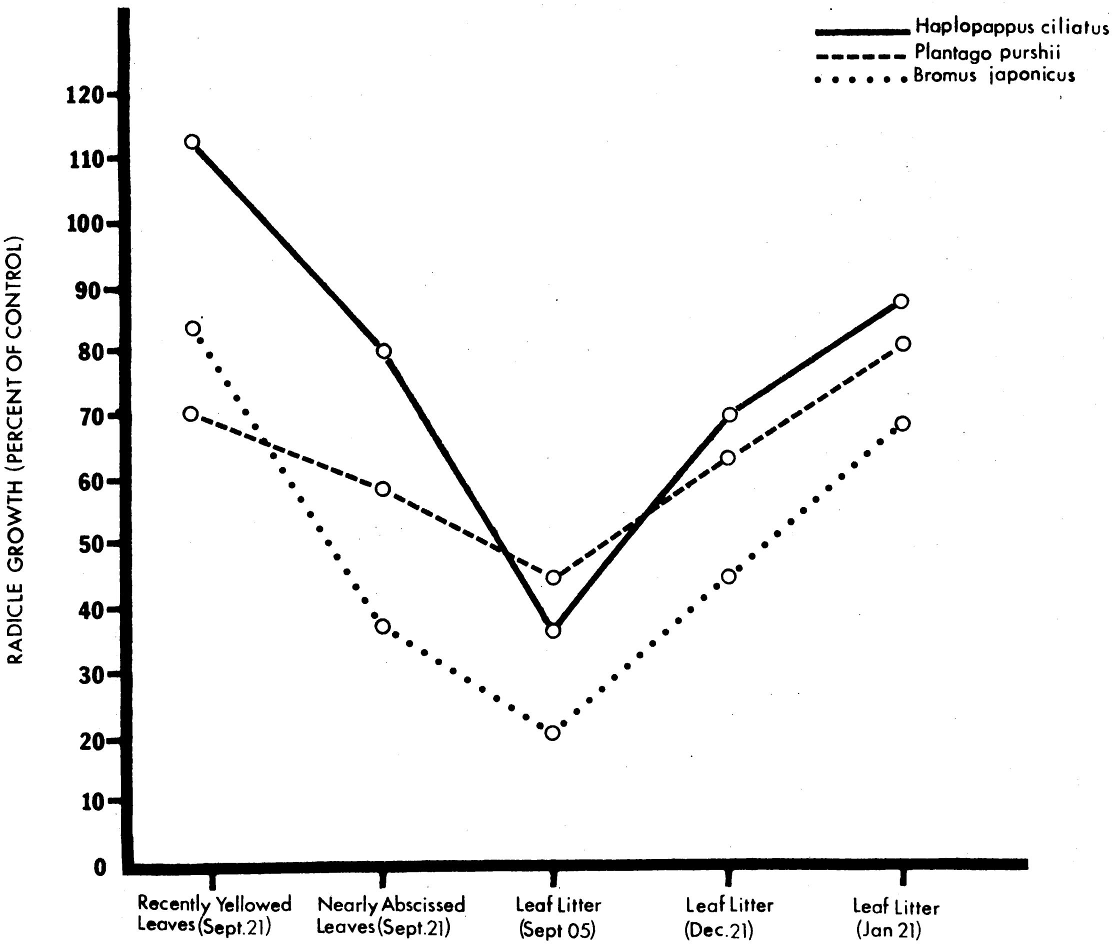


Figure 3. Chemical Inhibition of the Growth of Radicles of Three Test Species During Various Stages of Leaf Senescence and Decay

TABLE IX

THE EFFECTS OF LEACHATE FROM LEAF LITTER COLLECTED SEPTEMBER 5 ON THE GERMINATION AND RADICLE GROWTH OF TEN TEST SPECIES

Test Species	N of Control	Germination (% of Control)	Radicle Length (% of Control)
Andropogon scoparius	106	83**	75**
Panicum virgatum	53	102	82**
Sorghastrum nutans	59	100	110
Desmodium sessilifolium	24	54**	191
Lespedeza capitata	54	94	105
Lespedeza striata	33	58**	109
Achillea lanulosa	57	68**	70**
Plantago purshii	54	102	45**
Bromus japonicus	59	83**	21**
Haplopappus ciliatus	38	71**	36**

**Significant at $p < .01$

on most prairie species. Seed germination in these species generally occurs at the beginning of the growing season and tapers off as summer approaches and germination conditions become less favorable. By late summer soil moisture levels often become critical for plant growth to depths of 25-30 cm (Weaver 1968). Seedlings of prairie plants must therefore become established early in the growing season in order to develop a root system which is deep enough to insure the survival of the plant. The cumulative increase of toxins in the soil which is released from leaf litter during the winter months may serve as an effective inhibitor of seed germination or as a growth retardant of seedlings during the spring germination period.

Test of Rhizomes

Rhizomes collected 31 July from a 1 m^2 area of a clone were bioassayed for toxin production. A leachate was prepared by soaking rhizomes which had been cut into approximately 5 cm segments in distilled water for 24 hrs. (6:1 ratio). The leachate significantly inhibited the germination or radicle growth of five of the nine test species (Table X). Both climax and weedy species appeared to be equally inhibited. This experiment was repeated with rhizomes whose cut ends had been sealed with paraffin wax. *P. purshii*, *B. japonicus*, and *Haplopappus ciliatus* were used as test species. All three species were significantly inhibited by the leachate. There was no significant difference between the degree of inhibition of cut rhizomes and those that were sealed with paraffin which demonstrates that the toxins are able to move into the external environment surrounding the root under natural conditions.

TABLE X

THE EFFECTS OF LEACHATE FROM CUT RHIZOMES OF *RHUS COPALLINA* ON THE GERMINATION AND RADICLE GROWTH OF TEN TEST SPECIES

Test Species	N of Control	Germination (% of Control)	Radicle Length (% of Control)
Andropogon scoparius	163	107	75**
Panicum virgatum	54	96	87
Sorghastrum nutans	57	93	65**
Bouteloua curtipendula	29	83	70**
Psoralea tenuiflora	27	93	102
Lespedeza capitata	25	132	143
Achillea lanulosa	98	97	91
Haplopappus ciliatus	24	83	73**
Bromus japonicus	92	100	68**
Plantago purshii	39	107	73**

**Significant at $p < .01$

Flower Heads

Rhus copallina is polygamo-dioecious and produces rather bulky panicles. Each panicle is composed of hundreds of flowers which are shed simultaneously within a week or two after anthesis, in early to mid-July, so that the ground underneath a clone is blanketed with dead flowers. Leachate prepared from terminal thyrses significantly inhibited either the germination or radicle growth of all seven test species (Table XI). The weedy species tested showed particularly strong inhibition. Seed germination in *B. japonicus* was completely inhibited, while germination in *Achillea lanulosa* was reduced to 19% of the control. Radicle growth in *P. purshii* was reduced to 17% of control. Germination in climax prairie species was not significantly inhibited but a significant reduction in radicle growth occurred for all prairie species.

Fruits

Fruits of *R. copallina* generally turn a bright red color upon maturation and are very astringent to the taste. Leachate prepared from fruits produced inhibition similar to that for flowers (Table XII). Radicle growth in all test species was significantly reduced while germination was reduced only in weed species.

Field Evidence of Allelopathy

Seedling density increased dramatically during the winter months as several species of winter annuals made their appearance in the plots. Table XIII presents data on the number of seedlings found in

TABLE XI

THE EFFECTS OF LEACHATE FROM FLOWERS OF <u>RHUS COPALLINA</u> ON THE GERMINATION AND RADICLE GROWTH OF EIGHT TEST SPECIES

Test Species	N of Control	Germination (% of Control)	Racicle Length (% of Control)
Andropogon scoparius	37	151	62**
Panicum virgatum	56	88	48**
Bouteloua curtipendula	32	93	67**
Sorghastrum nutans	42	138	59**
Achillea lanulosa	32	19**	53**
Bromus japonicus	53	0**	--
Plantago purshii	66	92	17**
Haplopappus ciliatus	32	53**	49**

**Significant at $p < .01$

TABLE XII

THE EFFECTS OF LEACHATE FROM FRUITS OF *RHUS COPALLINA* ON THE GERMINATION AND RADICLE GROWTH OF EIGHT TEST SPECIES

Test Species	N of Control	Germination (% of Control)	Radicle Length (% of Control)
Andropogon scoparius	51	92	52**
Panicum virgatum	47	94	52**
Bouteloua curtipendula	27	95	48**
Sorghastrum nutans	57	100	28**
Achillea lanulosa	54	52**	50**
Haplopappus ciliatus	39	59**	28**
Bromus japonicus	39	49**	27**
Plantago purshii	51	89	68**

**Significant at $p < 0.1$

TABLE XIII

SEEDLING ABUNDANCE IN CONTROL AND TREATED PLOTS OF SEVEN EXPERIMENTAL CLONES OF RHUS COPALLINA

Clones***	Height Class	December 18		February 18		Total	
		Control	Treated*	Control	Treated*	Control	Treated*
1	>2.3m	9	2	0	0	155	23**
2	>2.3m	97	18	13	3		
3	>2.3m	0	0	0	0		
4	>2.3m	35	0	1	0		
5	<1.8m	3	0	0	0	12	2**
6	<1.8m	3	0	0	0		
7	<1.8m	6	2	0	0		

**Significant at $p < .01$

*Treated with leachate transferred to the plots

***Clone 8 destroyed by fire.

adjacent plots which were sampled 18 December and 18 February. Treated plots differed from control plots only in that leachate was applied throughout the growing season and leaf litter collected from a 1 m^2 area of the clone was transferred to the treated plot after autumnal leaf-drop.

Results

The data indicates very strong inhibition by *R. copallina* under field conditions. The treated plots contained only 14.35% of the number of seedlings found in the control plots. Over 90% of the seedlings occurred in the older clones where the percent cover of prairie vegetation was lowest and the amount of bare space was highest. The amount of inhibition exhibited in the plots was substantially greater than that obtained in the laboratory for other test species which suggests that toxins accumulate and increase in concentration in the soil following repeated leaching from the plant.

Summary

Laboratory tests reveal that the rhizomes, flowers, fruits, nearly abscissed leaves, and leaf litter of *R. copallina* produce toxins which significantly inhibit either seed germination or seedling growth in both climax prairie and weedy test species. Inhibition of radicle growth occurred in all taxa and ecological groups of test species except the Leguminosae. The radicle growth of most legumes either showed little inhibition or was stimulated. However, seed germination of several climax prairie legumes was significantly reduced. Sampling of vegetation composition of clones indicated a disproportionate reduction in the number of legumes found within clones of _R_. _copallina_. The inhibition of nodule formation by _R_. _copallina_ (Blum and Rice 1969) may be the most important factor in excluding many legumes from these clones.

Inhibition of seed germination was greatest among weedy species, but was not limited to these. Many of the climax prairie species were inhibited by one or more of the leachates prepared from various test materials.

Leachate from green foliage was not inhibitory to any of the test species, but the large amounts of tannins which can be readily leached from the foliage into the soil are, in all probability, biodegraded to form toxic decomposition products, particularly gallic and tannic acids. During the spring growing season, when seeds of most climax species germinate, the rhizomes, green foliage, and leaf litter may all contribute toxins or potentially toxic substances to the soil. Finally, the experimental manipulation of field plots has demonstrated the effectiveness of these toxins in inhibiting species under simulated natural conditions.

Light

Because of the very poor seedling response in the experimental plots during the growing season, little direct evidence was gained concerning the effects of shade produced by _R_. _copallina_ on the growth and reproduction of the surrounding climax prairie vegetation. However, measurements of light intensities in the eight clones under study together with reported shade tolerances of heliophytes in the literature offered substantial indirect evidence of the importance of this factor.

Light reduction by vegetation is generally not ecologically significant, even for heliophytes, until it is reduced by approximately 80% (Daubenmire 1974). Bohning and Burnside (1956) found the light compensation point for eight sun species to range from 100-150 ft-candles, while light saturation occurred at 2000-2500 ft. candles (76-80% reduction).

Measurements of light intensities were taken in all control plots of the eight study clones during mid-June soon after the clones had fully leafed-out. In each control plot 20 light readings were taken at predetermined points between the canopy and understory with a Model 756 Weston Illumination Meter. Measurements were taken on 10 June between 1200 and 1400 hrs when skies were clear and cloudless. In addition, estimates were made of the percent reduction in coverage of prairie vegetation in the control plots when compared to two plots in adjacent tall grass prairie (Table XIV).

Results

The reduction of light intensities in the control plots of clones > 2.3 m was greater than 90% in all four instances. These light intensities are less than that required for saturation but are higher than the compensation points reported for heliophytes by Bohning and Burnside (1956) and would result in very little or no growth in most climax prairie species. It is also very unlikely that seedlings of climax prairie species would be able to become successfully established under such low light intensities. The reduction in the percent

TABLE XIV

PERCENT REDUCTION IN LIGHT INTENSITIES AND COVERAGE OF PRAIRIE VEGETATION IN CONTROL PLOTS OF EIGHT STUDY CLONES

Clone Number	Height Class	% Light Reduction	Estimated % Reduction in Plant Cover*
1	>2.3m	91	30-40
2	>2.3m	90	60-70
3	>2.3m	97	90-100
4	>2.3m	92	70-80
5	<1.8m	81	20-30
6	<1.8m	57	10-20
7	<1.8m	65	10-20
8	<1.8m	74	10-20

*Coverage of prairie vegetation in plots as compared to plots established in adjacent tall grass prairie.

coverage of prairie vegetation was substantial in all plots and varied from an estimated 30-40% to 90-100% (avg. ~ 60-70%). The percent light reduction in the four younger clones (<1.8 m) was substantially less (avg. = 69%) and were above the light saturation point of most plants. In all but one clone the percent reduction in coverage of climax prairie vegetation was less than 20%. These younger clones generally form a patchwork or mosaic of various light intensities because of the incomplete canopy cover so that most areas of the clones appear to receive some direct sunlight during the day.

Soil Moisture

In tall grass prairie soil moisture generally reaches critically low levels for plant growth as the growing season progresses through the summer months. Weaver (1968) reported that critical water stress commonly develops to depths of 30 cm or more during July and August. It becomes apparent, therefore, that successful seedling establishment would require germination in early spring followed by rapid growth and development of a root system to a depth below the zone of critical water stress. Most prairie species have adapted such a mechanism and germinate at or soon after the onset of the growing season.

Earlier workers have shown that soil moisture conditions usually improve substantially as shrubs invade climax prairie. Weaver and Thiel (1917), Pool, Weaver, and Jean (1918), and Aikman (1927) demonstrated that the understory of shrubs generally have higher relative humidities, lower air and soil moistures, decreased evaporation and increased soil moisture so that conditions are much more favorable for seedling establishment. Critical water stress was still found to develop in shrub thickets, but to a lesser degree and at less frequent intervals. From this evidence it seems apparent that water stress alone would not limit the occurrence of prairie species under clones of R. copallina. However, if other factors reduce the rate of seedling growth, then roots may not penetrate deep enough to insure the survival of seedlings.

Both allelopathy and the effects of reduced light intensities may interact with soil moisture stress to exclude species from clones of R. copallina. When light levels are reduced below the saturation point of a plant, growth is reduced, and approaches zero as the compensation point is reached. Many of the light measurements from clones fell somewhere below the light saturation points reported for typical heliophytes so that a reduction in growth is very likely. Laboratory tests have also demonstrated that toxins produced by R. copallina retard the radicle growth of most climax prairie species. Although factor interaction in this manner seems implicit, the lack of seedling response in the experimental plots presented little evidence to demonstrate this phenomenon.

CHAPTER VI

DISCUSSION AND CONCLUSIONS

In the cross-timbers region of north-central Oklahoma _R_. _copallina_ often occupies ecotonal areas between hardwood forests and tall grass prairies. Clones frequently become established at forest edges and spread by the production of off-shoots from shallow rhizomes into adjacent prairie. Clones may also become established directly in climax prairie, presumably following local soil disturbances. Other workers have noted similar shrub zones between bottomland forests and prairies in Kansas and Nebraska (Aikman 1927, Fitch and McGregor 1956).

The invasion of R. copallina into climax prairie is characterized by a reduction in the density of prairie vegetation and a concomitant increase in tree seedlings, shrubs, and to a minor extent, herbs which comprise the surrounding hardwood forests. Several mechanisms are envolved in the successful invasion and replacement of an established climax prairie community by clones of _R_. _copallina_. Laboratory tests have demonstrated that the rhizomes, flowers, fruits, nearly abscissed leaves, and leaf litter of _R_. _copallina_ produce toxins which significantly inhibit either the seed germination or seedling growth in both climax prairie and weedy test species. Inhibition of radicle growth occurred in all taxonomic and ecological groups of test species with the exception of the Leguminosae, which generally showed little inhibition. Inhibition of seed germination was greatest among weedy species, but was by no means limited to these. The effectiveness of these inhibitors in the field was demonstrated by the seedling response in experimentally manipulated study plots.

Light intensities were found to reach critically low levels for growth in the control plots of the four older study clones (>2.3 m), but were above the light saturation point reported for heliophytes (Bohning and Burnside 1956, Daubenmire 1974) in the control plots of the four younger clones. The percent reduction in coverage of prairie vegetation at the centers of clones was rather high (avg. ~ 60-70%), while only a slight reduction occurred in the four younger clones (avg = <20%).

It is reasonable to assume that factor interactions occur between light or chemical inhibitors and soil moisture stress during the summer growing season as critical soil moisture levels are reached. A reduction in light intensities below the light saturation point as well as chemical inhibition would act to reduce the rate of root growth and increase the susceptibility of seedlings to stressful soil moisture conditions. Poor seedling response in the experimental plots throughout the growing season offered little evidence of the extent to which these interactions occur.

In most instances, bottomland forests appeared to be unable to effectively invade climax prairie without the prior invasion of *R. copallina* or other shrubs. Contrarily, most upland forest species were able to successfully invade climax prairie, but the invasion was enhanced by the prior invasion of shrubs. Field observations indicate that the successful establishment of hardwood seedlings is generally restricted to well formed clones with moderate to high stem densities.

Poorly formed or under-developed clones generally showed only a slight reduction in prairie vegetation and little or no hardwood establishment.

Weaver and Thiel (1917), Pool, Weaver, and Jean (1918), and Aikman (1927) demonstrated a general improvement in moisture conditions as shrubs of various species replace climax prairie. In addition, competition is alleviated within clones of *R. copallina* as climax prairie species are slowly eliminated. Both of these changes serve to improve the conditions for germination and establishment of hardwood species.

The aging of nine clones by ring counts indicated an average rate of encroachment of 1.25 m/year. Although frequently occurring fires generally act to halt the reinvasion of woody species, the reduced fire frequency (18-20 years) on the study sites tends to stimulate the invasion of *R. copallina*. Clones whose stems were destroyed by fire exhibited accelerated vertical and horizontal growth and generally appear to have greater vigor than unburned clones.

In conclusion, *Rhus copallina* appears to play a very important functional role in the dynamics of the forest-prairie ecotone in north-central Oklahoma.

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APPENDIX A

LEACHATE RATIOS (ML DISTILLED WATER/G DRY WT) FOR VARIOUS TEST MATERIALS

Test Material	Ratio (gm dry wt/ml distilled water)
Cut Rhizomes	6:1
Whole Rhizomes	6:1
Seed Heads	10:1
Male Flower Heads	10:1
Fresh Green Leaves	20:1
Freshly Yellowed Leaves (Summer)	48:1
Freshly Yellowed Leaves (Autumn)	33:1
Leaf Litter	33:1

APPENDIX B

GERMINATION REQUIREMENTS OF BIOASSAY SPECIES

Test Species	Minimum Test Length (Days)	Germination Requirements
Achillea lanulosa	5	1,3
Andropogon scoparius	7	1,3,5
Bromus japonicus	5	1,3,6
Bouteloua curtipendula	5	1,3,4
Cassia fasciculata	5	1,3,4
Desmodium sessilifolium	5	1,3,4
Haplopappus ciliatus	5	1,3
Lespedeza capitata	5	1,3,4
Lespedeza striata	5	1,3,4
Panicum virgatum	7	2,3,5
Plantago purshii	5	1,3
Psoralea tenuiflora	5	1,3,4
Sorgastrum nutans	7	1,3,5

1. Seeds germinated on sand
2. Seeds germinated on filter paper
3. Seeds germinated under photobank
4. Seeds scarified before treatment
5. Seeds cold stratified at 4°C for two weeks
6. Seeds cold stratified at 4°C for 17 hours

VITA

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Candidate for the Degree of

Master of Science

Thesis: A STUDY OF THE ROLE OF RHUS COPALLINA IN THE COMMUNITY DYNAMICS OF THE FOREST-PRAIRIE ECOTONE IN NORTH-CENTRAL OKLAHOMA

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