# ALLELOPATHIC INHIBITION OF WEED INVASION BY *ANDROPOGON SCOPARIUS* MICHX. IN CLIMAX PRAIRIES

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# CHAPTER I

## INTRODUCTION

In the study of plant community dynamics, a climax vegetational state is attained when the longest lived species continually replace themselves *in situ*. At this point the community is in dynamic equilibrium with the abiotic and biotic environment. When this climax vegetation is damaged or destroyed, secondary succession is initiated. In central Oklahoma grasslands secondary succession is divided into four phases: (1) weedy invaders; (2) annual grasses; (3) perennial bunch grasses; and (4) climax prairie (Booth 1941). Each phase is defined by the species which are present. *Andropogon scoparius* becomes predominant during the bunch grass phase and is also considered one of the four dominant species of the climax prairie. Once climax has been reached and the prairie remains undisturbed this closed community remains free of invasion by weedy species (Weaver and Hansen 1941; Weaver and Rowland 1952; Weaver 1968). The maintenance of this closed community has been attributed to interactions between environmental factors, both biotic and abiotic; including moisture, soil, temperature, and competition (Vogl 1964; Weaver 1968; Costello 1969; Sears 1969; Vesey-Fitz Gerald 1970). With the occurrence of localized or wide scale disturbances these closed communities are invaded by distinct weedy species; species which are considered by many workers to be indicators of disturbance (Clements and Shelford 1939; Weaver and Hansen 1941; Kelting 1954;

Ellison 1960; Petty and Jackson 1966; Weaver 1968).

Several reasons have been proposed to explain the resistance of undisturbed prairies to invading weedy species. Interspecific competition for light, water, or nutrients has been the most commonly accepted idea. Frequently weedy invaders are annual species (Weaver and Hansen 1941). However not all are restricted to the annual habit. Ecologically, a weed possesses several important characteristics: (1) ability to germinate in a wide variety of habitats; (2) great seed longevity and discontinuous germination; (3) rapid growth; (4) high and continuous seed production throughout the growing period under favorable habitat conditions; (5) high tolerance and plasticity; (6) possession of mechanisms for easy dispersability; e.g., a pappus; and (7) special adaptations for interspecific competition; e.g., rosette, allelochemics, $C_4$ photosynthesis (Black, Chen, and Brown 1969; Baker 1974). Additionally, if the weedy species is perennial it will possess vigorous vegetative reproduction and a "brittleness" characteristic to resist being totally withdrawn from the soil (Baker 1974). Weeds which invade perennial grasslands used for grazing or regular mowing (hay meadows) have a tendency to be more successful if they are rhizomatous or stoloniferous, even at the expense of becoming seed sterile (Bradshaw 1958). There are many excellent examples of ecological weedy invaders of perennial grasslands notable of which is the common dandelion, *Taraxacum officinale* (Baker 1974).

With the cessation of disturbance perennial grasslands again become closed communities and weedy invaders are resisted. Many of these perennial grasses have been found to be efficient competitors because of possession of various attributes, e.g., a $C_4$ photosynthetic pathway (Black, Chen, and Brown 1969; Black 1971; Downton 1971). Additionally, the second subdivision of interference, allelopathy, has been demonstrated in numerous studies of both weedy and climax species (Grummer and Beyer 1960; Muller 1966; Wilson and Rice 1968; Del Moral and Muller 1969; McPherson and Muller 1969; Rice 1971; Rice 1971; Whittaker and Feeny 1971; Gliessman and Muller 1972; Tinnin and Muller 1972; Rice 1974). These workers and others have shown that allelopathy can be a potent force influencing the composition of plant communities. Thus either competition or allelopathy, or some combination, could account for the observed resistance to invasion.

Muller (1966) found that _Salvia leucophylla_ shrubs produce several terpene compounds which are toxic to grassland species common in the California annual grasslands. Grassland species were found to grow within 1-2 m of the shrub stand, but were completely absent within the stand. Bioassays showed that the terpene compounds were inhibitory to seed germination and radicle growth. Muller concluded that volatilized terpenes released from the climax _Salvia leucophylla_ shrubs suppressed the establishment of a number of plants forming distinct patterns around mature stands of _S. leucophylla_. McPherson and Muller (1969) demonstrated that the absence of herbaceous species in mature _Adenostoma fasciculatum_ (chamise) stands was due to the release of several water soluble phenolic acids which are toxic to seed germination and radicle growth of some of these herbs. The phytotoxic compounds are released to the leaf surface, washed off with each rainfall and accumulated in the upper layers of the soil. The toxins effectively suppressed germination and growth of selected herbaceous species. These workers further found that herb seeds would germinate and flourish after a fire had destroyed the mature chamise stand. As the chamise stands matured sufficient toxins were released and accumulated in the soil to again suppress germination and growth of the herbaceous species. Studies performed by Muller (1966), McPherson and Muller (1969), and others have demonstrated that climax species can and do suppress the germination and growth of common field associates by allelopathic inhibition. There are, however, no studies involving the allelopathic potential of climax or near-climax dominants in mid-western prairies.

In studies of midwest prairies, numerous workers have noted the presence of thick mulch layers (Dyksterhuis and Schmutz 1947; Weaver and Rowland 1952; Hopkins 1954; Weaver 1968). Worker after worker has shown that this mulch layer possesses attributes which are both beneficial and detrimental. Many workers have suggested that this mulch layer is responsible for retarding weedy invaders and thereby maintaining pure stands of dominant prairie grasses (Weaver and Rowland 1952; Kelting 1954; Betz and Cole 1969). These studies have indicated that the probable mechanism of suppression is one of competition or mechanical effects; however, no specific mechanism of suppression has been advanced.

The presence of herbage and mulch in natural prairies yields several benefits to the soil and to the plants. Mulch favorably affects infiltration and runoff of rain water, soil moisture and soil temperature. One major advantage of a continuous mulch layer is the prevention of soil erosion; even an artificial layer of plant material prevents formation of a compact soil surface layer which enhances surface runoff from bare surfaces (Duley and Kelley 1939). Today, it is generally accepted that living plants are greatly benefitted by a layer of natural mulch which produces maximum rainwater infiltration and minimum soil erosion.

In addition to preventing soil erosion and enhancing water infiltration mulch prevents high soil surface temperatures thereby retarding evaporation (Weaver and Rowland 1952; Hopkins 1954). Furthermore, mulch improves the soil as a habitat for soil organisms (Hopkins 1954). A deep mulch layer, however, may also reduce establishment and retard growth initiation of plants principally by reducing soil temperature (Weaver and Rowland 1952). Ellison (1960) states that mulch affects the microclimate both above and below the soil and consequently influences both the macroorganisms and microorganisms which influence soil formation.

It has also been suggested that the heavy accumulations of mulch, in the absence of perturbations such as grazing, burning, or mowing, tend to: (1) produce pure stands of the dominant prairie grasses (Weaver and Rowland 1952; Kelting 1954); (2) reduce species diversity (Kelting 1954; Penfound 1964); (3) reduce the number of flower stalks (Burton 1944; Curtis and Parch 1950; Tomanek and Albertson 1953; Dix and Butler 1954); (4) greatly retard growth in the spring (Weaver and Fitzpatrick 1934; Weaver and Bruner 1948; Hopkins 1951; Penfound 1964); (5) decrease productivity and/or number of shoots per unit area (Dyksterhuis and Schmutz 1947; Albertson et al. 1957; Penfound 1964; Hulbert 1969); and (6) prevent the emergence of certain species (Weaver and Tomanek 1951; Weaver and Rowland 1952; Kelting 1954; Penfound 1964). In general, if a prairie is undisturbed, i.e., no grazing or mowing, weedy species do not become established; however, when one or more of these disruptive agents is added, a wide spectrum of weedy invaders can and does become established (Weaver and Hansen 1941;

Drew 1947; Kelting 1954; Ellison 1960; Weaver 1968).

Weaver and Hansen (1941) have described the process of degeneration under grazing pressure and have classified plant species according to their response to this grazing pressure. Those species that decrease in abundance under grazing pressure, "decreasers", include such species as *Andropogon gerardi*, *A. scoparius*, *Panicum virgatum*, *Sorghastrum nutans*, and many legumes. Species that increase under grazing pressure, "increasers", include such examples as *Buchloe dactyloides*, *Bouteloua* species, and *Achillea lanulosa*. Invaders are species that become established when grazing pressure is so intense as to handicap the increasers and include both grasses and forbs, many of which are annuals, such as species of *Bromus*, *Ambrosia*, *Cirsium*, and *Plantago*.

Kelting (1954) studied the effects of moderate grazing on species diversification in central Oklahoma prairies. He found a total of 36 species in a virgin prairie, of which 11 were exclusive species, and a total of 64 species in a grazed prairie of which 37 were exclusive. From this he determined that only 39% of the total species found in the virgin prairie were found in the grazed prairie. Kelting further concluded that grazing increased the total plant production and that the larger amount of dead plant material found in the virgin prairie may be partially responsible for the low living cover percentages reported for the area.

The above mentioned studies lend credence to the idea that protection from grazing results in accumulation of heavy mulch, nearly pure stands of dominant grasses, later spring growth, reduced flowering, and decreased forage yields (Weaver and Flory 1934; Weaver and Rowland 1952; Ellison 1960; Weaver 1968). Additionally, not only is there an actual diminution of the basal cover in virgin prairies, but also certain of the smaller and earlier species are severely handicapped and tend to disappear (Weaver and Fitzpatrick 1934; Betz and Cole 1969).

When prairies are undisturbed, most grass species show reduced growth, tillering, and flowering. Removal of the dead herbage by fire and/or grazing will eliminate this growth inhibition (Curtis and Partch 1950; Weaver and Rowland 1952; Dix and Butler 1954; Kucera and Ehrenreich 1962; Hadley and Kieckhefer 1963; Kucera et al. 1967; Weaver 1968; Hulbert 1969; Old 1969; Lloyd 1972). Curtis and Partch in 1950 indicated that the most important factor affecting the flowering of Andropogon gerardi was the presence of a cover of old litter on the crowns. Removal of this cover by either fire or clipping brought about a six-fold increase in flower production and a 60% increase in plant height. Old (1969) found that the addition of mulch to denuded areas caused an inhibition of both vegetative and flower stalk production. The response was proportional to the length of time that the mulch was in place, and the magnitude of inhibition depended on the thickness of the mulch layer. Other workers, such as Larson and Whitman (1942) have also reported that forage yields vary directly with the depth of natural mulch.

Suppression of weedy invaders in an undisturbed prairie has been attributed to either mechanical effects of the mulch layer or competition. Weight of mulch, reduced soil surface temperature, and reduced light are most commonly mentioned (Weaver and Rowland 1952; Hopkins 1954; Ehrenreich and Aikman 1963; Vogl and Bjusted 1968). However, the mechanism of suppression by mulch has not been thoroughly examined.

One objective of the current study was to examine the potential allelopathic interference by mulch as a mechanism of suppression of weedy invaders. The idea that allelopathy plays a major role in community structure and dominance is only about 20 years old, even though the concept of allelopathy has existed since 1832 (Rice 1974). Allelopathy has been demonstrated to be an operative mechanism in old field succession in Oklahoma. Rice, Penfound, and Rohrbaugh (1960) successfully showed that the slow return of climax species to an abandoned field was not related to seed dispersal or mineral nutrition. In 1964, Rice ascertained that some of the early invading weeds released compounds that were inhibitory to nitrogen-fixing and nitrifying bacteria. Inhibition of these bacterial species resulted in a decreased soil nitrogen level and a consequent slowing of the re-entry of climax species of high nitrogen requirement. Parenti and Rice (1969) reported that the weedy phase of succession was replaced by *Aristida oligantha* in two to three years. This replacement of the weedy phase was due primarily to phytotoxins released by some of the pioneer weeds such as *Helianthus annuus*, *Sorghum halepense*, and *Euphorbia supina*, which were effective against weedy seedlings, but not against *Aristida oligantha*. Furthermore, Rice (1964) has determined that *A. oligantha* also produces substances inhibitory to nitrogen-fixing and nitrifying bacteria, which leads to a longer persistence of the annual grass stage. Studies of this nature show that allelopathy greatly influences community structure and dominance.

There have been no comprehensive studies of the role of allelopathy in climax or near-climax prairies. However there are indications that phytotoxins may play a substantial role in maintaining dominant stands of climax prairie grasses. Semtner (1972) found that a leachate prepared from a mixture of *Andropogon scoparius* and *Sorghastrum nutans* significantly inhibited growth of Sorghum halepense, a weedy grass species. Semtner used leachates prepared from fresh green leaves and from dead, decomposing litter. The leachate was used to irrigate a seedbed containing S. halepense rhizome segments. Results of these experiments indicated that fewer plants emerged, those plants that did emerge were smaller, and height increase was slower, when compared with controls irrigated with distilled water. After leachate application was terminated, many new plants emerged and growth was comparable to the controls. Semtner's study indicates that climax grasses may release inhibitory compounds which interfere with potential invading weedy species in grass stands. One aspect of the current study was to ascertain which climax species have allelopathic potential, and the possible role played by allelopathy in maintenance of these dominant stands. The main objective of this study was to determine how prairie grasses are able to prevent weedy plants of similar habits from invading their intact stands.

# CHAPTER II

## SITE DESCRIPTIONS

Four field sites were selected in Payne County, Oklahoma, for field studies: climax tall grass prairie, native hay meadow, moderately grazed prairie, and a severely grazed prairie. All sites are located west of Stillwater, Oklahoma, and within an eight mile radius of each other. Each site will be described separately. Climatic factors will be discussed collectively.

### Climax Tall Grass Prairie

This study site is located 9.0 miles west of Stillwater, Oklahoma, in T19N-R1E-Sec 28 on the Oklahoma State University Ecology Preserve. The site is characterized by two major perennial grasses, _Andropogon scoparius_[1] and _Sorghastrum nutans_, one minor perennial grass, _Panicum oligosanthes_ var. _scribnerianum_, and a perennial forb, _Ambrosia psilostachya_. This site is in the prairie phase of an area characterized by a mosaic of upland forest and tall grass prairie. The site is part of the Redbed Plains and is characterized by fine soils that are well suited for the growth of grasses (Bruner 1931). The two dominant grasses, _A. scoparius_ and _S. nutans_, have been found by other workers to be of primary or secondary importance in Central Oklahoma tall grass

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[1] Nomenclature follows Waterfall, 1969, unless authority is given.

prairies (Booth 1941; Kelting 1954; Buck and Kelting 1962; Netherland 1972). Vegetational analysis showed that A. scoparius was the major dominant with 129 stems/sq. m and a percent frequency of 39.4.

The topography of the site is a gentle rolling plain with a very slight north-facing slope. Seedlings of climax upland and bottomland forest species are interspersed throughout the site.

This site is also part of the Renfrow-Zaneis-Vernon Association with characteristic residual soils derived from the Permian Redbeds (Gray and Galloway 1959). Gray and Roozitalab (1976) indicate that the site is located in the Central Reddish Prairies and that the Dominant Great Soils Groups are primarily Paleustolls, Argiustolls, and Ustochrepts. These soils occur on moderately sloping, well drained sites.

The area was settled during the late nineteenth and early part of the twentieth century. The area used as farmland was abandoned during the early 1930's and then utilized for cattle grazing. Examination of early aerial photographs suggests that the study site was not plowed. Because of the dense bottomland forests nearby which restrict access, the study site was probably grazed very lightly. Grazing by cattle was stopped during the 1960's and the area allowed to return to a primeval vegetational state. According to the classification scheme used by Booth (1941) the site would be considered late perennial bunch grass or early climax.

Evidence of lack of disturbance is indicated by the dominant grasses and the heavy layer of natural mulch present over the entire site. Small, localized, minor disturbances were indicated by the presence of Bromus japonicus and Chrysopsis pilosa, two common weedy invaders. Depth of the natural mulch layer varied, depending upon the density of vegetation, from one-half to five inches.

During the dormant season (October to April) the site is characterized by dead standing culms of both *Andropogon scoparius* and *Sorghastrum nutans*. During the growing season these culms still remain upright and give the site a ragged appearance. Standing culms several years old were found to be distinguished from younger culms by a grayish color and sometimes by marked decay lines at ground surface. Dead leaves of *A. scoparius* were found to remain attached to the root crown in most bunches that were examined. A bunch of *A. scoparius* would have dead, younger leaves on the outside of the crown and older leaves toward the center of the crown. As the leaves of the current growing season die, they fall to the nearest outside portion of the crown and form a closed canopy over the soil surface. When these dead leaves are removed bare soil or a very light mulch layer can be seen with few if any herbaceous plants present (Figure 1). Figure 2 is an aspect picture of part of the climax site used in this study.

## Native Hay Meadow

The hay meadow used for this study is located 17 miles west of Stillwater in T19N-R1W-Sec 30. Perennial grasses are the dominant vegetation. The major dominants are *Andropogon scoparius* and *Andropogon gerardi*, present in similar densities and frequencies. A number of increaser grass species are present indicating the effect of annual mowing. These increasers include: *Bouteloua curtipendula*, *Bouteloua hirsuta*, *Buchloe dactyloides*, and *Panicum oligosanthes*.

Topographically the site consists of slightly undulating hills sloped in a predominantly south-west facing direction. Soils of the area

Figure 1. Light Mulch Layer Present Between Two Bunches of Andropogon scoparius in the Climax Site. The herbaceous plants in the foreground are Achillea lanulosa and Ambrosia psilostachya.

Figure 2. Part of the Climax Prairie Site Used in This Study. Site is located on the OSU Ecology Preserve. Trees in the background are primarily members of the genus Quercus.

are identical to those of the climax site. The entire site during early spring is characterized by a conspicuous absence of standing dead culms and grass bunches of approximate equal height are present. This gives the site a smooth, even appearance. Height of the grasses in June is approximately 60 cm and vegetation is very dense. No bare soil areas were found in the entire site. No natural mulch layer was present. Formation of a mulch layer is prevented by the annual harvest and litter removal of the grasses in late June. The entire field is mowed and raked for hay. This effectively removes most of the litter and mulch from the field. However, a very light cover of small plant fragments is present after mowing. After spring mowing the field is not disturbed until the following spring. Rapid growth of the vegetation occurs following mowing and by September a continuous aereal coverage of the soil surface is complete. Basal area covered by _Andropogon scoparius_ is reduced because of the mowing, resulting in tiller formation from the center of each root crown. Therefore, during the active growing season there is no overlapping canopy of fallen leaves to interfere with light availability or herbaceous plant growth around the root crown area. Figure 3 shows an aspect picture of part of the hay meadow used in this study.

## Moderately Grazed Prairie

This site is located 10 miles west of Stillwater, in T19N-R1E-SEC 32. Perennial grasses, both decreasers and increasers are dominant or of secondary importance. _Andropogon scoparius_ and _Andropogon gerardi_ are the dominant grasses. _Andropogon scoparius_ occurs in the greatest density and frequency and is the major dominant. The grass increasers

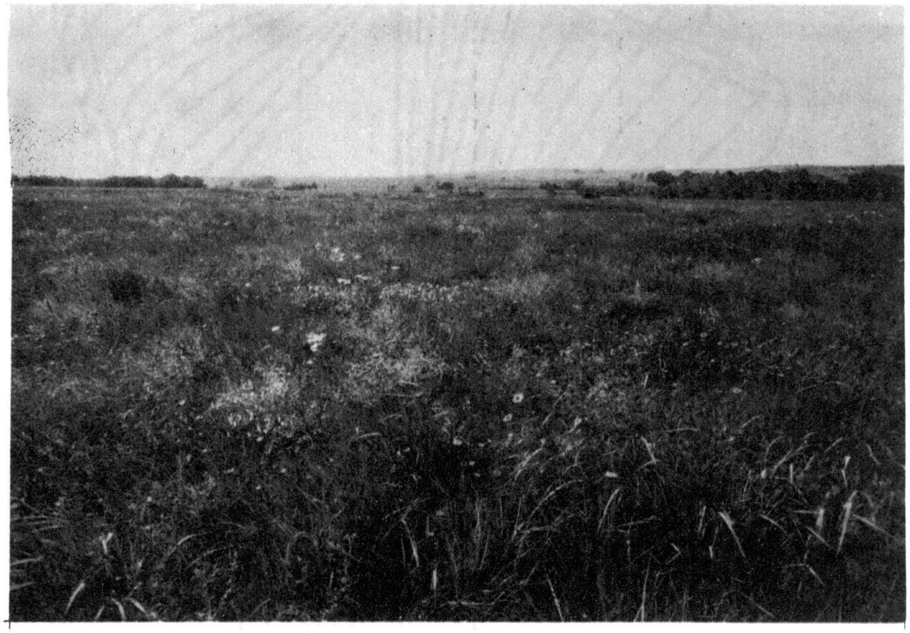

Figure 3. Partial View of Native Hay Meadow. Foreground grasses are primarily members of the Andropogoneae.

of secondary importance include Bouteloua curtipendula and Panicum oligosanthes. A number of species present are indicators of disturbance: Bromus japonicus, Digitaria sanguinalis and Andropogon saccharoides. The legume Amorpha canescens has a relatively high density. This species is locally regarded as indicating moderate grazing. The entire study area has a ragged, uneven appearance due to selective grazing by cattle. Many of the bunches of Andropogon scoparius were left ungrazed while the areas between bunches were grazed close to soil surface. This close grazing allows the shorter grasses, such as Bouteloua hirsuta, and forbs to become established.

This site is located on gently undulating hills which slope in a predominantly south-west facing direction. Soils of the area are similar to those of the climax site. Small rocky outcrops of Permian sandstone were found in scattered locations throughout the site.

The site is in the second growing season without grazing. Approximately four cattle per acre graze the site every two years during the spring and summer. The herd is removed during the fall. This rotation allows two years for litter and mulch to build up and become established. Around the clumps of Andropogon scoparius the layer of mulch and litter is similar to that found on the climax site. In areas between the clumps the mulch layer is very shallow. The soil surface, however, supports some type of litter cover in all areas except the rock outcrops. The areas between the clumps support a wide variety of weedy species. The A. scoparius bunches further supported old, dead, standing culms as did the climax site. Figure 4 shows an aspect picture of this site.

Figure 4. View of Moderately Grazed Prairie Site. The bunch grasses in the foreground are *Andropogon scoparius* and *A. gerardi*; other herbaceous plants are primarily legumes. This picture clearly shows the effects of selective grazing.

## Severely Grazed Prairie

This study site is located 9 miles west of Stillwater in T19N-R1E-Sec 28, approximately one-quarter mile east of the climax site. The site is dominated by characteristic weedy species including *Lespedeza stipulacea*, *Ambrosia psilostachya*, *Bromus japonicus*, *Andropogon saccharoides*, and species of *Eragrostis*. The major dominants are *L. stipulacea*, *A. psilostachya*, and *A. saccharoides* which have similar densities and frequencies. The entire site supports both perennial and annual species, however, annual species are more abundant. Numerous species used as indicators of disturbance are present, including: *Chrysopsis pilosa*, *Plantago purshii*, and *Gutierrezia dracunculoides*.

The site is located on a northwest sloping hill. Soils are similar to those found at the climax site. Reddish colored subsurface clay forms the surface soil in many places brought about by erosion of top soil due to the heavy grazing pressure (Figure 5). The soil is hard packed over much of the site and during rainfall, much runoff was observed. Very little organic material was present in the top part of the soil. There was very little natural mulch or litter present; much of the soil surface was bare.

Pure stands as well as mixed stands of *Bromus japonicus* were found throughout the site. These mixed stands contained a high proportion of *Ambrosia psilostachya* and in some areas depauperate representatives of *Andropogon gerardi* were present. *Andropogon scoparius* was also found in the field but density and frequency were very low. The bunches of *A. scoparius* that were present were small in stature and depauperate. Figure 6 shows the severely grazed site.

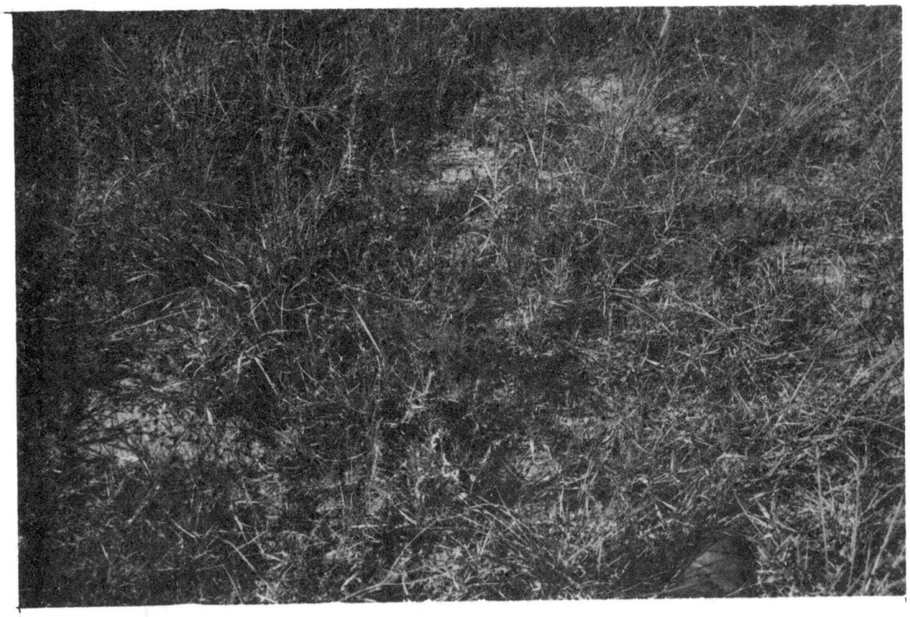

Figure 5. View of Bare Soil Surface in the Severely Grazed Prairie Site Caused by Erosion and Heavy Grazing Pressure. Grasses are primarily Andropogon saccharoides and Bromus japonicus.

Figure 6. Severely Grazed Prairie Site. Tall herbaceous plants in foreground are Vernonia Baldwinii; grasses around the Vernonia are primarily Bromus japonicus, Andropogon saccharoides, and Bouteloua gracilis.

## Climate

Figure 7 shows the relationship between average monthly ambient air temperature and precipitation based on a thirty year period for the Stillwater area. Highest temperatures occur in July, while the lowest average precipitation occurs in December/January. The average annual ambient air temperature for this area is 16.01 C with an average annual precipitation of 81.74 cm (Curry 1970). Table I shows average monthly ambient air temperatures (maximum and minimum) and precipitation values for 1975 with deviations from the mean for precipitation. The average length of the growing season is 211 days lasting from early April until late October.

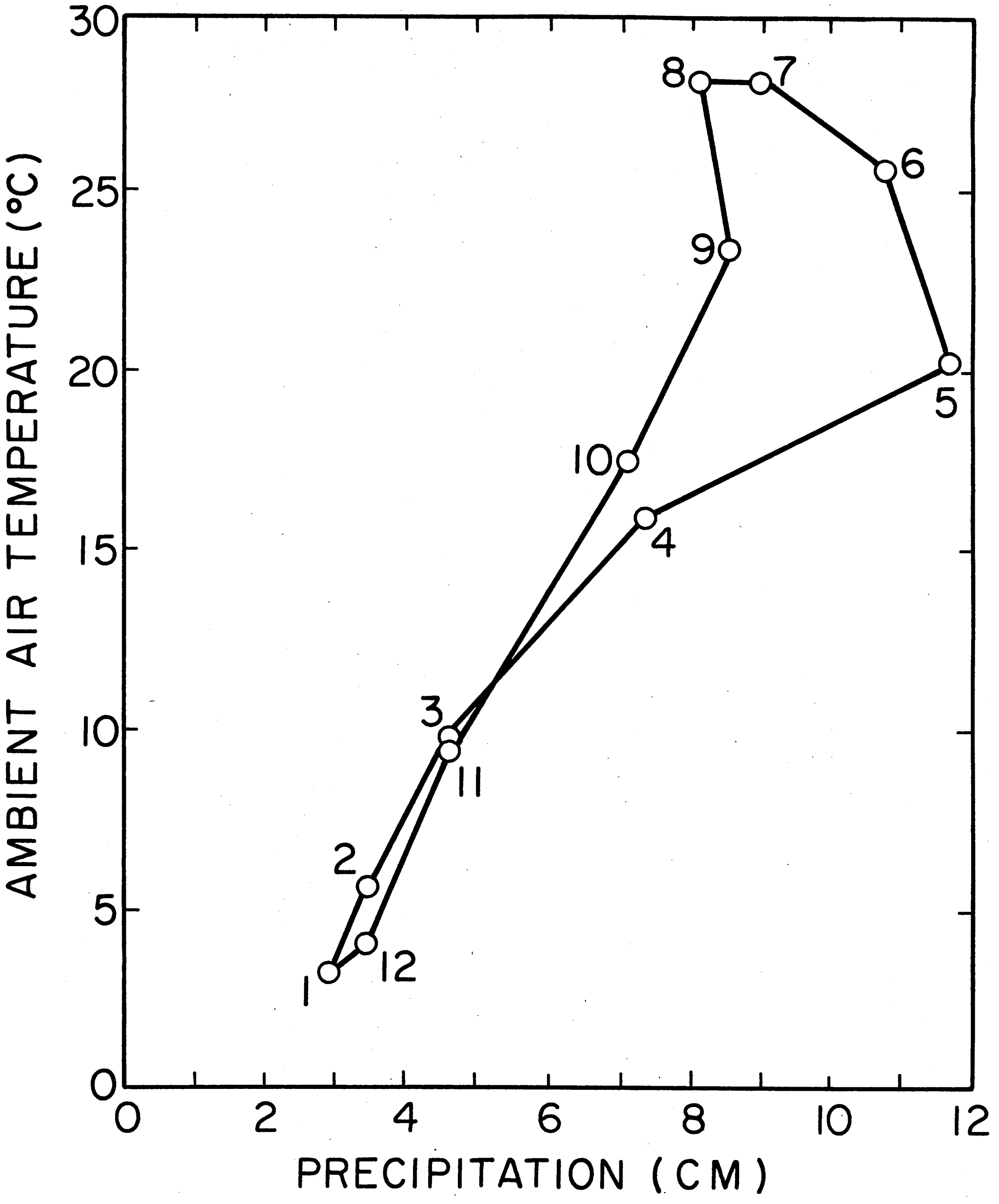

Figure 7. Climatogram Showing Relationship Between Average Monthly Ambient Air Temperature and Precipitation Based on 30 Year Period (1931-1960) for Stillwater, Oklahoma. Numbers correspond to months of the year. (Data from Curry, 1970; U. S. Department of Commerce, 1971.)

## TABLE I

## AVERAGE MONTHLY MAXIMUM AND MINIMUM AMBIENT AIR TEMPERATURE AND PRECIPITATION VALUES FOR 1975

| Month | Precipitation ** Average 1960-1974 (cm) | Precipitation ** Average 1975 (cm) | Precipitation ** Deviation From Mean (cm) | Ambient Air Temperature (°F)* Maximum | Ambient Air Temperature (°F)* Minimum |
|---|---|---|---|---|---|
| January | 2.04 | 6.96 | + 4.93 | 65 | 07 |
| February | 2.83 | 4.34 | + 1.52 | 69 | 08 |
| March | 4.91 | 7.19 | + 2.29 | 82 | 10 |
| April | 6.79 | 2.59 | - 4.19 | 89 | 18 |
| May | 10.21 | 22.53 | +12.32 | 89 | 40 |
| June | 8.52 | 9.42 | + 0.91 | 96 | 48 |
| July | 7.58 | 7.06 | - 0.51 | 99 | 48 |
| August | 8.73 | 5.51 | - 3.22 | 96 | 58 |
| September | 11.95 | 4.62 | - 7.34 | 101 | 39 |
| October | 6.70 | 6.63 | - 0.08 | 89 | 28 |
| November | 4.74 | 4.60 | - 0.15 | 81 | 25 |
| December | 3.34 | 3.15 | - 0.20 | 78 | 03 |
| YEARLY AVERAGE | 78.33 | 84.61 | + 6.27 | | |

*Temperature values recorded at OSU Ecology Preserve.

**Precipitation values recorded at Lake Carl Blackwell USDA Hydraulic Lab by USDA personnel.

# CHAPTER III

# SPECIES COMPOSITION

Species composition of the four sites was determined by the Point Centered Quarter sampling method and by observation.

## Point Centered Quarter Sampling

Each site was sampled during the period 01-15 August, 1975, by the point centered quarter method. Although this method was originally developed by Cottam and Curtis (1956) for determining tree composition of northern forests, the method was modified by Dix (1961) for use in determining species composition of grasslands. This plotless sampling technique is an efficient method of taking rapid, quantitative samples of grassland vegetation from which species composition, frequency, and density can be determined.

Since the point centered quarter technique involves the counting and identification of individual species a definition of an individual species is imperative. Results obtained by this method have been found to be completely dependent upon the definition of an individual (Walker 1970). Dix (1961) determined densities of North Dakota grasslands in terms of shoots per unit area and defined the shoot on a morphological basis. The shoot, as defined by Dix, consists of a stem and all its appendages. This definition is also used in the current study.

A steel stake was used as the point. To the stake were fastened steel bars which divided the circle centered on the stake into four equal quarters. Measurements were taken from the point of the stake to the nearest living shoot in each quarter. The shoot was then counted as one individual of that species. The distance from the point to the nearest shoot in each quarter was measured in centimeters and recorded.

At each of the four field sites five straight line transects, each 25 m long, were laid out. The location of each transect was located arbitrarily, but selected to pass through representative vegetation. On each transect 50 equally spaced sampling points were established. Thus a total of 250 sampling points were used for each site.

The following definitions and formulae are pertinent to the point centered quarter sampling technique and were therefore used in this study. The point-to-plant distance is the distance, in centimeters, from the point of the stake to the nearest living shoot in each quarter. The measured distance for each individual of each species is summed after sampling is completed. Totaling the summed point-to-plant distance values for all species and all points and obtaining an average gives the mean point-to-plant distance. Squaring the mean point-to-plant distance value yields the mean area per plant. Total density of all species is obtained by dividing the unit area by the mean area per plant. The unit area used in this study was 10,000, the number of square centimeters in one square meter. Relative frequency, the percentage of sampling points in which the species occurs, is determined by the formula:

$$\mathrm{RF} = \frac{\text{number of points at which the species occurs}}{\text{total number of points}} \times 100$$

Relative density, the number of individuals of a species expressed as a percentage of the total number of individuals, is determined by the formula:

$$RD = \frac{\text{number of shoots of species}}{\text{total number of shoots}} \times 100$$

Absolute density of each species is determined by multiplying the total density by the relative density of the individual species. The importance value (IV) for each species is determined by summing the relative density and relative frequency values of the individual species.

## Observation

In addition to measuring quantitative aspects of each habitat, a visual survey of species present at each site was carried out. Representative segments of each site were gridded off and unmarked straight line transects projected. The entire gridded section was traversed and essentially all species present were identified and recorded. This procedure was carried out between 01-15 August, 1975. Additionally, between 10-13 May, 1976, the vegetation was again surveyed, but with a slight modification; only those species not present in the August observations were recorded.

## Results and Discussion

Tables II through V show relative density, relative frequency, importance values, and density values for all species sampled by study site.

A total of 28 species were encountered in sampling the climax prairie site (Table II). The two most abundant species of this site

## TABLE II

## SPECIES DENSITIES, RELATIVE FREQUENCY, AND IMPORTANCE VALUES IN THE CLIMAX PRAIRIE SITE**

| Species | No. Shoots | Sum of point-to-plant Distances (cm) | Relative Frequency | Relative Density | Importance Value | Density* |
|---|---|---|---|---|---|---|
| Andropogon scoparius | 537 | 3478.8 | 39.40 | 53.70 | 93.10 | 128.92 |
| Sorghastrum nutans | 237 | 1674.1 | 26.32 | 23.70 | 50.02 | 56.90 |
| Ambrosia psilostachya | 45 | 223.2 | 7.07 | 4.50 | 11.57 | 10.80 |
| Panicum oligosanthes var. scribnerianum | 41 | 221.9 | 5.30 | 4.10 | 9.40 | 9.84 |
| Lespedeza virginica | 23 | 126.4 | 3.53 | 2.30 | 5.83 | 5.52 |
| Carex sp. | 23 | 140.6 | 3.36 | 2.30 | 5.66 | 5.52 |
| Panicum anceps | 15 | 93.6 | 2.12 | 1.50 | 3.62 | 3.60 |
| Achillea lanulosa | 13 | 96.1 | 2.30 | 1.30 | 3.60 | 3.12 |
| Andropogon gerardi | 13 | 83.0 | 1.59 | 1.30 | 2.89 | 3.12 |
| Symphoricarpos orbiculatus | 9 | 50.0 | 1.59 | 0.90 | 2.49 | 2.16 |
| Hieracium longipilum | 7 | 57.5 | 1.24 | 0.70 | 1.94 | 1.68 |
| Gerardia heterophylla | 6 | 37.4 | 0.88 | 0.60 | 1.48 | 1.44 |
| Lespedeza cuneata | 5 | 25.1 | 0.71 | 0.50 | 1.21 | 1.20 |
| Tragia ramosa | 4 | 18.4 | 0.71 | 0.40 | 1.11 | 0.96 |
| Solanum eleagnifolium | 3 | 17.6 | 0.53 | 0.30 | 0.83 | 0.72 |
| Chrysopsis pilosa | 3 | 10.3 | 0.53 | 0.30 | 0.83 | 0.72 |
| Cassia fasciculata | 3 | 13.4 | 0.53 | 0.30 | 0.83 | 0.72 |
| Lespedeza stipulacea | 2 | 13.3 | 0.35 | 0.20 | 0.55 | 0.48 |
| Artemisia ludoviciana | 2 | 9.0 | 0.35 | 0.20 | 0.55 | 0.48 |
| Others (9 species) | 9 | 64.3 | 1.62 | 0.90 | 2.52 | 2.16 |
| TOTAL | 1000 | 6454.0 | 100.03 | 100.00 | 200.03 | 240.06 |

Mean Distance = 6.45 cm Mean Area = 41.65 $cm^2$/shoot Total Density = 240.07 shoots/$m^2$

*Shoots/$m^2$ **Based on 250 points (1000 quarters).

## TABLE III

## SPECIES DENSITIES, RELATIVE FREQUENCY, AND IMPORTANCE VALUES IN THE NATIVE HAY MEADOW**

| Species | No. Shoots | Sum of point-to-plant Distances (cm) | Relative Frequency | Relative Density | Importance Value | Density* |
|---|---|---|---|---|---|---|
| Andropogon scoparius | 397 | 1706.5 | 32.44 | 39.70 | 72.14 | 237.55 |
| Andropogon gerardi | 341 | 1378.0 | 31.19 | 34.10 | 65.29 | 204.04 |
| Panicum oligosanthes var. scribnerianum | 84 | 312.3 | 12.48 | 8.40 | 20.88 | 50.26 |
| Bouteloua curtipendula | 65 | 213.2 | 9.62 | 6.50 | 16.12 | 38.89 |
| Bouteloua gracilis | 25 | 88.3 | 2.50 | 2.50 | 5.00 | 14.96 |
| Sorghastrum nutans | 22 | 90.3 | 2.50 | 2.20 | 4.70 | 13.16 |
| Panicum capillaris | 21 | 105.3 | 2.50 | 2.10 | 4.60 | 12.57 |
| Leptoloma cognatum | 15 | 69.5 | 1.96 | 1.50 | 3.46 | 8.98 |
| Bouteloua hirsuta | 9 | 32.6 | 1.43 | 0.90 | 2.33 | 5.39 |
| Achillea lanulosa | 4 | 13.1 | 0.71 | 0.40 | 1.11 | 2.39 |
| Hieracium longipilum | 4 | 23.3 | 0.71 | 0.40 | 1.11 | 2.39 |
| Schrankia uncinata | 3 | 12.3 | 0.53 | 0.30 | 0.83 | 1.80 |
| Panicum virgatum | 4 | 8.5 | 0.36 | 0.40 | 0.76 | 2.39 |
| Others (6 species) | 6 | 34.8 | 1.08 | 0.60 | 1.68 | 3.60 |
| TOTAL | 1000 | 4088.0 | 100.01 | 100.00 | 200.01 | 598.37 |

Mean Distance = 4.09 cm Mean Area = 16.71 $cm^2$/shoot Total Density = 598.37 shoots/$m^2$

*Shoots/$m^2$

**Based on 250 points (1000 quarters).

## TABLE IV

## SPECIES DENSITIES, RELATIVE FREQUENCY, AND IMPORTANCE VALUES IN THE MODERATELY GRAZED PRAIRIE SITE**

| Species | No. Shoots | Sum of point-to-plant Distances (cm) | Relative Frequency | Relative Density | Importance Value | Density* |
|---|---|---|---|---|---|---|
| Andropogon scoparius | 411 | 1273.8 | 30.28 | 41.10 | 71.38 | 466.67 |
| Andropogon gerardi | 212 | 619.8 | 22.67 | 21.20 | 43.87 | 240.72 |
| Bouteloua curtipendula | 117 | 351.1 | 12.58 | 11.70 | 24.28 | 132.85 |
| Panicum oligosanthes var scribnerianum | 103 | 288.0 | 13.20 | 10.30 | 23.50 | 116.95 |
| Ambrosia psilostachya | 35 | 81.6 | 5.28 | 3.50 | 8.78 | 39.74 |
| Bouteloua hirsuta | 30 | 81.3 | 3.26 | 3.00 | 6.26 | 34.06 |
| Leptoloma cognatum | 14 | 35.7 | 2.02 | 1.40 | 3.42 | 15.90 |
| Sporobolus asper | 13 | 45.0 | 2.02 | 1.30 | 3.32 | 14.76 |
| Amorpha canescens | 10 | 25.9 | 1.24 | 1.00 | 2.24 | 11.35 |
| Panicum virgatum | 8 | 28.9 | 0.93 | 0.80 | 1.73 | 9.08 |
| Sorghastrum nutans | 6 | 11.1 | 0.78 | 0.60 | 1.38 | 6.81 |
| Achillea lanulosa | 6 | 15.5 | 0.78 | 0.60 | 1.38 | 6.81 |
| Eragrostis intermedia | 6 | 19.7 | 0.78 | 0.60 | 1.38 | 6.81 |
| Hieracium longipilum | 3 | 9.9 | 0.47 | 0.30 | 0.77 | 3.41 |
| Andropogon ternarius | 3 | 10.4 | 0.47 | 0.30 | 0.77 | 3.41 |
| Psoralea tenuiflora | 3 | 5.0 | 0.47 | 0.30 | 0.77 | 3.41 |
| Dalea purpurea | 3 | 10.2 | 0.47 | 0.30 | 0.77 | 3.41 |
| Echinacea angustifolia | 3 | 7.3 | 0.47 | 0.30 | 0.77 | 3.41 |
| Digitaria sanguinalis | 2 | 11.0 | 0.31 | 0.20 | 0.51 | 2.27 |
| Bromus japonicus | 2 | 3.3 | 0.31 | 0.20 | 0.51 | 2.27 |
| Gerardia heterophylla | 2 | 2.2 | 0.31 | 0.20 | 0.51 | 2.27 |
| Plantago purshii | 2 | 6.9 | 0.31 | 0.20 | 0.51 | 2.27 |
| Andropogon saccharoides | 3 | 12.2 | 0.16 | 0.30 | 0.46 | 3.41 |
| Others (3 species) | 3 | 11.8 | 0.48 | 0.30 | 0.78 | 3.39 |
| TOTAL | 1000 | 2967.6 | 100.05 | 100.00 | 200.05 | 1135.44 |

Mean Distance = 2.97 cm    Mean Area = 8.81 $cm^2$/shoot    Total Density = 1135.46 shoots/$m^2$

*Shoots/$m^2$

**Based on 250 points (1000 quarters).

## TABLE V

## SPECIES DENSITIES, RELATIVE FREQUENCY, AND IMPORTANCE VALUES IN THE SEVERELY GRAZED PRAIRIE SITE**

| Species | No. Shoots | Sum of point-to-plant Distances (cm) | Relative Frequency | Relative Density | Importance Value | Density* |
|---|---|---|---|---|---|---|
| Lespedeza stipulacea | 229 | 727.5 | 21.01 | 22.90 | 43.91 | 184.26 |
| Ambrosia psilostachya | 200 | 660.4 | 19.32 | 20.00 | 39.32 | 160.93 |
| Andropogon saccharoides | 196 | 810.9 | 16.78 | 19.60 | 36.38 | 157.71 |
| Bromus japonicus | 93 | 329.2 | 8.46 | 9.30 | 17.76 | 74.83 |
| Andropogon gerardi | 63 | 210.6 | 7.48 | 6.30 | 13.78 | 50.69 |
| Bouteloua gracilis | 47 | 155.9 | 5.50 | 4.70 | 10.20 | 37.82 |
| Eragrostis intermedia | 34 | 125.5 | 4.51 | 3.40 | 7.91 | 27.36 |
| Achillea lanulosa | 26 | 88.0 | 3.24 | 2.60 | 5.84 | 20.92 |
| Andropogon scoparius | 28 | 159.1 | 2.82 | 2.80 | 5.62 | 22.53 |
| Aster ericoides | 16 | 45.3 | 2.11 | 1.60 | 3.71 | 12.87 |
| Hedeoma hispida | 15 | 35.5 | 2.11 | 1.50 | 3.61 | 12.07 |
| Eragrostis spectabilis | 15 | 40.7 | 1.97 | 1.50 | 3.47 | 12.07 |
| Diodia teres | 6 | 23.6 | 0.70 | 0.60 | 1.30 | 4.83 |
| Chrysopsis pilosa | 5 | 14.3 | 0.70 | 0.50 | 1.20 | 4.02 |
| Hypericum Drummondii | 5 | 22.7 | 0.56 | 0.50 | 1.06 | 4.02 |
| Tragia ramosa | 4 | 12.7 | 0.56 | 0.40 | 0.96 | 3.22 |
| Vernonia baldwinii | 5 | 20.6 | 0.28 | 0.50 | 0.78 | 4.02 |
| Plantago purshii | 3 | 10.4 | 0.42 | 0.30 | 0.72 | 2.41 |
| Haplopappus ciliatus | 2 | 6.1 | 0.28 | 0.20 | 0.48 | 1.61 |
| Rudbeckia hirta | 2 | 8.3 | 0.28 | 0.20 | 0.48 | 1.61 |
| Cassia fasciculata | 2 | 4.6 | 0.28 | 0.20 | 0.48 | 1.61 |
| Gutierrezia dracunculoides | 2 | 7.9 | 0.28 | 0.20 | 0.48 | 1.61 |
| Others (2 species) | 2 | 5.5 | 0.28 | 0.20 | 0.48 | 1.60 |
| TOTAL | 1000 | 3525.3 | 99.93 | 100.00 | 199.93 | 804.62 |

Mean Distance = 3.52 cm Mean Area = 12.43 $cm^2$/shoot Total Density = 804.63 shoots/$m^2$

*Shoots/$m^2$

**Based on 250 points (1000 quarters).

were *Andropogon scoparius* and *Sorghastrum nutans*. Thirty-nine percent of the species present were unique to this site and did not occur in the sampling of the other sites. Total density of this site was 240 stems/sq. m with two plant families, the Graminae (29%) and Leguminosae (21%), being predominant (Table VI). By observation an additional 44 species were found, giving a total of 72 species present in the climax site during August (Appendix A).

Table III shows results obtained on species composition for the native hay meadow. Total density for this site was determined to be 598 stems/sq. m with four abundant species: *Andropogon scoparius*, *Andropogon gerardi*, *Panicum oligosanthes* var. *scribnerianum*, and *Bouteloua curtipendula*. Nineteen species were found in sampling this hay meadow, of which 31% were unique. Fifty-eight percent of all species present in sampling were grasses, 10% were legumes, and 32% belonged to other families. Observation of the site showed an additional 37 species, bringing the total to 56 (Appendix A).

Table IV shows that the moderately grazed field has a total density of 1135 stems/sq. m. A total of 26 species were encountered during sampling of which 27% were unique to this site. The most abundant species were: *Andropogon scoparius*, *Andropogon gerardi*, *Bouteloua curtipendula*, *Panicum oligosanthes* var. *scribnerianum*, *Ambrosia psilostachya*, and *Bouteloua hirsuta*. The total number of species can be separated into 54% grasses, 11% legumes, and 35% other plant families. By observation 30 more species were found, giving a total species count of 56 for the moderately grazed site (Appendix A).

A total density of 804 stems/sq. m was determined for the severely grazed site (Table V). Sampling showed 24 species present, of which

## TABLE VI

## NUMBERS OF SPECIES AND THEIR DISTRIBUTIONS BY FAMILY IN THE FOUR STUDY SITES

| Measurement | Climax Prairie | | Native Hay Meadow | | Moderately Grazed Prairie | | Severely Grazed Prairie | |
|---|---|---|---|---|---|---|---|---|
| No. Species Present in Sampling | 28 | | 19 | | 26 | | 24 | |
| No. Species Present in August, 1975, Observation | 44 | | 37 | | 30 | | 10 | |
| No. Species Present in May, 1976, Observation | 12 | | 14 | | 12 | | 11 | |
| Total Number Species Present | 84 | | 70 | | 68 | | 45 | |
| Percent of Species Unique to Each Habitat by Sampling | 39 | | 31 | | 27 | | 46 | |
| Percentages of Plants Present in Sampling by Family | Number Individuals | % | Number Individuals | % | Number Individuals | % | Number Individuals | % |
| Gramineae | 8 | 28.6 | 11 | 57.9 | 14 | 53.9 | 8 | 33.3 |
| Leguminosae | 6 | 21.4 | 2 | 10.5 | 3 | 11.5 | 2 | 8.3 |
| Compositae | 7 | 25.0 | 2 | 10.5 | 6 | 23.1 | 7 | 29.2 |
| Cyperaceae | 1 | 3.6 | | | | | | |
| Solanaceae | 1 | 3.6 | 1 | 5.3 | | | 1 | 4.2 |
| Euphorbiaceae | 1 | 3.6 | | | | | 1 | 4.2 |
| Plantaginaceae | 1 | 3.6 | | | 1 | 3.8 | 1 | 4.2 |
| Malvaceae | 1 | 3.6 | | | 1 | 3.8 | 1 | 4.2 |
| Scrophulariaceae | 1 | 3.6 | 1 | 5.3 | 1 | 3.8 | | |
| Caprifoliaceae | 1 | 3.6 | | | | | | |
| Onagraceae | | | 1 | 5.3 | | | | |
| Asclepidaceae | | | 1 | 5.3 | | | | |
| Cruciferae | | | | | | | 1 | 4.2 |
| Rubiaceae | | | | | | | 1 | 4.2 |
| Labiatae | | | | | | | 1 | 4.2 |
| TOTAL | 28 | | 19 | | 26 | | 24 | |

46% were unique. The six most abundant species were: *Lespedeza stipulacea*, *Ambrosia psilostachya*, *Andropogon saccharoides*, *Bromus japonicus*, *Andropogon gerardi*, *Bouteloua gracilis*, and *Eragrostis intermedia*. Of the total number of species present 33% were grasses, 29% were composites, 8% were legumes, and 30% were in other families. An additional 10 species were added by observation giving a total of 34 present in the site (Appendix A).

Table VI shows that a total of 15 plant families were found when all four sites were examined. The three dominant families represented were the Gramineae, Leguminosae, and Compositae. All other families present were represented by only one species.

A visual search for uncommon species was again carried out in May, 1976, following the same procedure (Table VI). Only those species not observed during the August search or during the sampling were recorded as new species. A total of 12 new species were found in the climax site, 14 in the hay meadow, 12 in the moderately grazed prairie, and 11 in the severely grazed prairie. A comparison of species present by observation for both dates is shown in Appendixes A and B.

The major dominant of the climax site, hay meadow, and moderately grazed site, *Andropogon scoparius*, and the increaser forb *Achillea lanulosa*, were the only species common to all four sites. Fifteen plant families were found throughout the four habitats. Three of these families contain over 65% of all species present. The Gramineae were dominant in all sites with perennial grasses prevailing in all sites except the severely grazed site which contained mostly annual grasses. The Compositae had the next greatest number of species and the Leguminosae ranked third. One interesting trend found was the decrease in percent of legumes with increasing disturbance. The climax site had the greatest percentage of legumes at 21%, while the severely grazed site only contained 8%. The hay meadow and moderately grazed sites were approximately equal in legume composition at 10% and 11%, respectively. Other families were only represented by 3.6 to 5.3 percent of the total species.

There was a strong, progressive trend from mostly non-weedy, climax species in the climax prairie site to mostly weeds, many of them annuals, in the severely grazed site. Table VII shows the number of grass decreasers, increasers, and invaders, and the percent of each by site. A constant reduction in the number of decreasers and increase in the number of invaders with increasing severity of disturbance is evident.

## TABLE VII

## PERCENTAGE OF TOTAL GRASS SPECIES PRESENT BY SITE

| Degeneration Class | Climax Site | | Hay Meadow | | Moderately Grazed Prairie | | Severely Grazed Prairie | |
|---|---|---|---|---|---|---|---|---|
| | No. Species | % | No. Species | % | No. Species | % | No. Species | % |
| Decreasers | 6 | 75.0 | 4 | 36.4 | 5 | 35.7 | 2 | 25.0 |
| Increasers | 1 | 12.5 | 5 | 45.4 | 7 | 50.0 | 1 | 12.5 |
| Invaders | 0 | 0.0 | 1 | 9.1 | 2 | 14.3 | 5 | 62.5 |
| Unknown | 1 | 12.5 | 1 | 9.1 | 0 | 0.0 | 0 | 0.0 |
| TOTAL | 8 | 100.0 | 11 | 100.0 | 14 | 100.0 | 8 | 100.0 |

# CHAPTER IV

## SPECIES DIVERSITY

A species diversity index was calculated for each site based upon the absolute density of each species present and the total absolute density of all species present in each transect from the point centered quarter sampling. The diversity index used followed the Shannon-Wiener function,

$$H = - \sum_{i=1}^{s} p_i \log_2 p_i \ ,$$

where s is the total species and $p_i$ is the observed proportion of individuals that belong to the $i^{th}$ species (Shannon and Weaver 1963). According to Kochsiek and Wilhm (1969) the $p_i$ are equal to $N_i/N$, which are population values that can be estimated from the sample values $n_i/n$. Substituting the estimated sample values for the proportional values yields the equation

$$\bar{d} = - \sum_{i=1}^{s} (n_i/n) \log_2 (n_i/n)$$

which was used to calculate diversity indices for this study. In this equation $n_i$ is the absolute density of individuals of the $i^{th}$ species, n is the total absolute density of all species for each site, and s is the number of species.

The five transects used for determining species composition for each site were utilized in calculating a diversity index. A separate diversity index was calculated for each transect, the samples pooled and an overall diversity index determined for the site. Pielou (1966) suggests that for areas with sessile organisms which have a patch-like dispersion, samples be pooled for maximum effectiveness.

The Shannon-Weiner Diversity Index incorporates both species richness and equitability. Between these two components species equitability will have the greatest impact on the calculated diversity value when using numbers of individuals per species. To better determine the impact of each component to overall diversity, species equitability and species variety were calculated separately. Species equitability values were derived according to the manner described by Pielou (1966). This equation used the diversity values and the total number of species present. Five replicate and one pooled equitability value was calculated for each site using the equation

$$e = \frac{\bar{d}}{\log_2 n_i}$$

where $\bar{d}$ represents the diversity index and $n_i$ is the total number of species used to compute the diversity index. For this equitability index all values must lie between zero and one, with one representing the highest equitability, i.e., as a value of one is approached, all species present become more nearly equally abundant (Pielou 1966; Kocksiek and Wilhm 1969).

The second component of the diversity index value is species variety. According to Margalef (1958) this component can be determined by the equation

$$v = \frac{s - 1}{\mathrm{Ln}\ n_i}$$

where s is the number of species per sample and $n_i$ is the total number of individuals for all samples. To calculate the variety index values the number of species and the total number of individuals per transect from the point centered quarter sampling data were utilized.

## Results and Discussion

Species diversity within and between sites varied but was fairly consistent. The site with the lowest diversity index was the climax prairie while the severely grazed prairie had the highest diversity value. Individuals in plants are sometimes difficult to distinguish because of vegetative reproduction and this is especially true in grasslands. Accordingly this may have influenced the diversity results obtained.

The overall diversity value for the climax prairie site was calculated as 2.30 (Table VIII). The diversity values of samples within this site were relatively similar with a range of only 1.72-2.39. The two major dominants, _Andropogon scoparius_ and _Sorghastrum nutans_, exerted the greatest influence on the overall diversity value because of high abundance. The hay meadow site had an overall diversity value of 2.32 with a range of values between 1.74-2.53 (Table VIII). _Andropogon scoparius_ and _Andropogon gerardi_, the major dominants, exerted an influence comparable to the two dominants of the climax site. Likewise, _A. scoparius_ and _A. gerardi_ greatly influenced the overall diversity value of 2.70 in the moderately grazed site. Intra-site variability between diversity values in the moderately grazed site was much less than in any site, with a range of only 2.43-2.68 (Table VIII). The severely grazed site had the highest overall diversity value of all the

## TABLE VIII

## SPECIES DIVERSITY ($\bar{d}$), EQUITABILITY (e), AND VARIETY (v) OF GRASSES AND FORBS BY HABITAT

| Index | Replicate | Climax Prairie | Hay Meadow | Moderately Grazed Prairie | Severely Grazed Prairie |
|---|---|---|---|---|---|
| $\bar{d}$ | 1 | 2.06 | 1.74 | 2.65 | 2.79 |
| | 2 | 2.39 | 2.53 | 2.43 | 2.95 |
| | 3 | 2.21 | 2.39 | 2.68 | 3.37 |
| | 4 | 2.26 | 2.16 | 2.68 | 3.30 |
| | 5 | 1.72 | 2.19 | 2.61 | 2.88 |
| | $\bar{x}$ | 2.13 | 2.20 | 2.61 | 3.06 |
| | Pooled Value | 2.30 | 2.32 | 2.70 | 3.22 |
| e | 1 | 0.51 | 0.55 | 0.65 | 0.78 |
| | 2 | 0.62 | 0.70 | 0.66 | 0.77 |
| | 3 | 0.56 | 0.72 | 0.67 | 0.86 |
| | 4 | 0.55 | 0.63 | 0.64 | 0.80 |
| | 5 | 0.45 | 0.63 | 0.65 | 0.72 |
| | $\bar{x}$ | 0.54 | 0.65 | 0.65 | 0.79 |
| | Pooled Value | 0.48 | 0.54 | 0.58 | 0.70 |
| v | 1 | 2.83 | 1.51 | 3.02 | 2.08 |
| | 2 | 2.45 | 2.08 | 2.27 | 2.45 |
| | 3 | 2.64 | 1.70 | 2.83 | 2.64 |
| | 4 | 3.02 | 1.89 | 3.21 | 3.21 |
| | 5 | 2.45 | 1.89 | 2.83 | 2.83 |
| | $\bar{x}$ | 2.68 | 1.81 | 2.83 | 2.64 |
| | Pooled Value | 3.91 | 2.61 | 3.62 | 3.33 |

sites with a value of 3.22 (Table VIII). Variation between sample diversity is present but small, with the range being 2.79-3.30. The decreased abundance of the three main dominants of the severely grazed site influenced diversity by increasing the diversity index value because of the reduced number of individuals per species being encountered per sample.

Andropogon scoparius was found in all sites but the relative density and frequency decreased with increasing amount of disturbance. The climax site had the highest relative density and frequency of this species of the four sites. The hay meadow and moderately grazed sites were somewhat lower and were similar to each other, and the severely grazed site had very low values for this species. A. scoparius was present in the severely grazed site in the lowest density and frequency of all sites examined. With fewer individuals being encountered in fewer plots diversity would be increased by the rarer appearance of A. scoparius. This is in opposition to the influence found in the other sites where the abundance would cause an ultimate decrease in diversity.

Table VIII shows the resulting influence of equitability and variety on individual diversity values per transect and overall diversity values for each site. This table makes apparent the greater influence of equitability over variety in Shannon-Weiner calculations. This also accounts for the apparent discrepancy between high species richness and low diversity values. As equitability approaches the maximum value, distribution of individuals per species becomes more even regardless of total number of species present. Low equitability values indicate the influence of high numbers of individuals of a single species. With this increase in numbers of individuals of a single species the rarer species, which increase the diversity value, are encountered less often and abundant species are encountered more often. Consequently, diversity values are decreased. When density and frequency values of a single species decreases fewer individuals of the single species are encountered. Rather an increased number of different species are encountered. This, then, tends to increase the diversity value. The low diversity value for the climax prairie site is undoubtedly due to the greatly uneven distribution of individuals per species because of the high density and frequency values of the two major dominants. The considerably higher diversity value found in the moderately grazed site would be due to the decreased density and frequency of the dominants and subsequent increase in the rarer species, even though the variety index is lower than that of the climax site. When a large number of species are present and the frequency of the dominants is low, a more equitable distribution of individuals per species is attained resulting in a higher diversity value.

Table VIII further shows the influence of pooling samples on overall diversity. When the mean and total values for all replicate diversity and variety values are examined an apparent discrepancy is seen; the mean value is lower than the total value. This shows the influence of the interaction between the abundant species. When samples are pooled the rare species have more influence by increasing the overall number of species present. However, this pooling will also in effect increase the frequency of the abundant species and thereby decrease the diversity. Overall the rare species have a greater influence because they reduce the overall abundance of the dominant species. Equitability values, however, show means larger than totals. The abundant species have the greater influence in determining this equitability value. When samples are pooled the number of individuals of the abundant species is increased. This increased number of individuals of the abundant species reduces the evenness of distribution among the total species. Individual samples when analyzed for equitability show less impact from abundance and more from rare species. When samples are pooled the influence of the rare species is reduced because of the increase in the abundant species. The lower the frequency of the abundant species the greater the influence of the rare species. This can be seen in the severely grazed site results. There are more abundant species present but the frequency of each is reduced compared to the other sites. This indicates that the dominants play a smaller role in decreasing equitability but rather act more as rare species and tend to increase equitability and consequently diversity. There are fewer species present in the severely grazed site than in the climax site, but the evenness of distribution of individuals among species is greater resulting in a high equitability and diversity index.

# CHAPTER V

# COMPETITIVE FACTORS

In any study involving allelopathy, it is the responsibility of the researcher to clearly establish biochemical interference and show its relationship to other factors (Muller 1970). To do this, the researcher must evaluate the possibility of competition for physical factors. This possibility of competitive inhibition must be excluded or shown to function in conjunction with allelopathic effects.

Four physical factors, which could possibly become limiting and inhibit weed invasion, were evaluated to determine their role in exclusion of weedy invaders from prairie grasslands. In each of the four field sites soil nutrients, soil moisture, soil temperature, and light were measured to evaluate their potential inhibitory effects.

## Soil Nutrients

Soil nutrient content was determined once during the 1975 growing season. At each site three randomly located sampling points were selected and soil samples collected at the 2-30 cm depth. Each sample consisted of six soil cores collected with a standard T-bar soil corer within a one foot radius. All samples from each site were tested for pH, nitrate nitrogen, phosphorus, and potassium. One sample was additionally tested for calcium, magnesium, iron, zinc, and manganese, a routine micronutrient analysis.*

## Results and Discussion

Results of the soil nutrient assessment are presented in Table IX. A significant difference at the 95% level is shown for pH values between the hay meadow and both grazed sites. Likewise, a significant difference was found between the two grazed sites, with the severely grazed site being more acidic. The most acidic soil was found in the hay meadow with an average pH of 6.1; the least acidic was the moderately grazed site with an average pH of 6.9.

Nitrate nitrogen and phosphorus concentration (lbs/acre) were essentially the same in all sites (Table IX). However, significant differences were found in the amount of potassium present. A significant difference in potassium present (lbs/acre) was found between the climax and moderately grazed sites; hay meadow and moderately grazed sites; and severely grazed and hay meadow sites. The highest amount of potassium was found in the hay meadow and the lowest quantity found in the moderately grazed site.

The climax site had the highest concentrations of the micronutrients iron and manganese and the macronutrient calcium. The highest concentration of magnesium was found in the severely grazed site, while the hay meadow had the most zinc. The lowest concentrations of calcium and magnesium were found in the moderately grazed site; iron and zinc in the severely grazed site; and manganese in the hay meadow.

Soil pH in prairies has been found to range between 6.1-6.8 in virgin prairies and 5.8-6.8 in grazed prairies (Kelting 1954; Voigt and

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[*] Nutrient testing was performed by the Oklahoma State University Extension Soils Laboratory.

## TABLE IX

## AVERAGE VALUES OF pH AND MAJOR MACRONUTRIENTS AND INDIVIDUAL VALUES OF MAJOR MICRONUTRIENTS BY SITE*

| Site | pH | $NO_3$-N lbs/A | P lbs/A | K lbs/A | Ca lbs/A | Mg lbs/A | Fe ppm | Zn ppm | Mn ppm |
|---|---|---|---|---|---|---|---|---|---|
| Climax Prairie | 6.5 | < 5 | 4 | $233^{a}$ | 3350 | 830 | 46.0 | 0.44 | 45.9 |
| Hay Meadow | $6.1^{e,f}$ | < 5 | 3 | $255^{b,c}$ | 3200 | 780 | 24.0 | 0.66 | 12.0 |
| Moderately Grazed Prairie | $6.9^{d,f}$ | < 5 | 3 | $157^{a,b}$ | 3150 | 570 | 13.6 | 0.58 | 20.3 |
| Severely Grazed Prairie | $6.6^{d,e}$ | < 5 | 3 | $200^{c}$ | 3280 | 920 | 11.2 | 0.36 | 24.8 |

*Soil samples collected on 02 July, 1975, during active growing season (soil nutrient analysis performed by OSU Extension Soil and Water Laboratory).

[a-f] Duplicated superscript letters indicate a significant difference ($p < 0.05$ by t-test) between each pair.

Weaver 1951). A comparison of pH values between the climax and severely grazed sites shows no significant difference, even though a great difference in species composition was found. Likewise a significant difference between nutrient concentrations was not found between the climax site and the severely grazed site. In general the climax site contained higher amounts of nutrients than the severely grazed site. The presence of weedy invaders in the moderately grazed and severely grazed sites indicate that these lower amounts of nutrients are sufficient for growth. The pH of a soil can be used to indicate the availability of soil nutrients to plants. At pH values of approximately 6.5 all minerals needed by plants for growth are soluble enough for uptake and utilization (Truog 1947). The pH value obtained for each site indicates that mineral solubility would be sufficient for plant needs in each site.

## Soil Moisture

Soil moisture determinations were made weekly for the period June-September, 1975, and May-June, 1976, for all sites. All soil samples were collected between 9:30 a.m. and 1:00 p.m. on the same day. At each site three representative areas were marked off into one meter square plots. These plots were used for collection of all soil used for soil moisture determinations. Soil samples were collected with a standard T-bar soil corer from selected points within the plot at two depths: 2-10 cm and 20-30 cm. Two soil cores for each soil depth constituted one sample and both were collected immediately adjacent to each other. A total of three samples at each depth were collected for each site. Soil samples were placed in standard aluminum soil sample cans, returned to the laboratory and weighed. Samples were dried at 105 C for 72 hrs in a forced air oven and percent soil moisture determined gravimetrically. All percent soil moisture values were converted to bars for direct comparison.

Moisture retention of soils at specific pressures was measured by a Pressure Membrane Extractor (Black 1965). Intact soil cores were collected from each site and soil water content determined at pressures of 0.5, 1.0, 3.0, 5.0, 7.0, 9.0, 11.0, 13.0, 15.0, and 17.0 bars. At each pressure three replications were carried out.

## Results and Discussion

In general, soil moisture content in the 2-12 cm depth was related closely to precipitation. Three major rainfalls occurred during the summer months of 1975: 23 July (1.37 in.), 14 August (0.94 in.), and 11 September (1.77 in.). The consequent increases in soil moisture can be seen in Figure 8. A second trend seen in Figure 8 is the relationship between soil moisture and the presence or absence of a mulch layer. The presence of a mulch layer in general results in a lower moisture content at the 20-30 cm depth than the 2-12 cm depth. This can be clearly seen by comparing the climax and moderately grazed sites. The severely grazed site shows that soil water potential overall was lower in the 20-30 cm depth, while soil moisture stress was approximately the same at both depths in the hay meadow. This trend corresponds well with the soil structure and the type of vegetation present at each site. Interception and re-evaporation of rainwater by standing vegetation and mulch in the climax prairie resulted in less water reaching the ground. The hay meadow and moderately grazed sites intercepted much less

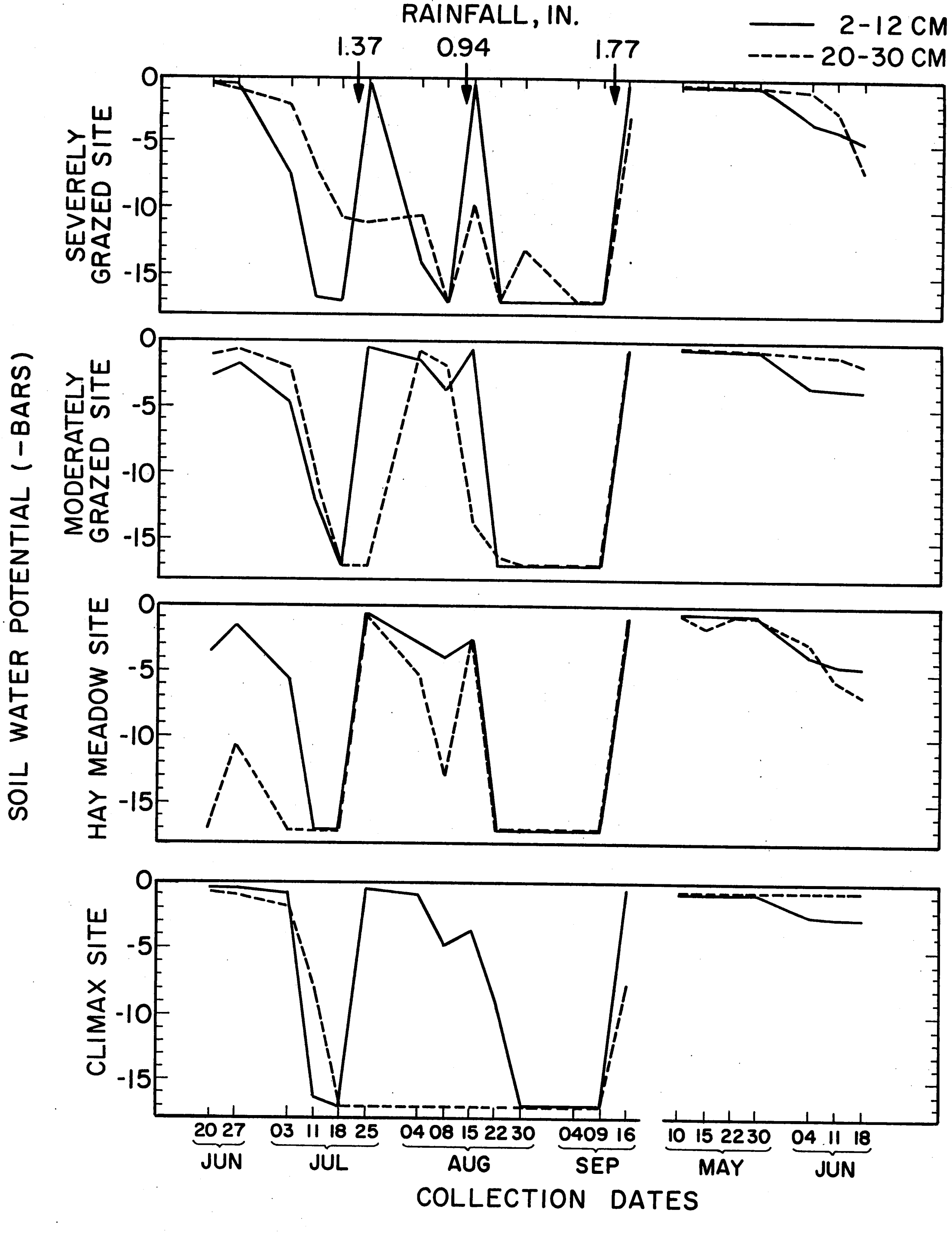

Figure 8. Comparison of Soil Moisture Pattern in All Field Sites For the Period May Through September at Two Depths: 2-12 cm and 20-30 cm. Values are Averages From Triplicate Samples.

rainfall, but soil structure was adequate to allow rapid infiltration. The severely grazed site on the other hand had soil compaction, poor soil structure, surface runoff and probably rapid evaporation which prevented moisture from penetrating downward.

Soil moisture stress showed a consistent increase as the growing period progressed with September showing the highest stress values (Appendix C). The highest soil moisture values for all sites occurred in May. These results correspond very well with the temperature and precipitation regimes for central Oklahoma; precipitation decreases and temperatures increase as summer progresses.

Figure 9 is a comparison of average monthly soil moisture potential in the 2-12 cm depth for each site. This figure shows that soil moisture stress is approximately the same for the climax and severely grazed sites during the months of June and July, 1975. After this time a large difference exists in the soil moisture stress for these two sites, with the severely grazed site showing the higher values. However, during the period of greatest seed germination and establishment soil moisture retention by the climax and severely grazed sites was essentially the same, indicating that sufficient water was available for establishment and survival of weedy species in the climax site. Even more moisture was retained and available in the climax site soil during August and September than in the severely grazed site. However, even though moisture availability was the same or higher in the 2-12 cm depth in the climax site as compared to the severely grazed site there was a conspicuous absence of the weedy annual species in the climax site.

The severely grazed site probably has reduced percolation and infiltration of rainwater because of the absence of a mulch layer and

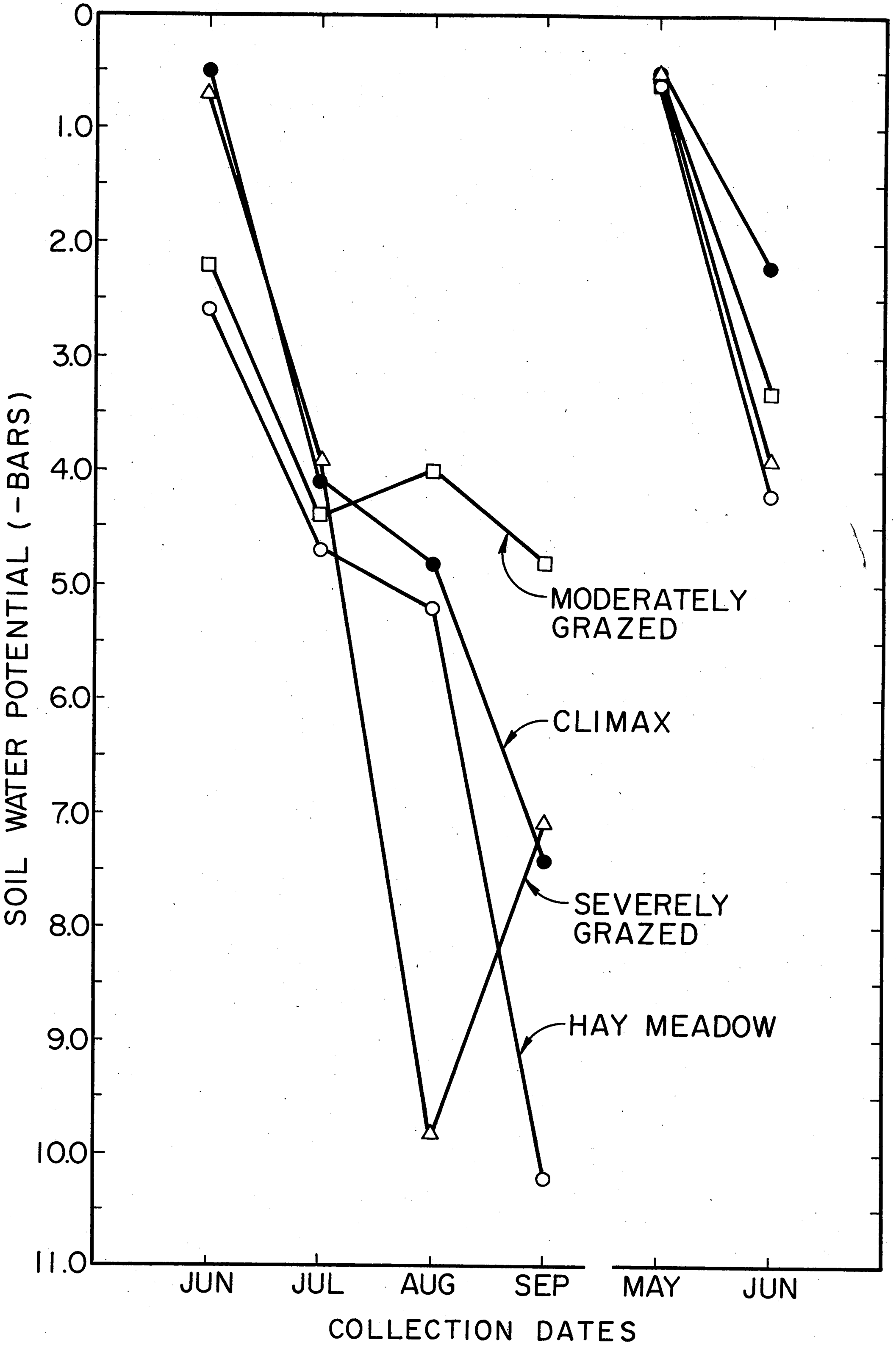

Figure 9. Comparison of Average Monthly Soil Water Potential at the 2-12 cm Depth

trampling by animals; however, soil moisture is sufficiently high to support growth of a number of annual weedy invaders. The moderately grazed site also supports some of the annual weedy species found in the severely grazed site. However, the site was dominated by *Andropogon scoparius* and *A. gerardi*. Overall this site had less soil moisture stress in the 2-12 cm zone than the climax site. These data indicate that sufficient moisture was available in the 2-12 cm zone in the climax site to support these weedy invaders.

### Soil Temperature

Soil temperature measurements were taken weekly for the period June-September, 1975, and May-June, 1976, for all sites with a Yellow Springs Telethermometer Model 42SC. Temperature readings for all sites were collected between the hours of 9:30 a.m. and 1:00 p.m. on the same day. Using the plots laid out for soil sampling, soil surface temperatures were measured with a Yellow Springs Model 401 General Thermometer Probe for all plots at each site. Sub-surface temperatures were measured at 2.0, 4.0, and 6.0 cm depths using a Yellow Springs Model 409 Soil Temperature Probe. Three representative readings within each plot were taken for each surface and sub-surface depth. This gave a total of nine replicate readings for each depth at each site.

#### Results and Discussion

Soil surface temperatures were highly variable at all field sites (Appendix D). The hay meadow and severely grazed sites showed the greatest range in surface temperatures, with overall variations of 17.4 C and 17.3 C, respectively. The least variation in surface temperature was shown by the climax site with an overall variation of only 11.7 C.

Temperature variation decreased with increasing depth in the soil. Least variability occurred at the 6.0 cm depth. Soil temperatures reached maximum values for all soil depths during August and early September. Table X shows average, maximum, and minimum temperatures for all depths and sites.

In early spring surface temperatures of the climax site were comparable to or higher than other sites. During this period the hay meadow had the lowest overall surface temperatures. The order of decreasing soil surface temperatures for May was: climax > severely grazed > moderately grazed > hay meadow.

Variation in soil surface temperatures was found with the climax site having the lowest overall average and the moderately grazed site having the highest overall average. However, there was considerable overlap in the range of temperature variations. Even on sunny days overall surface temperatures were similar in all sites. During May surface temperatures in the climax site were consistently higher than the other sites, including the severely grazed site. This corresponds to the period of greatest seed germination and establishment. These data indicate that temperature is not limiting to the establishment of the weedy species which are so prevalent in the severely grazed site.

## Light

Light measurements were collected monthly during the period July-September, 1975, and May-June, 1976, for all sites. At each site three straight line transects, oriented north to south and 20 m in length, were established across representative vegetation. Each transect was

## TABLE X

## MAXIMUM, MINIMUM, AND AVERAGE SOIL TEMPERATURES BY HABITAT FOR THE GROWING SEASON MAY-SEPTEMBER

| Temperature Range - °C | Climax Prairie | | | | Hay Meadow | | | | Moderately Grazed Prairie | | | | Severely Grazed Prairie | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | cm | | | | cm | | | | cm | | | | cm | | |
| | Surface | 2 | 4 | 6 | Surface | 2 | 4 | 6 | Surface | 2 | 4 | 6 | Surface | 2 | 4 | 6 |
| Maximum | 35.7 | 26.1 | 25.2 | 24.2 | 41.3 | 33.0 | 30.9 | 30.2 | 41.6 | 32.6 | 30.7 | 29.6 | 43.7 | 35.7 | 32.6 | 31.1 |
| Minimum | 24.0 | 19.3 | 19.0 | 17.1 | 23.9 | 19.0 | 17.9 | 17.3 | 27.8 | 23.6 | 20.9 | 20.4 | 26.4 | 20.7 | 19.5 | 18.9 |
| Average | 30.7 | 23.1 | 22.5 | 21.8 | 33.2 | 27.0 | 25.7 | 24.7 | 34.5 | 26.8 | 25.6 | 24.6 | 34.4 | 28.7 | 25.8 | 24.8 |

sub-divided and light readings were taken every 40 cm with a Weston Illumination Meter, Model 756.

Light readings were collected on two consecutive sunny, cloudless days and at two separate times of the day. The severely grazed and moderately grazed sites were measured on day one, and the hay meadow and climax prairie sites were measured on day two. Readings were collected between 7:00 a.m. and 9:00 a.m. and between 12:00 noon and 2:00 p.m. for each site on each collection day. The same order of collecting the readings was followed at each collection period. All readings were collected at ground surface or at mulch layer surface. For bunch grasses, readings were collected at ground surface, but beneath the over-hanging old and new leaves, next to the basal part of the crown. Care was exercised not to disturb the over-hanging leaves. The same procedure was rigorously adhered to for each site. All light readings were collected during the first half of each month.

## Results and Discussion

Available light beneath canopy level in prairies is clearly dependent upon the density of vegetation. The more dense the vegetation the less available light at soil surface. Light measurements taken at the four field sites showed a wide range of values and considerable variation within sites, even within sampled transects. Individual values ranged from less than 1% to 100% of full light. Transect values were pooled to obtain an average percent of full light for each site (Table XI). Data were arbitrarily divided into four light classes: Less than 26% full light; 26-50% full light; 51-75% full light; and greater than 76% full light. Each light reading was then placed into

## TABLE XI

## AVERAGE LIGHT VALUES* PER SITE AS PERCENT OF FULL LIGHT

| Date | Climax Prairie | | Hay Meadow | | Moderately Grazed Prairie | | Severely Grazed Prairie | |
|---|---|---|---|---|---|---|---|---|
| | a.m. | p.m. | a.m. | p.m. | a.m. | p.m. | a.m. | p.m. |
| May | 4.37 | 27.29 | 2.53 | 23.81 | 9.27 | 47.45 | 24.25 | 72.94 |
| June | 3.73 | 20.40 | 2.83 | 15.13 | 20.67 | 45.27 | 22.07 | 68.60 |
| July | 2.66 | 18.15 | 2.90 | 10.43 | 22.82 | 43.20 | 19.70 | 63.25 |
| August | 4.09 | 14.20 | 24.49 | 53.31 | 17.31 | 32.61 | 17.29 | 55.04 |
| September | 3.23 | 12.16 | 14.22 | 33.19 | 16.72 | 30.70 | 25.19 | 54.59 |

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[*] Values expressed are percentages. A.M. values are readings taken between 7:00-9:00 a.m.; p.m. values are readings taken between 12:00 noon and 2:00 p.m.

one of these four classes (Appendixes E and F).

Data presented in Table XI show several trends. Average site values for the early afternoon measurement show a consistent decrease over the sampling period May through September; the hay meadow site is an exception. This corresponds well with the increasing development of the vegetation. The severely grazed site consistently had the highest averages for all sites throughout the entire sampling period, while the hay meadow had the lowest until time of mowing in mid-July. After the hay meadow was mowed the climax site had the lowest values.

These data indicate that as vegetation develops over the growing season there is a constant decrease in available light at the soil surface. The hay meadow showed the greatest reduction, followed by the climax site, moderately grazed site, and severely grazed site, respectively. The available light data furthermore are comparable to values obtained by other workers for prairies (Steiger 1930; Flory, 1936; Weaver and Clements 1938). These data also show that as vegetation becomes dominated by fewer species light availability is decreased and as more weedy species become dominant, light availability is increased. This corresponds very nicely with the growth habit of these species. Bunch grasses, such as Andropogon scoparius, have standing dead litter which forms a closed canopy. If this canopy is not removed, standing dead material accumulates, increasing the effect of the closed canopy. The hay meadow, on the other hand, has a reduced light at ground level due to the greater number of plants present rather than the amount of standing dead litter present. The moderately grazed site has areas of dense vegetation and litter separated by areas of shorter, more sparse vegetation. This results in greater variability between samples, but a higher overall average value. The severely grazed site has more light available at the soil surface due to the small stature of the plants, reduced leaf surface, and greater variability in growth habit of species present.

The morning measurements of light show no consistent pattern. In each site light availability was variable from month to month and between sites. The severely grazed site had the highest value in May and June, moderately grazed site the highest in July, hay meadow the highest in August, and the severely grazed site the highest in September. With the exception of the May and June collections, the climax site showed the lowest values each month. Appendixes E and F show the number of individual values for each collection date and site.

Although light is important for germination and growth of many weedy species the data collected indicate there is sufficient light for growth. Semtner (1972) found that growth of Sorghum halepense under decreased light intensities was slower when compared to growth under higher intensities. Ryle (1967) found that temperate perennial grasses responded to shading by a decreased growth rate. Some weed species germinate under conditions of greatly reduced light intensities; other species, such as Bromus tectorum, require darkness for best germination; and others, such as Tragopogon pratensis, are indifferent to a light or dark requirement (Salisbury and Ross, 1969; Daubenmire 1974). As shown in Appendix F, light values for the climax site fell into all four light classes, indicating that sufficient light was available for growth of weedy invaders.

# CHAPTER VI

# ALLELOPATHY SURVEY

## Field Methods

Five prairie grasses were selected as test species: *Andropogon scoparius*, *A. gerardi*, *A. saccharoides*, *Sorghastrum nutans*, and *Panicum virgatum*. *Andropogon saccharoides* is a late successional species while the other four species are common climax dominants. Field sites for collection of these grasses were established on or near the Oklahoma State University Ecology Preserve located 16 km west of Stillwater, Oklahoma. Collections were taken from these sites for the 12-month duration of the study. During the growing season, from April through October, 1973, green leaves were collected each month, from each species on the same date of each month. During the dormancy period, from November, 1973, to March, 1974, the dead, standing leaves were collected. Samples were clipped from living or dormant grass plants, bagged, and returned to the laboratory where they were immediately oven-dried at 40 C for 48 hrs. No fallen or decomposing litter was included in this part of the study. Leachates were made from these dried samples within four weeks of the collection date.

## Bioassay Procedures

### Leachate Preparation

The bioassay procedure followed in this study is similar to that described by McPherson and Muller (1969). In order to simulate field conditions as closely as possible, whole green grass leaves or whole dead grass leaves and distilled water were used in a ratio of 10 g of dry leaf material to 100 ml of distilled water. These preparations were allowed to soak for three hours. The leachate was then filtered and used as the irrigating agent. Leachate was prepared fresh for each experiment and if storage was required, it was refrigerated and used within 12 hrs. Petri dishes (100 x 15 mm) containing 70 g of washed commercial river sand, were utilized for the bioassay chambers.

### Assay Species

A preliminary screening yielded twelve weedy species which had readily collectable seeds, germinated well, and with one or two exceptions, could occur with the prairie species in nature. Assay seed species used and growth time of each species is shown in Table XII. These weedy species can be divided into two ecological groupings: (1) disturbed prairie species which are commonly found in areas of natural disturbance and commonly occur with native prairie vegetation, and (2) disturbed soil weeds which are primarily agricultural weeds and usually do not interact with native prairie plant species. These are species which commonly invade agricultural fields, roadways, lawns, and waste areas.

## TABLE XII

## SPECIES AND GROWTH PERIOD* OF SEEDS USED IN LEACHATE EXPERIMENTS

| Prairie Weed Species | Growth Period in Days | Disturbed Soil Weed Species | Growth Period in Days |
|---|---|---|---|
| Achillea lanulosa | 9 | Rumex crispus | 5 |
| Chrysopsis pilosa | 14 | Datura stramonium | 5 |
| Desmodium sessilifolium | 9 | Lolium perenne | 5 |
| Elymus canadensis | 16 | Chenopodium album | 10 |
| Hieracium longipilum | 17 | Amaranthus retroflexus | 10 |
| Plantago purshii | 9 | Bromus secalinus | 10 |

*Growth period is the incubation time allowed for development of a useable seedling.

### Bioassay Technique

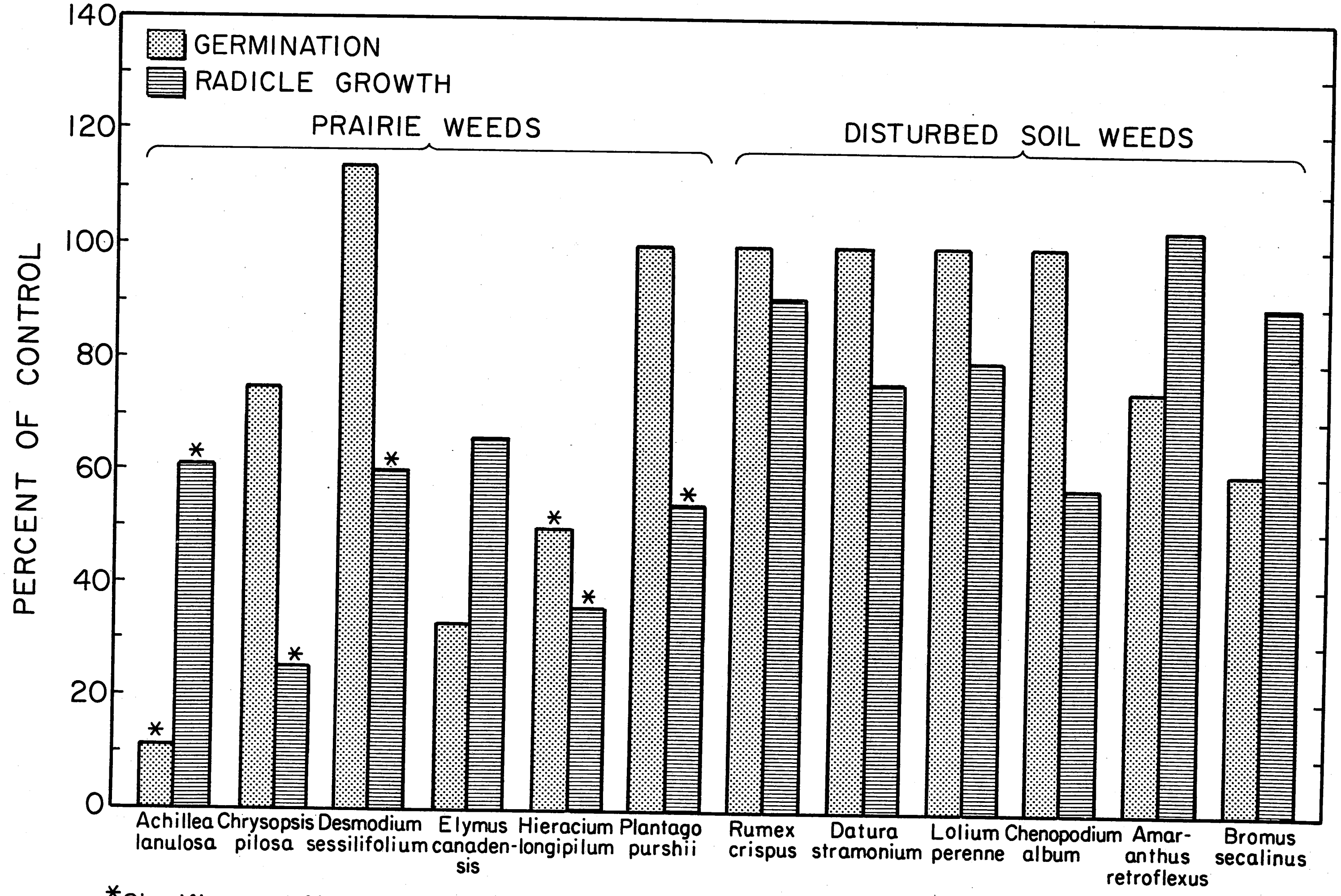
Ten seeds of an assay species were placed on the sand seedbed in a radial arrangement. Three treatment replications and three control replications of each assay species were set up for each test species collected on each collection date. Treatments were irrigated with 10 ml of leachate and controls were irrigated with 10 ml of distilled water. Bioassay chambers were covered with plastic wrap and placed under a 12-12 hr light/dark regime at 27 ± (3) C for the required growth period.

### Results and Discussion

Leaf leachate from all five test grasses significantly inhibited either radicle growth or germination in the majority of assay species at some time during the 12 month duration of the survey. Most species were inhibited with leachate prepared from test species collected during the spring and summer months. *Andropogon scoparius* inhibited 10 of the 12 assay species, *A. gerardi* and *A. saccharoides* inhibited 8, *Panicum virgatum* inhibited 9, and *Sorghastrum nutans* inhibited only 7 species. Species that were considered affected were significantly inhibited at least once during the 12 month survey (Appendixes G through K). Species most affected were the prairie weed species; the disturbed soil weed species were minimally affected.

### Bioassay Results

*Green Leaf Leachate Bioassays*. Leachate from *Andropogon scoparius* collected in June and applied to the 12 weedy species yielded the results shown in Figure 10. The six prairie weed species suffered strong inhibition in radicle growth with *Chrysopsis pilosa* and *Hieracium longipilum*



*Significant difference from control at $p < 0.05$ by t-test.*

Figure 10. Germination Response and Radicle Growth of Twelve Weedy Species as Influenced by Leachate of Andropogon scoparius Collected in June

being affected the most. *Chrysopsis pilosa* was inhibited to 25% of control and *H. longipilum* was inhibited to 36% of control. Three species, *Achillea lanulosa*, *Elymus canadensis*, and *Hieracium longipilum* also suffered strong inhibition of germination. *Achillea lanulosa* was inhibited to 33% of control, and *H. longipilum* to 50% of control. The six disturbed soil weed species appear to suffer no detrimental effects from application of this leachate. Germination and radicle growth were essentially unaffected with only two exceptions: radicle growth of *Chenopodium album* was inhibited to 58% of control and germination of *Bromus secalinus* was inhibited to 60% of control.

Application of a leachate prepared from *Andropogon gerardi* collected in June has in general essentially no effect on either prairie weed species or disturbed soil species. Germination of *Elymus canadensis* and *Chenopodium album* and radicle growth of *Desmodium sessilifolium* show a slight reduction when compared with controls. Germination of *Plantago purshii*, *Rumex crispus*, and *Amaranthus retroflexus* and radicle growth of *A. retroflexus*, *R. crispus*, and *Datura stramonium* show a slight stimulation (but not significant) when compared with controls (Table XIII).

Leachates of *Panicum virgatum* collected in June produced strong inhibition of radicle growth in four prairie weed species, *Chrysopsis pilosa*, *Desmodium sessilifolium*, *Hieracium longipilum*, and *Plantago purshii*, and strong inhibition of germination in *Elymus canadensis* and *H. longipilum*. Disturbed soil weed species showed only one indication of strong inhibition, that being germination of *Chenopodium album* (Table XIII).

Leachate from *Sorghastrum nutans* collected in June only inhibited germination of *Chrysopsis pilosa*. Other assay species were affected

## TABLE XIII

### GERMINATION (germ) AND RADICLE GROWTH (rad grow), AS PERCENT OF CONTROL, OF TWELVE WEEDY SPECIES AS INFLUENCED BY LEACHATE OF FOUR GRASS SPECIES COLLECTED IN JUNE

| Species | *A. gerardi* | | *P. virgatum* | | *S. nutans* | | *A. saccharoides* | |
|---|---|---|---|---|---|---|---|---|
| | germ | rad grow | germ | rad grow | germ | rad grow | germ | rad grow |
| *Achillea lanulosa* | 88 | 90 | 133 | 80* | 75 | 81* | 100 | 94 |
| *Chrysopsis pilosa* | 80 | 79 | 168 | 38* | 60* | 110 | 100 | 144 |
| *Desmodium sessilifolium* | 78 | 64 | 75 | 57 | 100 | 109 | 111* | 111 |
| *Elymus canadensis* | 50 | 77 | 40 | 67* | 100 | 107 | 86 | 89 |
| *Hieracium longipilum* | 80 | 87 | 40* | 38* | 75 | 109 | 50* | 84 |
| *Plantago purshii* | 125* | 93* | 89 | 51* | 100 | 66* | 112 | 55* |
| *Rumex crispus* | 129 | 107 | 100 | 99 | 100 | 97 | 89 | 118 |
| *Datura stramonium* | 100 | 103 | 89 | 71* | 120 | 79 | 140 | 69 |
| *Lolium perenne* | 100 | 93 | 100 | 108 | 90 | 91 | 111 | 88 |
| *Chenopodium album* | 60 | 86 | 50 | 70* | 140 | 88 | 50 | 111 |
| *Amaranthus retroflexus* | 168 | 143 | 80 | 117 | 100 | 117 | 80 | 103 |
| *Bromus secalinus* | 80 | 89 | 87 | 100 | 100 | 134 | 80 | 99 |

*Significant difference at $p < 0.05$ by t-test.

very little, if at all (Table XIII).

*Andropogon saccharoides* leachates reduced germination of *Hieracium longipilum* and *Chenopodium album* and radicle growth of *Plantago purshii*. Response of the remaining nine species was similar and essentially equal to that of the controls (Table XIII).

These results indicate that two test species, *Andropogon scoparius* and *Panicum virgatum*, are allelopathic to a large percentage of the assay species for this time period. If the results from a longer time period are studied, a pattern begins to emerge. *Hieracium longipilum*, a prairie forb increaser, was the species most affected over a four month period. Table XIV indicates the effects of leachate application from the five test species on *H. longipilum* radicle growth for May through August. The table shows that with time the inhibitory effects of *A. scoparius* and *P. virgatum* are diminished. *Andropogon scoparius* inhibited radicle growth to 62% of control in May, to 36% in June, to 44% in July, and to 50% in August. This decrease in inhibitory effect continued until April (Appendix G). *Panicum virgatum* inhibited radicle growth to 82% of control in May, to 38% in June, to 50% in July, and to 69% in August. After August there were no significant times of inhibition (Appendix I). The data indicate, therefore, that for this time period, there is a definite trend toward reduction of inhibition. *Andropogon gerardi*, *A. saccharoides*, and *S. nutans* show no obvious trends in inhibition for this period. Table XIV indicates that for this period *A. gerardi* does not significantly inhibit either radicle growth or germination. *Sorghastrum nutans* shows a significant inhibition of radicle growth only during August while *Andropogon saccharoides* significantly inhibits germination during June and germination and radicle

# TABLE XIV

## EFFECTS OF AN AQUEOUS LEAF LEACHATE ON RADICLE LENGTH OF *HIERACIUM LONGIPILUM*, A PRAIRIE FORB INCREASER**

| Grass Species | May | | June | | July | | August | |
|---|---|---|---|---|---|---|---|---|
| | Germ | Radicle length | Germ | Radicle length | Germ | Radicle length | Germ | Radicle length |
| Andropogon scoparius | 100 | 62* | 50* | 36* | 75 | 44* | 60 | 50* |
| Andropogon gerardi | 100 | 108 | 80 | 87 | 50 | 91 | 67 | 80 |
| Panicum virgatum | 250 | 82 | 40* | 38* | 57* | 50* | 83 | 69* |
| Sorghastrum nutans | 33 | 105 | 75 | 110 | 80 | 83 | 67 | 79* |
| Andropogon saccharoides | 80 | 43 | 50* | 84 | 100 | 114 | 50* | 58* |

*A significant difference from control at $p < 0.05$ by t-test.

**Values are expressed as percent of control. Each value is the average of 30 seedlings.

growth in August.

*Plantago purshii*, a weedy invader of disturbed prairies, also showed a significant reduction in radicle length for this time period. Radicle growth of this species was significantly inhibited by all five test grass species; however, the greatest amount of inhibition occurred during June through August by *Andropogon scoparius* (Table XV). With the exception of *Andropogon gerardi*, test grasses exhibited greastest overall inhibition of radicle growth in June. After June, the trend was a reduction in inhibitory power of the test grasses. *Andropogon gerardi*, however, yielded an increasing degree of radicle growth inhibition from June to August. This test species significantly inhibited radicle growth for all four months (Table XV). *Plantago purshii* radicle growth was significantly inhibited every month of this period by *Andropogon gerardi* and *A. saccharoides*. Germination of *Plantago purshii* was not significantly altered by the test grasses when compared with controls (Table XV).

The radicle growth of *Achillea lanulosa*, a forb increaser, was significantly inhibited by four of the test grasses: *Andropogon scoparius*, *A. gerardi*, *Panicum virgatum*, and *Sorghastrum nutans* (Table XVI). Leachate from *A. saccharoides* affected neither radicle growth nor germination for the period May through August. Radicle growth was significantly inhibited all four months only by *A. scoparius*; *Panicum virgatum* inhibited radicle growth for May through July; *Sorghastrum nutans* was inhibitory only for May and June. However, *P. virgatum* and *S. nutans* were significantly inhibitory to germination (Table XVI). *Andropogon scoparius* exerted the greatest consistent inhibitory effect and the most inhibitory collection was June, which produced a reduction

## TABLE XV

## EFFECTS OF AN AQUEOUS LEAF LEACHATE ON RADICLE LENGTH OF *ACHILLEA LANULOSA*, A PRAIRIE FORB INCREASER**

| Grass Species | May | | June | | July | | August | |
|---|---|---|---|---|---|---|---|---|
| | Germ | Radicle length | Germ | Radicle length | Germ | Radicle length | Germ | Radicle length |
| Andropogon scoparius | 88 | 70* | 11 | 61* | 33 | 62* | 117 | 74* |
| Andropogon gerardi | 100 | 78* | 88 | 90 | 75 | 104 | 78 | 98 |
| Panicum virgatum | 112 | 54* | 133 | 80* | 80 | 73* | 67* | 91 |
| Sorghastrum nutans | 67 | 78* | 75 | 81* | 67* | 112 | 78* | 90 |
| Andropogon saccharoides | 80 | 100 | 100 | 94 | 75 | 92 | 100 | 100 |

*Significant difference from control at $p < 0.05$ by t-test.

**Values are expressed as percent of control and are averages ($n = 30$).

## TABLE XVI

## EFFECTS OF AN AQUEOUS LEAF LEACHATE ON RADICLE LENGTH OF *PLANTAGO PURSHII*, A PRAIRIE FORB INVADER**

| Grass Species | May | | June | | July | | August | |
|---|---|---|---|---|---|---|---|---|
| | Germ | Radicle length | Germ | Radicle length | Germ | Radicle length | Germ | Radicle length |
| Andropogon scoparius | 112 | 94 | 100 | 54* | 125 | 67* | 100 | 69* |
| Andropogon gerardi | 90 | 83* | 125 | 93* | 114 | 79* | 100 | 65* |
| Panicum virgatum | 111 | 77* | 89 | 51* | 90 | 88* | 100 | 94 |
| Sorghastrum nutans | 100 | 94 | 100 | 66* | 100 | 78* | 100 | 98 |
| Andropogon saccharoides | 112 | 69* | 112 | 55* | 80 | 75* | 100 | 81* |

*Significant difference from control at $p < 0.05$ by t-test.

**Values are expressed as percent of control and are averages ($n = 30$).

in radicle length to 61% of control. Panicum virgatum produced the largest overall reduction, 54% of control, with the May collection. The inhibitory effect on radicle length within each test grass was fairly consistent through this time period.

One grass species which decreases with disturbance, Elymus canadensis, was used as an assay species. Table XVII indicates that Andropogon scoparius has no significantly inhibitory effect on either radicle growth or germination. One exception to this occurred for germination in May. Leachate from Sorghastrum nutans had no effect on germination or radicle growth while radicle growth was significantly inhibited in July by Andropogon gerardi. Panicum virgatum and A. saccharoides both had two periods when leachate was inhibitory to radicle growth. Panicum virgatum leachate significantly inhibited radicle growth in June and July; radicle growth was less than control in August, but not significantly.

Leachate prepared from green leaves of the test grasses, overall, had no significant inhibitory effects on the disturbed soil assay species. Andropogon scoparius and A. saccharoides showed no consistent inhibitory trends on any of the six assay species. One species, Lolium perenne, was inhibited by three of the test grasses. Andropogon gerardi significantly inhibited radicle growth in April, May, and August; June was less than control, but not significant; July growth was same as control (Appendix H). Panicum virgatum tended to inhibit radicle length of Lolium perenne from April to December, while Sorghastrum nutans inhibited radicle growth from March to September (Appendixes I and J, respectively). No other inhibitory trends are obvious.

## TABLE XVII

## EFFECTS OF AN AQUEOUS LEAF LEACHATE ON RADICLE LENGTH OF *ELYMUS CANADENSIS*, A PRAIRIE GRASS DECREASER**

| Grass Species | May | | June | | July | | August | |
|---|---|---|---|---|---|---|---|---|
| | Germ | Radicle length | Germ | Radicle length | Germ | Radicle length | Germ | Radicle length |
| Andropogon scoparius | 62* | 106 | 33 | 66 | 100 | 83 | 112 | 79 |
| Andropogon gerardi | 100 | 100 | 50 | 77 | 56 | 76* | 90 | 101 |
| Panicum virgatum | 117 | 102 | 40 | 67* | 78 | 83* | 100 | 91 |
| Sorghastrum nutans | 150 | 99 | 100 | 107 | 90 | 95 | 100 | 88 |
| Andropogon saccharoides | 100 | 66* | 86 | 89 | 143 | 76* | 50 | 102 |

*Significant difference from control at $p < 0.05$ by t-test.

**Values are expressed as percent of control and are averages ($n = 30$).

*Dead Leaf Leachate Bioassays*. Leachates prepared from dead standing leaves collected during the period of December through April were designated dead leaf leachate material. This time period corresponds to the dormancy period of all five test grass species.

Table XVIII compares radicle length of *Achillea lanulosa* and *Plantago purshii* as affected by dead leaf leachate and green leaf leachate from the five test grasses. Leachate prepared from dead leaves of *A. scoparius* and *P. virgatum* showed no significant inhibitory trends on the radicle length of either *Achillea lanulosa* or *Plantago purshii*. *Plantago purshii* was significantly inhibited by the March leachate of *Andropogon scoparius*, however, the other three dead leaf leachates showed stimulatory effects. This is in contrast to the green leaf leachate which demonstrated significant inhibition on both these assay species. *Panicum virgatum* dead leaf leachate also stimulated radicle growth of *Plantago purshii*. Effect of dead leaf leachate from *A. scoparius* and *Panicum virgatum* on *Achillea lanulosa* showed no significant deviation from controls.

Dead leaf leachates prepared from the February and March collections of *Andropogon gerardi* were significantly inhibitory to radicle growth of both *Achillea lanulosa* and *Plantago purshii* (Table XVIII). Leachate from the December and January collections was inhibitory, but was not significant to *P. purshii*. Green leaf leachate of *A. gerardi* was significantly inhibitory to radicle growth of *P. purshii* from all collections, while only the May leachate was significantly inhibitory to *A. lanulosa*. *Andropogon saccharoides* showed a similar trend in inhibitory power (Table XVIII). Dead leaf leachate from January and February were significantly inhibitory to *P. purshii* while leachate from

## TABLE XVIII

## COMPARISON OF EFFECTS ON RADICLE LENGTH BY DEAD AND GREEN LEAF AQUEOUS LEACHATE FROM FIVE GRASS SPECIES**

| Test Grass and Month of Collection | Achillea lanulosa | | | | Plantago purshii | | | |
|---|---|---|---|---|---|---|---|---|
| | Length (mm) | | SE of Mean | | Length (mm) | | SE of Mean | |
| | control | test | control | test | control | test | control | test |
| Andropogon scoparius | | | | | | | | |
| May | 11.1 | 8.3* | 0.58 | 0.66 | 23.1 | 21.8 | 1.39 | 0.78 |
| June | 11.4 | 7.0* | 0.72 | 1.22 | 21.9 | 12.0* | 1.39 | 1.89 |
| July | 5.6 | 3.5* | 0.33 | 0.33 | 21.9 | 14.8* | 1.26 | 0.56 |
| Aug. | 9.6 | 7.1* | 0.44 | 0.67 | 20.8 | 14.4* | 1.24 | 0.55 |
| Dec. | 9.9 | 9.4 | 0.58 | 0.46 | 19.8 | 20.0 | 1.07 | 0.71 |
| Jan. | 10.6 | 12.7 | 0.86 | 1.20 | 19.4 | 20.1 | 0.99 | 0.58 |
| Feb. | 8.1 | 6.0 | 0.50 | 0.65 | 22.0 | 23.3 | 1.53 | 1.03 |
| Mar. | 8.8 | 8.3 | 0.65 | 0.57 | 25.9 | 21.0* | 0.88 | 0.92 |
| Panicum virgatum | | | | | | | | |
| May | 11.3 | 6.0* | 0.56 | 0.35 | 25.5 | 19.6* | 0.41 | 0.86 |
| June | 8.5 | 6.8* | 0.55 | 0.44 | 27.5 | 13.9* | 0.59 | 0.88 |
| July | 11.6 | 8.4* | 0.71 | 0.60 | 25.9 | 22.8* | 0.93 | 1.04 |
| Aug. | 10.9 | 9.9 | 0.86 | 0.95 | 26.5 | 24.8 | 1.10 | 1.13 |
| Dec. | 11.0 | 9.9 | 0.62 | 0.53 | 23.5 | 24.1 | 1.03 | 0.65 |
| Jan. | 7.3 | 8.4 | 0.78 | 0.74 | 21.2 | 19.5 | 0.73 | 0.77 |
| Feb. | 10.1 | 10.6 | 0.65 | 0.62 | 20.9 | 21.4 | 0.60 | 0.49 |
| Mar. | 10.1 | 9.3 | 0.38 | 0.40 | 22.7 | 24.6 | 1.12 | 0.58 |
| Andropogon gerardi | | | | | | | | |
| May | 10.3 | 8.0* | 0.57 | 0.59 | 27.5 | 22.8* | 0.94 | 1.33 |
| June | 6.9 | 6.2 | 0.53 | 0.36 | 25.8 | 20.5* | 1.32 | 0.98 |
| July | 13.1 | 13.6 | 0.52 | 0.79 | 26.6 | 21.0* | 1.16 | 1.01 |
| Aug. | 11.3 | 10.7 | 0.68 | 0.59 | 21.4 | 14.0* | 1.24 | 0.79 |
| Dec. | 10.6 | 11.6 | 0.79 | 0.75 | 24.9 | 23.0 | 0.77 | 0.59 |
| Jan. | 7.7 | 7.7 | 0.99 | 1.03 | 19.6 | 18.9 | 0.88 | 0.80 |
| Feb. | 11.4 | 6.1* | 0.75 | 1.18 | 26.2 | 21.4* | 1.25 | 1.62 |
| Mar. | 13.0 | 11.5* | 0.52 | 0.47 | 24.9 | 22.9* | 0.67 | 0.59 |
| Sorghastrum nutans | | | | | | | | |
| May | 11.9 | 9.6* | 0.55 | 0.79 | 27.0 | 26.2 | 0.52 | 1.27 |
| June | 10.4 | 8.4* | 0.45 | 0.68 | 27.9 | 18.5* | 1.00 | 0.99 |
| July | 9.4 | 10.5 | 0.44 | 0.47 | 27.6 | 22.3* | 1.46 | 1.43 |
| Aug. | 9.3 | 8.3 | 0.65 | 0.58 | 21.2 | 20.6 | 1.28 | 0.75 |
| Dec. | 10.8 | 9.6 | 0.48 | 0.45 | 24.8 | 28.1* | 1.06 | 0.87 |
| Jan. | 7.6 | 6.5 | 0.51 | 0.66 | 21.7 | 20.9 | 1.32 | 1.64 |
| Feb. | 9.9 | 9.0* | 0.33 | 0.31 | 22.2 | 20.1 | 1.17 | 1.29 |
| Mar. | 11.2 | 9.7* | 0.57 | 0.36 | 25.3 | 28.1* | 0.93 | 0.78 |
| Andropogon saccharoides | | | | | | | | |
| May | 14.4 | 14.4 | 0.32 | 0.77 | 30.7 | 20.6* | 1.66 | 1.56 |
| June | 12.9 | 12.1 | 0.68 | 0.57 | 28.2 | 15.6* | 0.89 | 0.64 |
| July | 11.9 | 11.0 | 0.81 | 0.79 | 29.2 | 22.3* | 1.27 | 0.96 |
| Aug. | 9.3 | 9.4 | 0.60 | 0.59 | 25.2 | 20.4* | 0.73 | 0.98 |
| Dec. | 8.8 | 9.1 | 0.58 | 0.69 | 20.5 | 19.2 | 0.73 | 0.56 |
| Jan. | 7.9 | 7.2 | 0.55 | 0.42 | 18.8 | 14.7* | 1.25 | 1.52 |
| Feb. | 9.8 | 8.6* | 0.37 | 0.45 | 19.9 | 16.5* | 0.74 | 0.96 |
| Mar. | 10.0 | 9.7 | 0.65 | 0.48 | 20.7 | 19.6 | 0.69 | 0.56 |

*Significant difference from control at $p < 0.05$ by t-test.

**Values are averages of 30 seedlings.

December and March caused a reduction in growth but not significantly. The February leachate of *A. saccharoides* was significantly inhibitory to *Achillea lanulosa*; December, January, and March leachates did not differ significantly from controls. Green leaf leachate of *Andropogon saccharoides* was significantly inhibitory to radicle growth of *Plantago purshii* from all collections, while leachates from the same period had no effect on *Achillea lanulosa*.

Table XVIII further shows the effects of a dead leaf leachate prepared from *Sorghastrum nutans*. The December and March leachates were significantly stimulatory to radicle growth of *Plantago purshii*. The January and February leachates showed no significant effects. *Achillea lanulosa* radicle length was significantly reduced by dead leaf leachates from the February and March collections. Radicle growth of *A. lanulosa* was reduced but not significantly by the December and January leachates. Green leaf leachate applied to *P. purshii* was significantly inhibitory only from the June and July collections. However, the May and August leachates did cause a reduction in radicle length. *Achillea lanulosa* radicle length was significantly inhibited only by the May and June green leaf leachates.

Overall trends that can be seen in Table XVIII indicate that: (1) *Plantago purshii* radicle length is inhibited by green leaf leachate and stimulated by dead leaf leachates of *Sorghastrum nutans*; *Achillea lanulosa* radicle length is inhibited by both green and dead leaf leachates; (2) *Plantago purshii* radicle length is significantly inhibited by green and dead leaf leachates of *Andropogon saccharoides*; *Achillea lanulosa* is not affected by either leachate; (3) green leaf leachate of *Panicum virgatum* inhibits radicle growth of *A. lanulosa* and *Plantago* *purshii*; dead leaf leachate is stimulatory to *P. purshii* and has no significant effect on *A. lanulosa*; (4) dead leaf leachate of *Andropogon gerardi* is significantly inhibitory to radicle growth of *Achillea lanulosa* and *P. purshii*; green leaf leachate is inhibitory to *P. purshii*; and (5) green leaf leachate of *Andropogon scoparius* significantly inhibits radicle growth of both *Achillea lanulosa* and *Plantago purshii*; dead leaf leachate is stimulatory to *P. purshii* and causes no significant changes in *A. lanulosa*.

Table XIX shows the percent (n = 12) of assay species inhibited by leachate of the five test grass species over the one year survey. As indicated, the decreasing order of inhibitory power is: *Andropogon scoparius* > *Panicum virgatum* > *Andropogon saccharoides* > *Andropogon gerardi* > *Sorghastrum nutans*. *Andropogon scoparius* inhibited the largest number of species of all the test grasses in June; 59% of all assay species were strongly inhibited and 33% were slightly inhibited. *A. scoparius* leachate strongly inhibited more species for the period June through September than any other time of the year. The period of lowest strong inhibition occurred between November and March with two months showing no species inhibited and two months showing only one species inhibited. This period, however, corresponds to the period of highest slight inhibition of species.

*Panicum virgatum* follows the same pattern as *A. scoparius* but with lower percent values. A number of months show strong inhibition, but the majority of months only showed slight inhibition. However, the number of months of strong inhibition and the percent species inhibited by far exceed the other three test grasses. *Andropogon gerardi*, *A. saccharoides*, and *Sorghastrum nutans* show only occasional strong

## TABLE XIX

## PERCENT (n = 12) OF ASSAY SPECIES INHIBITED BY AQUEOUS LEAF LEACHATE OF FIVE GRASS SPECIES OVER ONE YEAR

| Test Species | J | J | A | S | O | N | D | J | F | M | A | M |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Andropogon scoparius | | | | | | | | | | | | |
| Strongly Inhibited[a] | 59 | 42 | 8 | 33 | 17 | 0 | 8 | 8 | 17 | 0 | 33 | 33 |
| Slightly Inhibited[b] | 33 | 25 | 59 | 8 | 58 | 50 | 25 | 42 | 33 | 58 | 42 | 42 |
| Unaffected or Stimulated | 8 | 33 | 33 | 59 | 25 | 50 | 67 | 50 | 50 | 42 | 25 | 25 |
| Panicum virgatum | | | | | | | | | | | | |
| Strongly Inhibited[a] | 33 | 17 | 16 | 33 | 8 | 17 | 8 | 17 | 8 | 8 | 42 | 25 |
| Slightly Inhibited[b] | 33 | 67 | 25 | 25 | 33 | 33 | 33 | 17 | 25 | 33 | 17 | 50 |
| Unaffected or Stimulated | 34 | 16 | 59 | 42 | 59 | 50 | 59 | 66 | 67 | 59 | 41 | 25 |
| Andropogon saccharoides | | | | | | | | | | | | |
| Strongly Inhibited[a] | 8 | 8 | 8 | 8 | 0 | 0 | 8 | 8 | 8 | 0 | 8 | 8 |
| Slightly Inhibited[b] | 33 | 42 | 59 | 42 | 42 | 25 | 42 | 50 | 33 | 50 | 25 | 50 |
| Unaffected or Stimulated | 59 | 50 | 33 | 50 | 58 | 75 | 50 | 42 | 59 | 50 | 67 | 42 |
| Andropogon gerardi | | | | | | | | | | | | |
| Strongly Inhibited[a] | 8 | 8 | 8 | 17 | 8 | 0 | 8 | 8 | 8 | 0 | 8 | 8 |
| Slightly Inhibited[b] | 50 | 33 | 33 | 8 | 33 | 25 | 25 | 42 | 33 | 8 | 58 | 58 |
| Unaffected or Stimulated | 42 | 59 | 59 | 75 | 59 | 75 | 67 | 50 | 59 | 92 | 34 | 34 |
| Sorghastrum nutans | | | | | | | | | | | | |
| Strongly Inhibited[a] | 0 | 8 | 8 | 8 | 8 | 8 | 0 | 8 | 0 | 0 | 0 | 0 |
| Slightly Inhibited[b] | 33 | 33 | 33 | 33 | 25 | 33 | 50 | 25 | 33 | 17 | 50 | 42 |
| Unaffected or Stimulated | 67 | 59 | 59 | 59 | 67 | 59 | 50 | 67 | 67 | 83 | 50 | 58 |

[a] Radicle growth up to 65% of control.

[b] Radicle growth 66-90% of control.

inhibition, this occurring principally during the summer months.

*Andropogon scoparius* Leaf Leachate Effects. *Andropogon scoparius* exhibited the strongest inhibitory effects of all the test grasses; additionally it inhibited the largest percentage of assay species and had the greatest number of months of inhibitory activity (Table XIX and Appendix G).

*A. scoparius* leaf leachate was tested on three additional grass species: *Bromus tectorum*, *Bromus japonicus*, and *Eragrostis trichoides*. *B. tectorum* and *B. japonicus* are common weedy invaders of disturbed prairies. Additionally, leachate was prepared from weekly collections of *A. scoparius* during May and June. This procedure was carried out to determine a more precise time of greatest inhibitory activity of *A. scoparius* leachate.

Figures 11 through 15 show the effects of monthly collections of leachate on radicle length of five assay species. These five species were strongly inhibited in from five to 10 months of the survey. The least affected was *Achillea lanulosa* (Figure 11). This species was significantly inhibited for only five different months, April through August. This time period corresponds to the main growing season of *Andropogon scoparius*, indicating that leachate from the green leaves of *A. scoparius* is significantly inhibitory to some weedy invaders. The greatest significant inhibition of *Achillea lanulosa* radicle growth occurred in late May (41% of control) and the least inhibition which was statistically significant occurred in April (78% of control). Leachate prepared from dead leaves of *A. scoparius* had no significant effect on *Achillea lanulosa* radicle growth.

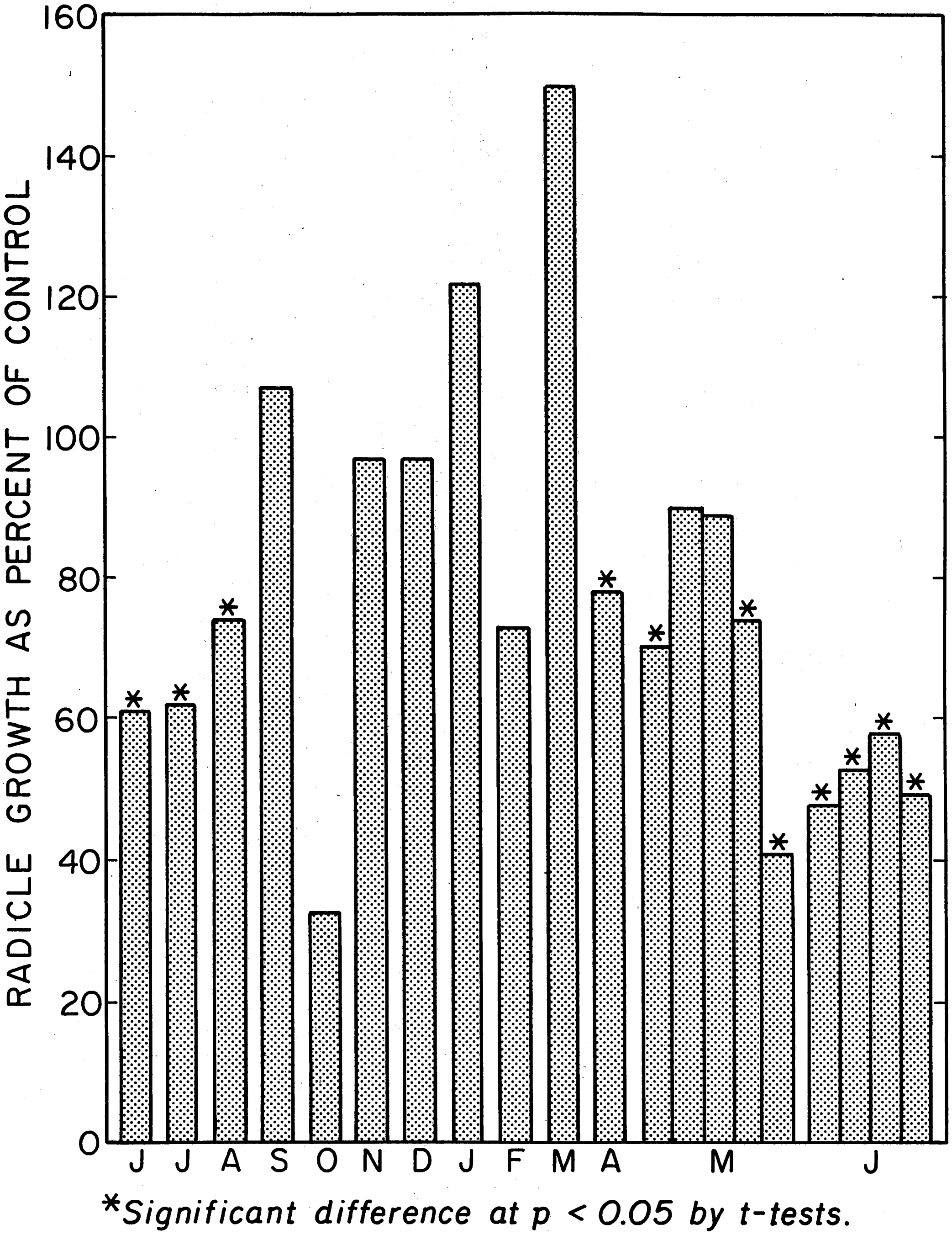


Figure 11. Achillea lanulosa Radicle Growth as Influenced by Leachate From Monthly Collections of Andropogon scoparius

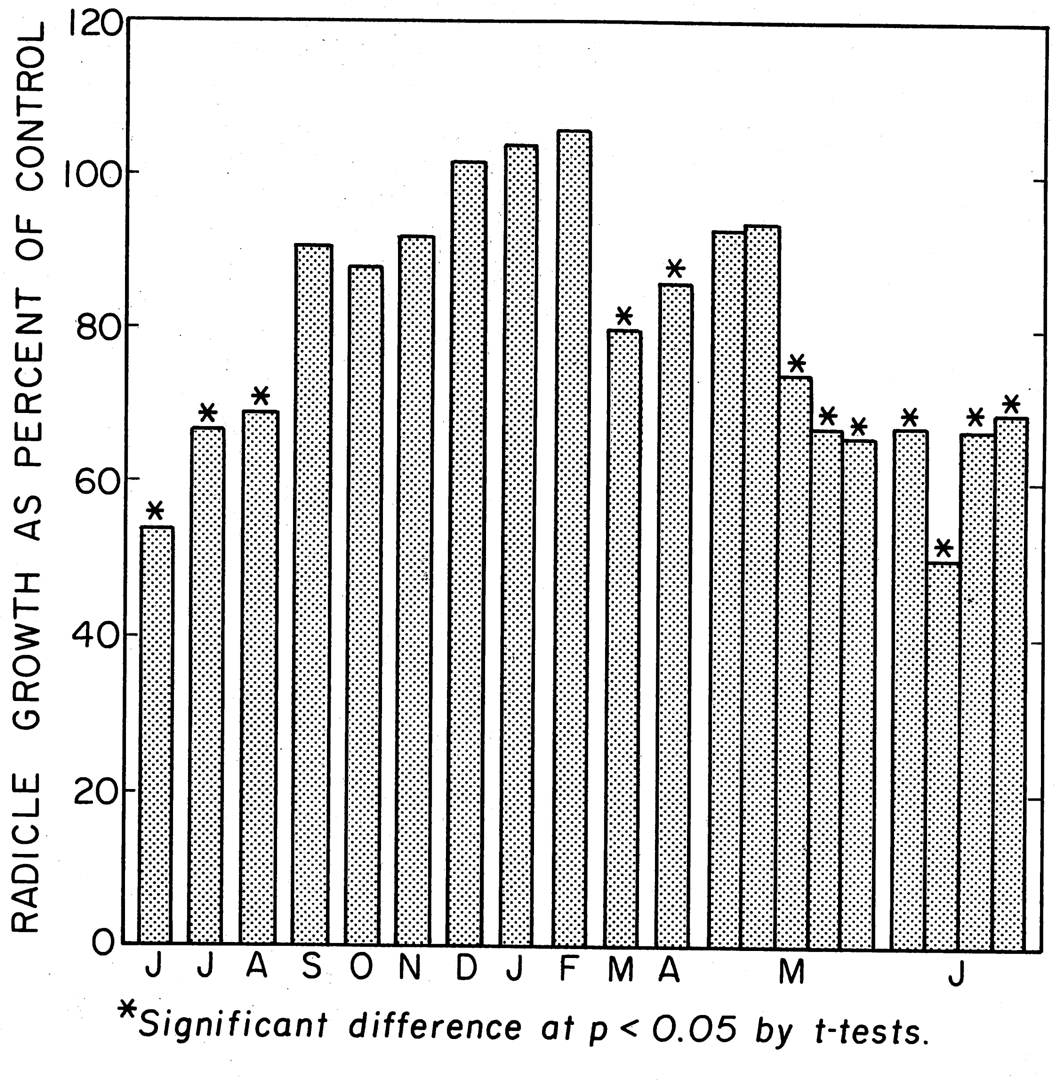


Figure 12. Plantago purshii Radicle Growth as Influenced by Leachate From Monthly Collections of Andropogon scoparius

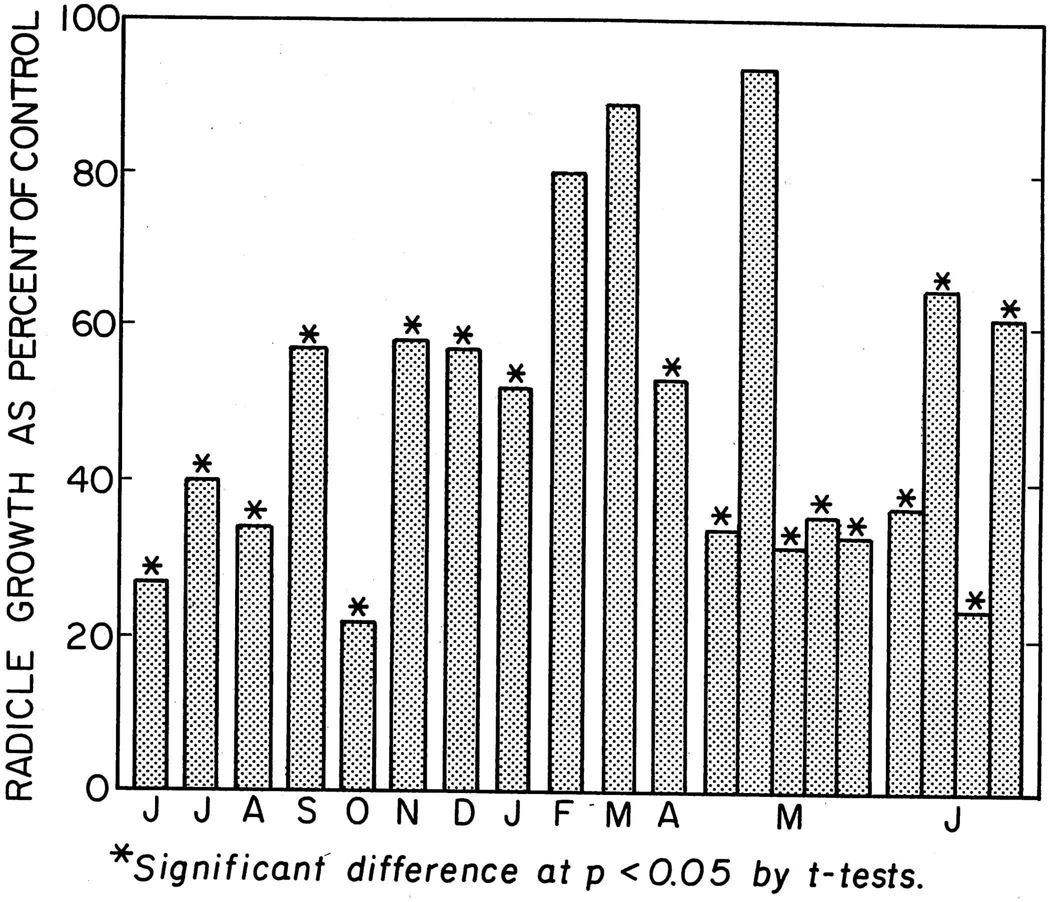


Figure 13. Bromus japonicus Radicle Growth as Influenced by Leachate From Monthly Collections of Andropogon scoparius

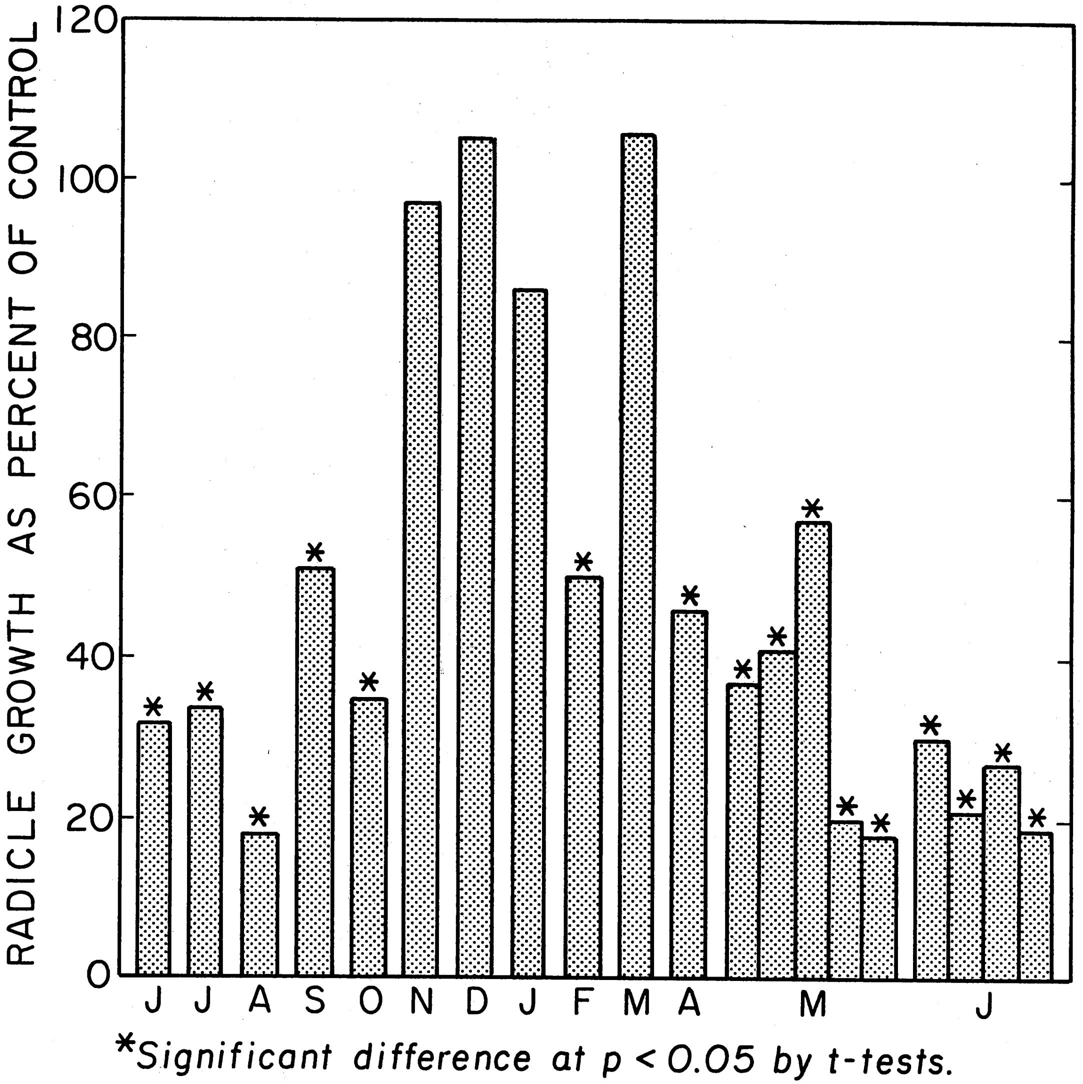


Figure 14. Eragrostis trichoides Radicle Growth as Influenced by Leachate From Monthly Collections of Andropogon scoparius

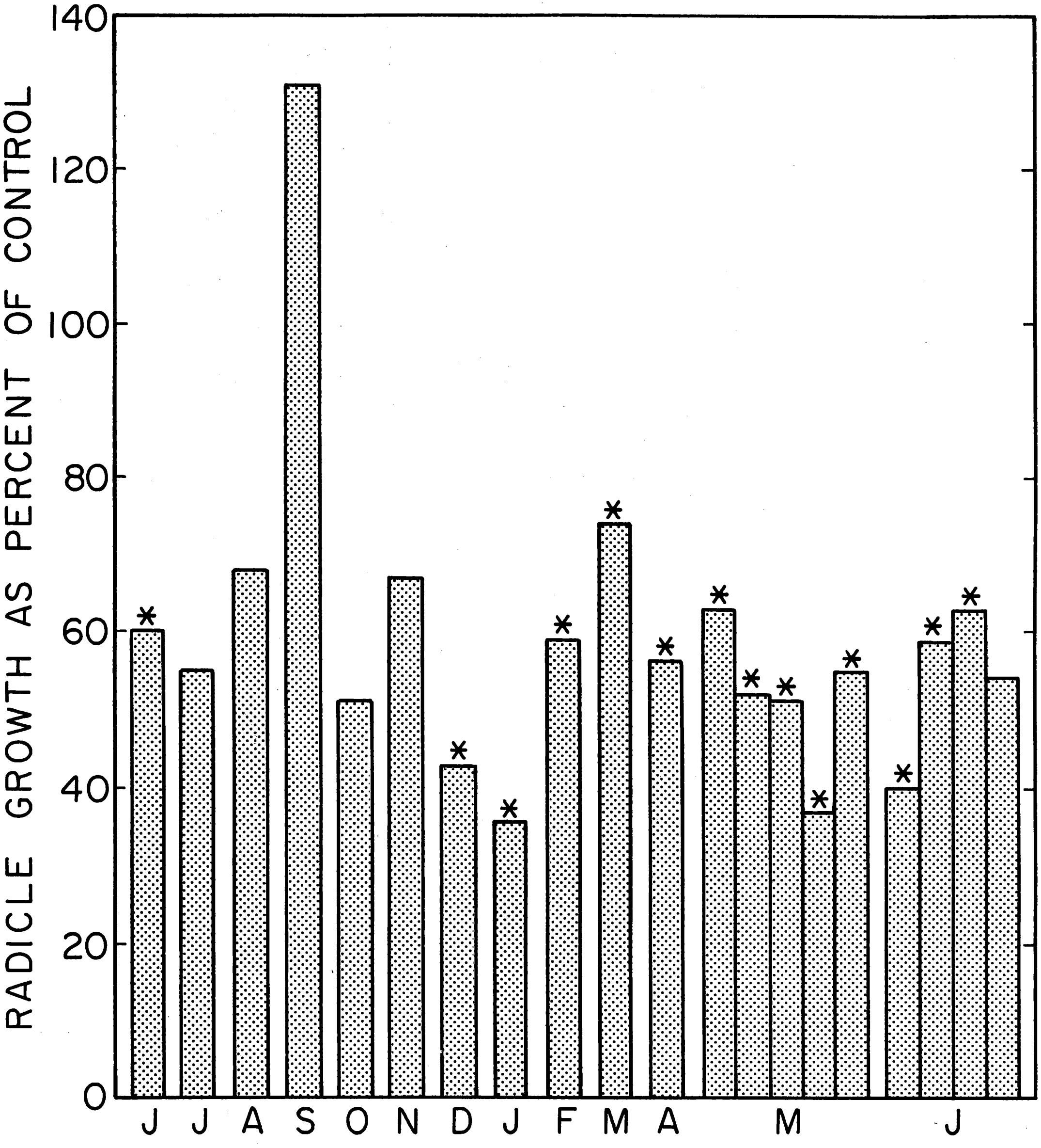


Figure 15. Desmodium sessilifolium Radicle Growth as Influenced by Leachate From Monthly Collections of Andropogon scoparius

Radicle growth of Plantago purshii was significantly inhibited by leachate from six different monthly preparations, March through August (Figure 12). This corresponds quite well with inhibition of Achillea lanulosa. However, the month with the greatest significant inhibition was June (50% of control) and the lowest statistically significant inhibition occurred in April (86% of control). Leachate prepared from dead leaves was significantly inhibitory only once, in March (80% of control).

Bromus japonicus radicle growth was affected most often and strong inhibition was evident (Figure 13). Radicle growth was significantly inhibited for 10 of the 12 collections. The only months not showing significant inhibition were February and March; however, growth was less than control for these two months. The period of greatest consistent inhibition occurred in mid to late May, while the least inhibition occurred in November/December. Bromus japonicus is a weedy invader of disturbed prairies and is a winter annual which makes its appearance in the fall, grows slowly during the winter, and blooms in early spring. Inhibition is maximal during seed set, and thus probably interferes with this crucial process. There is also considerable inhibition during the fall germination period.

Significant inhibition of Eragrostis trichoides occurred during eight of the 12 monthly collections (Figure 14). Only leachate made during the months of November, December, January, and March proved to be non-inhibitory. The greatest significant inhibition occurred during August, while the lowest statistically significant inhibition occurred in mid-May.

The only legume assay species tested, Desmodium sessilifolium, was significantly inhibited for seven of the 12 collection months, December through June (Figure 15). Only one collection, September, showed no inhibition. The months of July, August, October, and November showed a reduction in radicle length, however, variability between replicates was great enough to yield statistically nonsignificant differences. Though great variation occurred, a large proportion of the seedlings were strongly inhibited compared to the controls. Thus in nature many of the plants would not have lived past the seedling stage, and it seems reasonable to attach substantial biological significance to the inhibition observed. The greatest inhibition was found in late May while the least inhibition was found in March.

Table XX shows a comparison between the inhibitory effects of dead leaf versus green leaf leachate on radicle length of *Bromus japonicus* and *Eragrostis trichoides*. As shown green leaf leachate is strongly inhibitory to both species while dead leaf leachate causes only a reduction in *B. japonicus* during February and March. Dead leaf leachate appears to cause a slight stimulation of radicle growth of *E. trichoides* from the December and March collections, while inhibiting radicle growth from the January and February collections.

Appendix H reveals the effect of green leaf leachate on germination and radicle length of five assay species during collection months of April through August. As previously indicated, this is the period of greatest inhibitory activity of *Andropogon scoparius*. All five assay species were inhibited during the period 31 May through 13 June. This is the period of greatest inhibition to radicle growth for these weedy species. Furthermore, during this time period germination of three assay species is significantly inhibited. Only germination of *Bromus*

## TABLE XX

## EFFECTS OF DEAD AND GREEN LEAF AQUEOUS LEACHATE FROM A. SCOPARIUS ON RADICLE GROWTH OF TWO WEEDY INVADERS OF DISTURBED PRAIRIES**

| Collection Month | Bromus japonicus | | | | Eragrostis trichoides | | | |
|---|---|---|---|---|---|---|---|---|
| | Length (mm) | | SE of Mean | | Length (mm) | | SE of Mean | |
| | Control | Test | Control | Test | Control | Test | Control | Test |
| May | 16.6 | 5.8* | 1.63 | 0.92 | 23.5 | 7.1* | 1.33 | 0.71 |
| June | 12.1 | 3.1* | 1.70 | 0.66 | 20.9 | 6.6* | 1.35 | 0.70 |
| July | 9.9 | 3.9* | 1.44 | 0.80 | 19.6 | 6.7* | 1.39 | 0.50 |
| Aug. | 10.4 | 3.6* | 1.49 | 0.90 | 23.6 | 4.2* | 1.37 | 0.61 |
| Dec. | 16.8 | 9.4* | 1.55 | 1.04 | 19.4 | 20.4 | 2.11 | 1.94 |
| Jan. | 15.8 | 8.2* | 1.84 | 1.16 | 19.2 | 16.4 | 1.42 | 1.35 |
| Feb. | 13.3 | 10.5 | 1.76 | 1.20 | 23.2 | 11.4* | 1.45 | 1.51 |
| Mar. | 18.0 | 16.1 | 1.54 | 1.45 | 19.1 | 20.2 | 1.60 | 1.52 |

*Significant difference from control at $p < 0.05$ by t-test.

**Values are averages of 30 seedlings.

*tectorum* and *Plantago purshii* were not inhibited during the entire period April through August. Germination of *Achillea lanulosa* was significantly inhibited from 13 June through 27 June; *Hieracium longipilum* germination was significantly inhibited from 20 May through 27 June. These periods of greatest inhibition of germination further correspond well to the period of greatest radicle length reduction.

*Summary of All Survey Leachate Experiments*. *Andropogon saccharoides*, *A. gerardi*, and *Sorghastrum nutans* show occasional low intensity inhibition; *Panicum virgatum* and *Andropogon scoparius* are inhibitory to *Chrysopsis pilosa*, *Desmodium sessilifolium*, *Hieracium longipilum*, *Plantago purshii*, *Elymus canadensis*, and *Achillea lanulosa*, all prairie weed species, and occasionally to some of the disturbed soil weed species. The phytotoxic material is produced during the early part of the growing season and is present in sufficiently high concentrations to cause strong inhibition of both radicle growth and seed germination in mid-May to late June. One major avenue of release of this phytotoxic material is leaching from the green leaves of the plant. The compound(s) could be released onto leaf surfaces and because of water solubility be removed from the leaves and deposited on the soil surface by precipitation. Furthermore, this period of high inhibitory activity corresponds to the period of highest average rainfall for this part of Oklahoma.

*Andropogon scoparius* was found to have the greatest inhibitory activity. Green leaf leachate from this species inhibited the greatest number of weedy species and also produced the most severe radicle growth inhibition. Leachates prepared from dead leaves showed a low degree of inhibitory power. Many of the weedy invaders of damaged prairies are summer annuals and reproduce by seed. Growth of these species begins in early spring which corresponds with the breaking of dormancy by Andropogon scoparius. Since allelopathic compounds usually are effective only against seeds and young seedlings, the period of seed germination and early seedling growth would be the most susceptible to inhibitory activity. The period of greatest inhibitory activity of Andropogon scoparius leachate occurred from mid-May to late June, the same time of seed germination and early seedling growth of the weedy invaders.

Prairie weed species were inhibited most often and effectively. The disturbed soil weed species were essentially unaffected by either green leaf or dead leaf leachates from any of the test grass species. These disturbed soil weed species are species which are commonly associated with cultivated fields or other areas of very severe disturbance involving the moving of the soil substrate. Several of these species are also common lawn invaders. Apparently these species have evolved mechanisms capable of tolerating high levels of severe disturbance without being adversely effected.

Dead leaf leachate produced some inhibitory activity against a few of the assay species, especially Bromus japonicus. Andropogon scoparius leachate was inhibitory to B. japonicus radicle growth for 10 of the 12 collection dates. This indicates that the inhibitory compound may be released slowly over a period of time from the standing dead litter. As indicated in Figure 13, B. japonicus is most strongly inhibited during spring and summer and then a decrease in inhibitory activity occurs with the least inhibition occurring during February and March. This corresponds well with the precipitation regime of the region. Lowest average monthly precipitation occurs during the winter months from December to February. Water to leach inhibitors from the leaves would be least available during this period.

The curve of inhibitory activity for Andropogon scoparius and Panicum virgatum was found to peak in spring and early summer. The number of species inhibited and the severity of inhibition was about constant for the 12 month survey period for the other three test grasses.

# CHAPTER VII

# ADDITIONAL *ANDROPOGON SCOPARIUS* BIOASSAYS

## Crown Mulch

Bunches of *Andropogon scoparius* were selected which showed no growth at the center of the crown but possessed numerous tillers around the periphery of the crown. Dead material from the center of the crown was collected during the early active growing season from several bunches, combined, returned to the lab, and dried for 72 hrs in a forced air oven at 40 C. Ten g of this material was soaked in 100 ml distilled water for 3 hr. The prepared leachate was used to irrigate seeds in a bioassay to determine its effects upon biological activity. Twenty seeds of *Bromus japonicus* and *Eragrostis trichoides* were positioned in a radial manner in separate petri dishes on filter paper seedbeds. Each test species seedbed was irrigated with 2 ml of the prepared leachate, the dishes were sealed and stratified at 4 C for 18 hr. Bioassays were then incubated in the dark at 26 C for 72 hr. Controls were identical except 2 ml of distilled water was used as the irrigating solution. Twenty seeds of *Achillea lanulosa* and *Plantago purshii* were positioned in a radial manner in separate petri dishes containing 70 g of washed commercial river sand. Seedbeds of the assay species were irrigated with 10 ml of the prepared leachate, the dishes were sealed and placed in a 12/12 hr light/dark regime at 27 ± (3) C for nine days. Controls were irrigated with 10 ml distilled water. The assay and controls were replicated five times in each experiment and the experiment was duplicated.

### Soil Surface Mulch

Well separated bunches of *Andropogon scoparius* were located which had abundant soil surface mulch between and around them. This mulch was characterized by being free from the bunch, grayish in color, and partially decomposed. Fresh organic material on this mulch layer was discarded and only the partially decomposed material used. The older more completely decomposed mulch was not tested. Bioassay procedure followed was as described above in "Crown Mulch" section.

### Dead Standing Litter

During the early growing season bunches of *Andropogon scoparius* were located which possessed few green tillers but had considerable standing, dead material from the previous growing season. Material which touched the mulch layer or soil surface was not collected. Only standing dead leaves from the periphery of the crown were collected and utilized. Bioassays were prepared as described in "Crown Mulch" section above.

## Results and Discussion

Crown mulch, soil surface mulch, and dead standing litter produced no statistically significant inhibition in the assay species tested (Table XXI). Radicle growth was stimulated by the dead standing litter leachate in all species but was not statistically significant; crown mulch leachate stimulated germination in *Bromus japonicus* and radicle

## TABLE XXI

## EFFECTS OF AQUEOUS LEACHATE PREPARED FROM THREE TYPES OF *ANDROPOGON SCOPARIUS* MATERIAL ON GERMINATION AND RADICLE GROWTH OF FOUR ASSAY SPECIES**

| Bioassay Material | *Bromus japonicus* | | | *Eragrostis trichoiodes* | | | *Achillea lanulosa* | | | *Plantago purshii* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | % of control | | treatment average rad. length in mm | % of control | | treatment average rad. length in mm | % of control | | treatment average rad. length in mm | % of control | | treatment average rad. length in mm |
| | germ | radicle length | | germ | radicle length | | germ | radicle length | | germ | radicle length | |
| Soil Surface Mulch | | | | | | | | | | | | |
| Exp. 1 | 102 | 119 | 18.24 | 94 | 87 | 6.58 | 98 | 102 | 10.6 | 102 | 107 | 21.7 |
| Exp. 2 | 101 | 115 | 18.48 | 97 | 94 | 6.73 | 100 | 97 | 9.7 | 97 | 104 | 19.9 |
| Crown Mulch | | | | | | | | | | | | |
| Exp. 1 | 102 | 98 | 17.45 | 90* | 105 | 6.38 | 100 | 96 | 11.1 | 98 | 111 | 22.3 |
| Exp. 2 | 100 | 103 | 18.14 | 94 | 109 | 6.81 | 100 | 103 | 10.3 | 94 | 108 | 21.8 |
| Dead Standing Litter | | | | | | | | | | | | |
| Exp. 1 | 98 | 110 | 18.78 | 107 | 116 | 6.46 | 98 | 109 | 10.9 | 112 | 97 | 20.6 |
| Exp. 2 | 102 | 106 | 18.57 | 98 | 122 | 6.89 | 103 | 111 | 10.5 | 106 | 102 | 20.2 |

*Significant difference at $p < 0.05$ by t-test.

**Values are averages of five replicates (n = 100).

growth in all species but also not statistically significant; crown mulch leachate did, however, significantly inhibit germination of *Eragrostis trichoides*; soil surface mulch leachate stimulated both germination and radicle growth in *B. japonicus* and *Plantago purshii*, and radicle length in *Achillea lanulosa*; leachate from soil surface mulch did reduce germination and radicle growth in *E. trichoides* but the reduction was not statistically significant. These data indicate the leachate prepared from these different materials show no overall trend in inhibitory activity against the weedy species used and in fact may even be stimulatory. Leachate prepared from soil surface mulch did reduce germination and radicle growth of *E. trichoides* but there was no statistically significant difference between test and control. One exception to the overall trend was exhibited by *E. trichoides*; a statistically significant inhibition of germination was found in one experiment using leachate prepared from crown mulch.

The water soluble toxin(s) demonstrated in the green leaf leachate experiments appear to be lost over a period of time after the leaves die. All material used in these experiments was greater than one year of age and had, therefore, been exposed to considerable precipitation. Water soluble toxins, present when the green leaves died, would have had ample time to be completely leached away or decomposed by microbial action. The inhibitor(s) apparently persist for a short period after the growing season, as indicated by the allelopathic survey, but with time the inhibitory activity is lost.

### Green Leaves Leached Immediately

Actively growing leaves of Andropogon scoparius were collected from the field on 07 June, 1976. Leaves were returned to the lab and leached within 30 minutes after clipping. Ten g of leaves were soaked in 100 ml distilled water for three hr, the solution was then filtered and used as the irrigating solution. Additionally, a portion of the collection was set aside to air dry for seven days. The portion set aside to be air dried was separated into sets each weighing 10 g wet weight. Leachate was prepared from the air dried leaves in the same way. Leachate from fresh leaves was concentrated 1X, 2X, 5X, and 10X to determine the effects of increasing concentration. Concentration of the leachate solution was accomplished by flash evaporation *in vacuo*. Four bioassay species were tested: Bromus japonicus, Eragrostis trichoides, Achillea lanulosa, and Plantago purshii. Bioassay technique followed was as described in "Crown Mulch" section above.

#### Results and Discussion

Overall 1X concentrated fresh leaf leachate appeared to have little inhibitory activity on the four assay species tested (Table XXII). However, statistically significant inhibition of radicle growth in Achillea lanulosa and germination of Plantago purshii was found indicating the presence of an inhibitor. Concentrations of 2X, 5X, and 10X produced statistically significant inhibition in all test species. When the effects of leachate prepared from fresh leaves is compared with the effects of leachate prepared from air dried leaves there apparently is less inhibition from the fresh leaf leachate. Leachate from the air

# TABLE XXII

# EFFECTS OF CONCENTRATED LEACHATE FROM GREEN, GROWING LEAVES OF A. SCOPARIUS LEACHED IMMEDIATELY AFTER CLIPPING COMPARED WITH LEACHATE PREPARED FROM LEAVES OF THE SAME COLLECTION AIR DRIED ONE WEEK*

| Bioassay Species | Fresh Leachate Concentration | | | | | | | | | | | | Leachate From Air Dried Leaves | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1X | | | 2X | | | 5X | | | 10X | | | | | |
| | % of control | | treatment average rad. length in mm | % of control | | treatment average rad. length in mm | % of control | | treatment average rad. length in mm | % of control | | treatment average rad. length in mm | % of control | | treatment average rad. length in mm |
| | germ | radicle length | | germ | radicle length | | germ | radicle length | | germ | radicle length | | germ | radicle length | |
| Bromus japonicus | 93.3 | 94.0 | 23.5 | 105.6 | 85.9$^{a}$ | 15.6 | 94.4 | 75.1$^{a}$ | 12.7 | 97.7 | 66.1$^{a,b}$ | 12.8 | 91.6 | 26.0$^{a,b}$ | 3.9 |
| Eragrostis trichiodes | 100.0 | 98.3 | 9.7 | 92.0 | 68.3$^{a}$ | 1.92 | 92.9 | 76.0$^{a}$ | 4.7 | 93.4 | 76.1$^{a}$ | 5.6 | 101.2 | 45.9$^{a,b}$ | 2.6 |
| Achillea lanulosa | 102.4 | 83.6$^{a,b}$ | 6.5 | 98.9 | 70.1$^{a,b}$ | 6.2 | 81.0$^{a,b}$ | 68.9$^{a,b}$ | 6.7 | 60.9$^{a,b}$ | 67.9$^{a,b}$ | 7.4 | 43.2$^{a,b}$ | 56.1$^{a,b}$ | 6.3 |
| Plantago purshii | 71.2$^{a}$ | 105.9 | 24.9 | 92.1 | 67.9$^{a,b}$ | 17.4 | 93.3 | 56.9$^{a,b}$ | 12.6 | 85.0$^{a,b}$ | 51.9$^{a,b}$ | 14.1 | 101.1 | 49.5$^{a,b}$ | 11.6 |

*Values are averages of five replicates (n = 100).

[a] Significant difference at $p < 0.05$ by t-test.

[b] Significant difference at $p < 0.01$ by t-test.

dried leaves significantly inhibited radicle growth of all the bioassay species and germination of Achillea lanulosa. Fresh leaf leachate significantly reduced ($p < 0.01$) radicle growth of A. lanulosa at all concentrations; radicle growth of Plantago purshii at 2X, 5X, and 10X; and radicle growth of Bromus japonicus at 10X. Additionally, fresh leaf leachate significantly reduced ($p < 0.05$) radicle growth of B. japonicus at 2X and 5X; and radicle growth of Eragrostis trichodes at 2X, 5X, and 10X (Table XXII).

It is apparent from these data that one or more inhibitors are present in the fresh leaf leachate, but the concentration is low. During May and June monthly average precipitation is high. It is likely that phytotoxins are released onto the leaf surfaces and are quickly leached into the soil where they build up concentrations to inhibitory levels. Additionally, tillers of A. scoparius are constantly dying through the growth period under field conditions. These dead tillers do not fall to soil surface but remain standing. Under these conditions they would become air dried and larger concentrations of the inhibitor(s) would be leached and deposited. Furthermore, field observations have shown that parts of tillers may die, especially the tips, while the remainder of the tillers remain viable. This dead portion would also release the inhibitor(s).

## Soil Leachates

To confirm the results of the fresh leaf leachate experiments, a series of soil leachate bioassays were carried out. Aqueous leachate was prepared from Andropogon scoparius leaves which were air dried one week. One hundred ml of leachate was poured onto 70 g of soil from a cultivated field, filtered, using a Buchner funnel and collected. The soil filtered leachate and the soil were then tested for inhibitory activity. Species used in the bioassays were Bromus japonicus, Eragrostis trichoides, Achillea lanulosa, Plantago purshii, and Desmodium sessilifolium. Bioassay technique was the same as in "Crown Mulch" section above.

The cultivated field soil irrigated with the air dried leaf leachate was also utilized as a bioassay seedbed. Soil was removed from the Buchner funnel with care to avoid breaking or crumbling the resulting soil disk. Twenty seeds of each of the above assay species were sown directly on separate soil disks, placed in petri dishes, sealed, and grown for the appropriate time periods. Controls consisted of 70 g cultivated field soil watered with 100 ml of distilled water and filtered using a Buchner funnel. Controls and tests were run in triplicate.

## Results and Discussion

Table XXIII indicates that leachate prepared from air dried leaves was inhibitory before being passed through the soil. After passage through the soil segment the filtrate exhibited no statistically significant inhibitory activity on the assay species tested. The soil segment, however, exhibited considerable inhibitory activity. Inhibition of radicle length of seeds grown on the soil seedbed was as high as 51% of control. These data indicate that soil can trap released inhibitors. With sporadic precipitation throughout the active growing season, the small concentration of inhibitor released to the leaf surface would be deposited on the soil surface, eventually reaching concentrations high enough to inhibit germination and growth of invading species trying to

## TABLE XXIII

## EFFECTS OF LEACHATE FROM A. SCOPARIUS AFTER BEING PASSED THROUGH CULTIVATED FIELD SOIL*

| Bioassay Species | Leachate From Air Dried Leaves | | | Soil Leachate | | | Soil Seedbed | | |
|---|---|---|---|---|---|---|---|---|---|
| | % of control | | treatment | % of control | | treatment | % of control | | treatment |
| | germ | radicle length | average rad. length in mm | germ | radicle length | average rad. length in mm | germ | radicle length | average rad. length in mm |
| Bromus japonicus | 76.3$^{a,b}$ | 33.3$^{a,b}$ | 5.47 | 94.8 | 92.5 | 14.42 | 82.1$^{a}$ | 49.1$^{a,b}$ | 8.00 |
| Eragrostis trichoides | 96.5 | 32.6$^{a,b}$ | 6.60 | 98.3 | 98.9 | 19.20 | 98.2 | 43.4$^{a,b}$ | 8.48 |
| Achillea lanulosa | 92.5 | 59.3$^{a,b}$ | 6.65 | 94.6 | 96.4 | 10.30 | 91.1 | 61.5$^{a,b}$ | 6.53 |
| Plantago purshii | 98.1 | 51.2$^{a,b}$ | 11.44 | 100.0 | 92.3 | 24.21 | 89.7 | 52.1$^{a,b}$ | 12.15 |
| Desmodium sessilifolium | 93.6 | 62.6$^{a}$ | 8.68 | 90.0 | 99.1 | 15.02 | 96.2 | 67.2$^{a}$ | 9.70 |

*Values are averages from three replicates (n = 60). Soil leachate is leachate from air dried leaves that was passed through cultivated field soil and collected; soil seedbed was cultivated field soil that had leachate from air dried leaves filtered through.

$^{a}$Significant difference at $p < 0.05$ by t-test.

$^{b}$Significant difference at $p < 0.01$ by t-test.

become established. Numerous workers have concluded that released inhibitors are accumulated in the soil (Muller and Del Moral 1966; Wilson and Rice 1968; McPherson and Muller 1969; Del Moral and Muller 1970; Chou and Muller 1972; Rice 1974). Wilson and Rice (1968) found that aqueous leaf leachate of *Helianthus annuus* was not inhibitory to test species when quartz sand was used as the seedbed. However, when a mixture of soil and sand (2:1) was used, inhibition was obtained. This led to the suggestion that the colloidal nature of the soil influenced the concentration of inhibitors, leading to levels high enough to demonstrate phytotoxicity. Other workers have demonstrated that identified inhibitory compounds present in foliage can be recovered from soil beneath the plant (Guenzi and McCalla 1966a, 1966b; Blum and Rice 1969; McPherson, Chou, and Muller 1971; Chou and Muller 1972). Although the soil was not analyzed for inhibitory compounds in this study the inhibition of assay species sown on soil watered with a leachate of demonstrated toxicity indicates that the inhibitor(s) may be active in the upper layer of soil and presumably are deposited on soil surface by rainfall.

# CHAPTER VIII

# CHEMICAL IDENTIFICATION AND INHIBITORY ACTIVITY

## Identification of Inhibitors

Green, living leaves of Andropogon scoparius were collected on 07 June and returned to the laboratory. Ten g of leaf material was immediately soaked in 100 ml distilled water for three hrs; this was replicated six times. After soaking, 500 ml of the leachate was placed in a flash evaporator (water bath temperature was 40 C) and concentrated to one-tenth the original volume. Leachate was extracted three times with an equal volume of diethyl ether and the ether layers combined. The ether was allowed to evaporate to dryness and the residue taken up with three ml of 95% EtOH. The ethanolic solution was then spotted on 2 x 57 cm strips of Whatman No. 3 MM chromatography paper. The same procedure was carried out on leaves air dried for one week. Descending chromatograms were developed in n-butanol:acetic acid:water (63:10:27, v:v:v, called BAW), viewed under UV light and sprayed with diazotized p-nitraniline (DPN) or diazotized sulphanilic acid (DSA) followed immediately with a 10% solution of $Na_2CO_3$ (Bray et al. 1950). Fluorescence, reagent colors, and $R_f$ values were determined.

Freshly developed chromatogram strips were cut into segments as indicated by fluorescence spots under UV light and by calculated $R_f$ values from other sprayed strips. These segments were eluted in 95%

EtOH for 12 hrs. The EtOH was evaporated to dryness using nitrogen gas. The residue was redissolved in three ml 95% EtOH and spotted on new Whatman No. 3 MM paper. These strips were developed in two solvent systems, BAW and 6% aqueous acetic acid (called 6% AA) by the descending chromatographic technique. $R_f$ values, fluorescence under UV light, and reaction colors with DPN and DSA were determined for each solvent system. Chromatograms of 12 commercial standard compounds of demonstrated allelopathic activity were run in the same way and used to check the identity of the unknown compounds present in the leachate. Standards and tests were run simultaneously.

## Chromatogram Bioassays

The biological activity of these compounds was determined by chromatogram bioassays using lettuce seeds (Grand Rapids variety). Freshly developed BAW strips were cut into segments as indicated by UV light and DPN spot appearance on duplicate strips. Identified segment spots were placed in separate petri dishes and moistened with two ml distilled water. Twenty-five lettuce seeds were sown on each segment and grown at 26 C for 48 hrs. Percent germination and radicle length were used as indicators of inhibitory activity. Controls were prepared from developed but unspotted strips cut into segments identical to the tests. Controls and tests were replicated three times.

## Results and Discussion

Leachates were prepared from fresh green leaves and air dried leaves as described previously. The leachate was used to confirm toxicity in bioassays and for chromatographic processes. Results from the bioassays show that both types of leachate are toxic to the bioassay species tested (Table XXII).

Using descending paper chromatography both types of prepared leachate were examined and inhibitors identified. Two phenolic compounds, caffeic acid, and ferulic acid were identified from the leachates. Both compounds were present in each type of leachate. $R_f$ values and color responses are given in Table XXIV.

Biological activity of the absorption zones was determined for both types of leachate (Table XXV). The absorption zones from the fresh leachate showed no inhibition of germination or radicle length. However, the same zones from the air dried leaf leachate did show statistically significant inhibition. Apparently the concentration of toxins present in the fresh leaf leachate was not great enough to cause significant inhibition. These data appear to be contradictory to those presented in Table XXII. However, the inhibition shown in Table XXII represent results when all toxins present are acting together, not individually. The data in Table XXV represent the effects of individual eluted spots. Apparently a synergistic effect exists between two or more toxins which is greater than either one individually.

The results, shown in Table XXVI, indicate considerable toxicity between $R_f$ 0.1-0.8. This corresponds to the determined $R_f$ of caffeic acid (0.29, 0.52, 0.30, and 0.54) and ferulic acid (0.37, 0.61, 0.39, and 0.62). The greatest inhibition of radicle growth occurred at segments 0.1-0.2 and 0.5-0.6. $R_f$ 0.5-0.6 corresponds to the zone occupied by caffeic acid. The zone 0.1-0.2 does not correspond to any of the phenolic acids tested nor does it yield phenolic characterization by the reagents used. Apparently other phytotoxins are present which are

## TABLE XXIV

## CHROMATOGRAPHIC RESULTS FROM FRESH LEAF AND AIR DRIED LEAF LEACHATES PREPARED FROM ANDROPOGON SCOPARIUS.

| Compound | $R_f$'s on Whatman No. 3 MM[a] | | Fluorescence | | Reagent Colors[b,c] | |
|---|---|---|---|---|---|---|
| | BAW | 6% AA | Long UV | Short UV | DPN | DSA |
| Fresh Leachate | | | | | | |
| Unknown #1 | .84 | .29, .52 | S. bt. abs. | S. bt. abs. | red. br. | pl. yel. |
| Caffeic Acid | .82 | .28, .59 | S. bt. abs. | S. bt. abs. | red. br. | pl. yel. |
| Unknown #2 | .97 | .37, .61 | S. bt. abs. | S. bt. abs. | br. bk. | ft. or. |
| Ferulic Acid | .88 | .34, .64 | S. bt. abs. | S. bt. abs. | br. bk. | ft. or. |
| Air Dried Leachate | | | | | | |
| Unknown #1 | .81 | .30, .54 | S. bt. abs. | S. bt. abs. | red. br. | pl. yel. |
| Caffeic Acid | .82 | .28, .59 | S. bt. abs. | S. bt. abs. | red. br. | pl. yel. |
| Unknown # 2 | .96 | .39, .62 | S. bt. abs. | S. bt. abs. | br. bk. | ft. or. |
| Ferulic Acid | .88 | .34, .64 | S. bt. abs. | S. bt. abs. | br. bk. | ft. or. |

[a] Refer to text for solvent systems; $R_f$'s are averages of 8-12 replications.

[b] DPN = diazotized p-nitroaniline (Bray, et al., 1950).
DSA = diazotized sulfanilic acid (Bray, et al., 1950).

[c] abs - absorption; v - very; bt - bright; red - reddish; br - brown; pl = pale; yel - yellow; or - orange; ft - faint; tan - tan; S - strong; bk - black.

## TABLE XXV

## GERMINATION AND RADICLE GROWTH RESPONSE OF LETTUCE SEEDS PLANTED ON CHROMATOGRAM SEGMENTS TAKEN FROM STRIPS SPOTTED WITH LEACHATE FROM *ANDROPOGON SCOPARIUS*[*]

| Compound | Spot Centered $R_f$ | Mean Radicle Length (mm) | | | Mean Germination (%) | | |
|---|---|---|---|---|---|---|---|
| | | Control | Test | % Control | Control | Test | % Control |
| Fresh Leaf Leachate | | | | | | | |
| Presumed Caffeic Acid | .84 | 11.7 | 10.6 | 91 | 92 | 91 | 99 |
| Presumed Ferulic Acid | .97 | 10.7 | 10.5 | 98 | 95 | 92 | 97 |
| Air Dried Leaf Leachate | | | | | | | |
| Presumed Caffeic Acid | .81 | 12.3 | 6.1 | $50^{a,b}$ | 95 | 81 | $86^{a}$ |
| Presumed Ferulic Acid | .96 | 11.2 | 7.2 | $64^{a,b}$ | 92 | 85 | 93 |

[*] Developed in BAW (n = 75).

[a] Significant difference at $p < 0.05$ by t-test.

[b] Significant difference at $p < 0.01$ by t-test.

## TABLE XXVI

## GERMINATION AND RADICLE GROWTH RESPONSE OF LETTUCE SEEDS PLANTED ON CHROMATOGRAM SEGMENTS FROM STRIPS SPOTTED WITH AIR DRIED LEAF LEACHATE FROM *ANDROPOGON SCOPARIUS**

| $R_f$ Segment | Mean Radicle Growth (mm) | | | Mean Germination (%) | | |
|---|---|---|---|---|---|---|
| | Control | Test | % Control | Control | Test | % Control |
| 0.0 - 0.1 | 9.8 | 10.1 | 103 | 85 | 77 | 91 |
| 0.1 - 0.2 | 10.0 | 4.2 | 42[a,b] | 91 | 77 | 85[a] |
| 0.2 - 0.3 | 9.6 | 5.8 | 60[a,b] | 93 | 84 | 90[a] |
| 0.3 - 0.4 | 10.4 | 5.1 | 49[a,b] | 91 | 84 | 93 |
| 0.4 - 0.5 | 13.0 | 6.2 | 48[a,b] | 95 | 65 | 69[a,b] |
| 0.5 - 0.6 | 13.7 | 5.7 | 42[a,b] | 93 | 71 | 76[a,b] |
| 0.6 - 0.7 | 12.2 | 7.1 | 58[a,b] | 93 | 88 | 94 |
| 0.7 - 0.8 | 10.6 | 5.8 | 55[a,b] | 95 | 88 | 93 |
| 0.8 - 0.9 | 8.8 | 6.3 | 71[a,b] | 93 | 85 | 91 |
| 0.9 - 1.0 | 7.8 | 6.9 | 88[a] | 89 | 69 | 78 |

*Values are averages from three replications.

[a] Significant difference at $p < 0.05$ by t-test.

[b] Significant difference at $p < 0.01$ by t-test.

non-phenolics. Germination was inhibited greatest in the caffeic acid $R_f$ zone (0.5-0.6) and in the zones 0.4-0.5 and 0.9-1.0. Again these latter two zones do not represent phenolic compounds as determined in this study. Germination was essentially unaffected in the other segment zones. Attempts to further characterize the non-phenolic toxins present were not carried out at this time. Results shown in Appendix M are characterization parameters for 12 standard commercial phenolic compounds tested during this study.

The two identified phenolic compounds have been shown to exhibit ecological impact in other allelopathic studies (Rice and Parenti 1967; McPherson and Muller 1969; Lodhi and Rice 1971; McPherson et al. 1971; Rasmussen and Rice 1971; Chou and Muller 1972; Rice 1974). These workers have shown or concluded that these compounds are released from a producer plant, mainly through precipitation, deposited and accumulated in the upper layers of the soil, and detrimentally affect germination and/or growth of various plant species. These two compounds are apparently removed from *Andropogon scoparius* by rainfall and deposited on the soil surface where they adversely affect various species of weedy invaders. In this manner climax grassland communities are better able to maintain an intact stand. Upon disturbance the colloidal nature of the soil is rearranged, thus removing or altering the toxic nature of the compounds. The means by which disturbance disrupts the allelopathic effect was not studied. Other investigations suggested by this research are: the characterization of the non-phenolic compounds; the precise source of the toxins within the plant; the method of release to the leaf surface; the mechanism of inhibition on the victim plant; the effects on microbial activity in the soil and rhizosphere of *Andropogon scoparius* and other climax species; and the effects on population regulation of the producer plant.

# CHAPTER IX

# DISCUSSION AND CONCLUSIONS

The literature contains numerous examples of plant species which influence the establishment, survival, and/or growth of other plant species in a community. This influence can occur by one of the two means of interference (as defined by Muller 1969, as any deleterious effect of one plant on another and encompassing both allelopathy and competition) or by a synergistic interaction between the two components of interference. Curtis (1959) states that hawkweed becomes a complete local dominant in the bracken-grassland of Wisconsin by production of a potent allelopathic agent which retards establishment of other species. Levy (1970) suggests that the bracken-grassland retards invasion of specific tree species because of the introduction, by resident plants, of a chemical compound detrimental to tree germination and growth. Subsequently, Dawes and Maravolo (1973) stated that *Hieracium aurantiacum* stabilizes the bracken-grassland and impairs tree invasion by the release of several phenolic compounds of demonstrated allelopathic impact. Numerous other examples of allelopathic inhibition of species invasion into a community can be found (Muller 1966; McPherson and Muller 1969; Del Moral and Muller 1970; Semtner 1972; Tinnin and Muller 1972; others). Muller (1966) states that the process of allelopathy slows succession by interfering with the natural processes of migration, ecesis, or competition. If allelopathy can retard the migration of species, this process then can influence species composition and diversity of established communities. Only those species tolerant of the released allelochemic will become established in the community (Whittaker 1971; Whittaker and Feeny 1971).

The literature contains studies which have shown that grasslands are capable of deterring invasion and/or of regulating population size of certain species. Sagar and Harper (1961) showed that the presence of weedy *Plantago* species was determined by the presence or absence of grass communities in England. These grass communities furthermore were able to limit the population size of the *Plantago*. Putwain and Harper (1970) demonstrated that population size of species of *Rumex* was regulated by the presence of grasses. Semtner (1972) concluded that two grass species of Oklahoma prairies appear to restrict growth of the weedy grass *Sorghum halepense*. Parenti and Rice (1969) concluded that the first phase of old field succession was rapidly replaced because of the presence of certain weedy species which released phytotoxins. Rasmussen and Rice (1971) showed that *Sporobolus* stands prevented weed invasion by phytotoxins which were released and were deleterious to germination and growth of weedy species. Tinnin and Muller (1971) concluded that certain shrub and herb species of the California chaparral are excluded from the annual grasslands of California by allelopathic substances released from *Avena fatua*. Rice (1972) found that aqueous extracts of fresh roots and shoots of *Andropogon virginicus* were inhibitory to both higher plants and nitrogen-fixing bacteria. Parks and Rice (1969) found that the roots of *Andropogon scoparius* released a substance which inhibited the blue-green alga *Anabaena* sp.

Many studies involving the midwest prairies have dealt with the influence of litter and mulch accumulation. Kelting (1954) showed that a grazed prairie contained more species than an ungrazed prairie. Weaver and Fitzpatrick (1934) reported that early spring growth was retarded by heavy mulch accumulation. Weaver and Rowland (1952) found that prairies with heavy litter or mulch accumulations supported a very sparse understory. This understory sparsity was attributed to decreased light availability and the actual weight of the mulch. Vogl and Bjusted (1968) and Ehrenreich and Aikman (1963) stated that in undisturbed prairies litter accumulation decreased yields of grasses and delayed spring growth. Old (1969) has shown that the application of litter to denuded areas caused an inhibition of both vegetative and flower stalk production; the magnitude of inhibition was dependent upon the thickness of the mulch layer. Semtner (1972) demonstrated that litter composed of Andropogon scoparius and Sorghastrum nutans had inhibitory effects on growth of a weedy grass. If germination and/or seedling growth is slowed by an inhibitor in early spring this will result in a distinct disadvantage to the seedling under ordinary competitive situations. Competition, then, would enhance the detrimental effects of allelopathy by acting as a feedback mechanism (Rice 1974).

In order to establish the mechanism of allelopathy, Muller (1974) states that five basic requirements must be met: (1) the suspected plant must produce a toxin; (2) there must exist a mechanism of release from the plant into the adjacent environment; (3) a mechanism must exist for the movement and concentration of the released toxin; (4) the susceptibility of juxtaposed species in the field must be determined; and (5) physical factors and non-chemical factors which could cause a deleterious effect on plants must be eliminated. One method that is used to indicate a potential allelopathic species is field observation of the vegetational patterns associated with the species. A vegetation pattern under these conditions is the spatial arrangement of individuals which are visually apparent in the field at that period in time (Funke 1943; Muller et al. 1964; Muller 1966; Wilson and Rice 1968). This would include the exclusion of individual species from particular areas (Muller 1966; McPherson and Muller 1969; Rasmussen and Rice 1971; Tinnin and Muller 1971; Dawes and Moravals 1973; others), the increased growth of individual species with increased distance from the suspected plant (Wilson and Rice 1968); and the ordering of different species into distinct zones around the suspected plant (Tinnin and Muller 1971).

In climax tall grass prairies of Oklahoma certain weedy species are virtually excluded until some sort of disturbance occurs. With increasing severity of disturbance a wider variety of weedy invaders become established. The undisturbed climax site in this study contained fewer weedy species than did the severely grazed site, which had the greatest degree of disturbance and the greatest number of weedy species. Data presented in the current study show that there is a reduction in the total number of species present which corresponds to the degree of disturbance. A total of 84 species were found in the climax site but only 45 species were found in the severely grazed site. These results agree with those of Kucera (1956) and Drew (1947). Additionally the number of weedy invaders increase with increasing disturbance. This is especially prevalent among the grasses. These results agree with those of Kucera (1956), Kelting (1954), and Drew (1947) who found a great increase in "invaders" with grazing pressure.

This decrease in total species present appears to be correlated with the abundance of <u>Andropogon</u> <u>scoparius</u> in these sites. As the importance value of *A. scoparius* decreases the number of different species occurring increases, thus changing the diversity value. The lowest diversity index was found in the climax site while the largest occurred in the severely grazed site. Upon first inspection this appears to be contradictory to theory which states that species diversity increases with increasing stability of the environment (Odum 1971; Pielou 1974; Pielou 1975; Whittaker 1975). However, the influence exerted by the dominant species by their abundance must be considered. Competition could lead to dominance of a few species in an area or an allelopathic species could become dominant due to the intolerance of potentially invading species (Harper 1961; Muller 1969; Singh and Misra 1969; Odum 1971; Muller 1974). McNaughton (1967) indicates that there is an inverse relationship between dominance and diversity, and that an increase in the number of species in a community results in decreased efficiency probably through competition. Singh and Misra (1969) concluded that dominance is attained through interspecific competition and that the suppressive influence of a limited number of dominants decreases diversity by some competitive mechanism. Data gathered in the current study indicate that diversity is inversely correlated with the density of *Andropogon scoparius*. Furthermore the density of *A. scoparius* is also correlated with the severity of the disturbance. A heavily grazed field is severely disturbed resulting in a greatly reduced density of *A. scoparius* while a hay meadow mowed annually is relatively undisturbed. The degree of disturbance alters not only the mulch layer but also various physical factors thereby allowing change in community composition to occur.

Many workers have noted that when a climax prairie is disturbed weedy invaders can and do become established. The mechanism(s) whereby these invaders have been retarded, until disturbance, has been previously attributed to competition or mechanical effects. The presence of a layer of mulch does alter several environmental parameters but these mostly benefit the community. Physical factors measured in this study were found not to be limiting.

During the active growing season *Andropogon scoparius* releases several phenolic compounds from the green leaves. These compounds are released to the leaf surface where they are washed off by rainfall. Leachate prepared from these leaves proved to be inhibitory to germination and/or growth of representative weedy invaders under laboratory conditions. Leaves which had been air dried and thereby simulated dead standing litter in the field showed an even greater degree of inhibitory power. Field soil watered with this leachate showed an inhibition of radicle growth when used as a seedbed. This agrees with other workers who have found that phytotoxins can be accumulated in the soil to a toxic level (Wilson and Rice 1968; Del Moral and Muller 1970; McPherson et al. 1971; Rice 1974).

A one year study on the allelopathic effects of *Andropogon scoparius* shoots indicates that the greatest period of inhibition occurs in late spring and early summer. During this period a slowing of germination or growth would yield a definite disadvantage to the affected plant. This slowing of growth would render the plant more susceptible to competitive pressures from the faster growing adjacent plants. Either factor acting independently would not exert as great an influence as the synergistic interaction between the two factors.

The data obtained here support the hypothesis that *Andropogon* scoparius has an allelopathic influence on potential weedy invaders when the prairie is intact. Upon perturbation of this closed community the effect is disrupted, allowing invasion and establishment of weedy species. In areas dominated by A. scoparius, Andropogon gerardi, Panicum virgatum, and Sorghastrum nutans, a wider spectrum of potential invaders are inhibited because of the nature of differential susceptibility of individuals to various toxins and concentrations of toxins. Additionally these four grasses exhibit phytotoxicity during various seasons of the year on the same species of invader. In this manner weedy invaders are excluded from climax prairies during both the growing and dormant seasons of the climax dominants. The individual dominant exhibiting the greatest degree of phytotoxicity is A. scoparius, which has its greatest impact during spring and summer. This is the season during which the greatest number of invaders would germinate. By either complete inhibition of germination or a greatly decreased rate of growth these potential invaders are placed at a competitive disadvantage and are thus eliminated by a synergistic interaction between the two forms of interference.

Chemical analysis of leachates from both green and air dried leaves of Andropogon scoparius revealed the presence of two identifiable phenolic acids, caffeic and ferulic acid. These compounds are present in sufficient concentration to induce toxicity and have been shown to be potent allelopathic agents (Rice and Parenti 1967; Lodhi and Rice 1971; Rice 1974). Air dried shoots, because they exhibited a greater amount of inhibition, are presumed to have higher concentrations of these acids. Since these compounds were found in aqueous leachates there is little doubt that they are inhibitors. No attempt was made to isolate or identify these compounds from the soil. Ferulic acid, however, has been isolated and identified from soil by other workers (Wang, Yang, and Chuang 1967; McPherson et al. 1971; McCalla 1971; Wang et al. 1971; Chou and Muller 1972).

Ferulic acid has been found to increase IAA decarboxylation and thereby decrease growth in higher plants (Zenk and Muller 1963). At low concentrations Gortner and Kent (1958) found ferulic acid to be an activator of IAA oxidase, but at high concentrations it proved to be inhibitory. Numerous phenolic acids have also been found to inhibit higher plant growth indirectly by inhibiting nitrogen-fixing and nitrifying bacteria (Rice 1964, 1965). Phenolic acids then can influence plant growth directly or indirectly.

Many plants release various metabolites into the environment which may have either a positive or negative effect on other species (Tukey 1966). Those compounds which act negatively have been shown in many cases to be allelopathic substances. These substances, and the ecological process of allelopathy, then are important ecologically as one aspect of the environmental complex which may aide in determining the distribution of species and the overall diversity of plant communities.

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# APPENDIXES

# APPENDIX A

## SPECIES PRESENT BY OBSERVATION METHOD AND ARRANGED BY HABITAT

Observations made during the period 01-15 August, 1975

**Climax Prairie**

Acacia angustissima
Andropogon saccharoides
Andropogon ternarius
Aristida oligantha
Aster ericoides
Baptisia leucophaea
Bromus japonicus
Callirhoe involucrata
Cercis canadensis
Commelina erecta
Conyza canadensis
Desmanthus illinoensis
Desmodium sessilifolium
Echinacea angustifolia
Elymus canadensis
Elymus viginicus
Eupatorium serotinum
Euphorbia marginata
Gnaphalium obtusifolium
Hedeoma hispida
Juncus interior
Juniperus virginiana
Lactuca scariola
Lechea mucronata
Lespedeza capitata
Liatris punctata
Neptunia lutea
Opuntia sp.
Panicum oligosanthes
  var. lindheimeri
Physalis sp.
Polygala incarnata
Psoralea tenuiflora
Ratibida columnifera
Rhus copallina
Rudbeckia hirta
Schrankia uncinata
Setaria geniculata
Solidago rigida
Strophostyles helvola
Teucrium canadensis
Torilis arvensis
Ulmus americana
Vernonia baldwinii

*OTHERS:

Cirsium arvense
Desmodium paniculatum
Erigeron strigosus
Hypericum drummondii
Krameria secundiflora
Panicum virgatum
Plantago purshii
Sporobolus asper
Tridens flavus

**Hay Meadow**

Ambrosia psilostachya
Amorpha canescens
Andropogon saccharoides
Andropogon ternarius
Aristida oligantha
Artemisia ludoviciana
Asclepias tuberosa
Baptisia tenuiflora
Bromus japonicus
Bromus unioloides
Buchloe dactyloides
Cassia fasciculata
Chloris verticillata
Cirsium arvense
Cyperus ovularis
Echinacea angustifolia
Elymus canadensis
Eragrostis cilianensis
Erigeron strigosus
Eupatorium serotinum
Gerardi heterophylla
Gnaphalium obtusifolium
Helianthus maximiliana
Lactuca scariola
Lespedeza virginica
Linum sulcatum
Neptunia lutea
Oenothera serrulata
Paspalum dilatatum
Psoralea tenuiflora
Sorghum halapense
Spiranthes gracilis
Thelesperma trifidum
Torilis arvensis
Trifolium repens
Vernonia baldwinii
Vicia villosa

*OTHERS:

Asclepias viridis
Gerardia heterophylla
Nedeoma hispida
Oenothera serrulate
Ratibida columnifera
Solanum eleagnifolium

**Moderately Grazed Prairie**

Asclepias tuberosa
Aster eriocoides
Baptisia leucophaea
Bromus unioloides
Callirhoe inolucrata
Chloris verticillata
Chrysopsis pilosa
Desmodium sessilifolium
Eragrostis cilianensis
Eragrostis srectabilis
Erigeron strigosus
Euphorbia prostrata
Gaillardia puchella
Gaura sinuata
Gutierrezia dracunculaides
Haplopappus ciliatus
Lespedeza virginica
Linum sulcatum
Neptunia lutea
Oenothera serrulatus
Paspalum dilatum
Plantago virginica
Ruellia penduncul ata
Sabatia campestris
Salvia azurea
Schrankia uncinata
Seteria geniculata
Solidago missouriensis
Sporobolus asper
Vicia villosa

*OTHERS:

Hypericum drummondii
Liatris punctata
Rudbeckia hirta

**Severely Grazed Prairie**

Asclepias tuberosa
Croton capitatus
Diodia teres
Erigeron strigosus
Gaillardia pulchella
Hypericum drummondii
Panicum oligosanthes
  var. lindheimeri
Sporobolus cryptandrus
Tridens flavus
Xanthisma texana

*OTHERS:

Lepidium densiflorum
Solanum eleagnifolium

*Others are genera found during sampling which were represented by only one individual.

# APPENDIX B

## SPECIES PRESENT BY OBSERVATION METHOD AND ARRANGED BY HABITAT

Observations made during the period 01 April - 01 June, 1976. Only those species not observed during the August, 1975, observation are listed.

| Climax Prairie | Hay Meadow | Moderately Grazed Prairie | Severely Grazed Prairie |
|---|---|---|---|
| Andropogon virginicus | Allium canadense | Buchloe dactyloides | Cirsium undulatum |
| Cirsium undulatum | Cirsium undulatum | Cirsium undulatum | Geranium carolinianum |
| Diodia teres | Eleocharis sp. | Cyperus ovularis | Krameria secundiaflora |
| Geum canadensis | Geranium carolinianum | Geranium carolinianum | Melilotus officinalis |
| Linum sulcatum | Lepidium densiflorum | Juniperus virginiana | Oenothera serrulata |
| Lithospermum incisum | Nothoscordum bivalve | Krameria secundiflora | Oxalis stricta |
| Oenothera oklahomensis | Oenothera oklahomensis | Nothoscorum vivalve | Pyrrhopappus grandiflorus |
| Oxalis stricta | Oxalis stricta | Oenothera oklahomensis | Schrankia uncinata |
| Petalostemum purpureum | Oxytropis lambertii | Oxalis stricta | Sibara virginica |
| Plantago virginica | Pyrrhopappus grandiflorus | Penstemon sp. | Tradescantia ohiensis |
| Sabatia campestris | Senecio sp. | Sisyrinchium campestre | Tragopogon pratensis |
| Strophostyles leiosperma | Sisyrinchium campestre | Trifloium procumbens | |
| | Tradescantia ohiensis | | |
| | Tragopogon pratensis | | |

# APPENDIX C

## SOIL WATER POTENTIAL VALUES (in bars) FOR ALL FIELD SITES EXAMINED

| Collection Date | Climax Prairie Depth | | Hay Meadow Depth | | Moderately Grazed Prairie Depth | | Severely Grazed Prairie Depth | |
|---|---|---|---|---|---|---|---|---|
| | 2-12 cm | 20-30 cm | 2-12 cm | 20-30 cm | 2-12 cm | 20-30 cm | 2-12 cm | 20-30 cm |
| 20 June 75 | >- 0.5 | - 0.8 | - 3.4 | <-17.0 | - 2.8 | - 1.1 | - 0.6 | - 0.7 |
| 27 June 75 | >- 0.5 | - 0.9 | - 1.4 | -10.8 | - 1.9 | - 0.8 | - 0.6 | - 1.0 |
| 03 July 75 | - 0.9 | - 1.8 | - 5.6 | <-17.0 | - 4.8 | - 2.0 | - 7.2 | - 2.2 |
| 11 July 75 | -16.2 | - 8.0 | <-17.0 | <-17.0 | -12.0 | -10.8 | -16.4 | - 7.0 |
| 18 July 75 | <-17.0 | <-17.0 | <-17.0 | <-17.0 | -17.0 | <-17.0 | <-17.0 | -10.8 |
| 25 July 75 | - 0.5 | <-17.0 | - 0.6 | - 0.9 | - 0.6 | <-17.0 | >- 0.5 | -11.0 |
| 04 Aug. 75 | - 0.9 | <-17.0 | - 2.8 | - 5.2 | - 1.2 | - 0.8 | -14.0 | -10.6 |
| 08 Aug. 75 | - 4.8 | <-17.0 | - 4.0 | -13.0 | - 3.5 | - 1.8 | <-17.0 | <-17.0 |
| 15 Aug. 75 | - 3.6 | <-17.0 | - 2.8 | - 2.5 | - 0.6 | -13.6 | - 0.5 | - 9.5 |
| 22 Aug. 75 | - 9.2 | <-17.0 | <-17.0 | <-17.0 | <-17.0 | -16.6 | <-17.0 | <-17.0 |
| 30 Aug. 75 | <-17.0 | <-17.0 | <-17.0 | <-17.0 | <-17.0 | <-17.0 | <-17.0 | -13.0 |
| 04 Sept. 75 | <-17.0 | <-17.0 | <-17.0 | <-17.0 | <-17.0 | <-17.0 | <-17.0 | <-17.0 |
| 09 Sept. 75 | <-17.0 | <-17.0 | <-17.0 | <-17.0 | <-17.0 | <-17.0 | <-17.0 | <-17.0 |
| 16 Sept. 75 | >- 0.5 | - 7.8 | - 0.7 | -10.1 | - 0.5 | - 1.3 | - 0.5 | - 3.0 |
| 10 May 76 | >- 0.5 | >- 0.5 | - 0.6 | >- 0.5 | - 0.5 | >- 0.5 | - 0.5 | >- 0.5 |
| 15 May 76 | >- 0.5 | >- 0.5 | - 0.6 | - 1.5 | - 0.6 | >- 0.5 | - 0.5 | >- 0.5 |
| 22 May 76 | >- 0.5 | >- 0.5 | - 0.6 | - 0.8 | - 0.6 | >- 0.5 | - 0.6 | >- 0.5 |
| 30 May 76 | >- 0.5 | >- 0.5 | - 0.7 | - 0.8 | - 0.7 | >- 0.5 | - 0.7 | >- 0.5 |
| 04 June 76 | - 2.2 | >- 0.5 | - 3.8 | - 3.0 | - 3.2 | - 0.9 | - 3.5 | - 1.0 |
| 11 June 76 | - 2.3 | >- 0.5 | - 4.3 | - 5.6 | - 3.3 | - 1.0 | - 4.0 | - 2.4 |
| 18 June 76 | - 2.4 | >- 0.5 | - 4.7 | - 6.8 | - 3.5 | - 1.7 | - 4.9 | - 7.0 |

# APPENDIX D

## SOIL TEMPERATURE VALUES (°C) FOR ALL FIELD SITES EXAMINED

| Collection Date | Climax Prairie Depth (cm) | | | | Hay Meadow Depth (cm) | | | | Moderately Grazed Prairie Depth (cm) | | | | Severely Grazed Prairie Depth (cm) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Surface | 2 | 4 | 6 | Surface | 2 | 4 | 6 | Surface | 2 | 4 | 6 | Surface | 2 | 4 | 6 |
| 20 June 75 | 35.7 | 25.1 | 24.7 | 23.8 | 35.0 | 27.9 | 27.0 | 26.1 | 34.7 | 28.7 | 27.9 | 27.3 | 39.0 | 31.8 | 30.6 | 29.1 |
| 27 June 75 | 29.9 | 23.9 | 23.6 | 23.4 | 34.4 | 25.7 | 25.1 | 24.3 | 35.1 | 27.3 | 26.7 | 26.0 | 34.8 | 27.9 | 27.1 | 26.4 |
| 03 July 75 | 30.2 | 24.6 | 23.9 | 23.6 | 34.1 | 27.9 | 26.6 | 25.7 | 33.9 | 26.7 | 26.2 | 25.6 | 36.5 | 29.6 | 28.4 | 27.1 |
| 11 July 75 | 24.0 | 23.2 | 23.2 | 22.7 | 24.8 | 22.9 | 22.2 | 23.0 | 37.5 | 28.7 | 27.1 | 26.6 | 43.7 | 31.6 | 27.9 | 26.8 |
| 18 July 75 | 31.2 | 23.8 | 23.5 | 23.1 | 34.6 | 26.7 | 25.7 | 25.2 | 34.1 | 27.2 | 26.5 | 25.3 | 36.1 | 31.0 | 29.4 | 28.5 |
| 25 July 75 | 26.7 | 22.7 | 22.4 | 22.1 | 36.9 | 28.2 | 26.4 | 24.8 | 30.6 | 25.0 | 24.4 | 23.9 | 28.6 | 26.1 | 25.7 | 25.3 |
| 04 Aug. 75 | 32.7 | 22.6 | 22.8 | 22.2 | 38.8 | 32.4 | 30.2 | 28.6 | 37.4 | 27.7 | 26.2 | 24.8 | 36.8 | 27.7 | 26.3 | 25.2 |
| 08 Aug. 75 | 30.7 | 24.3 | 24.0 | 23.4 | 35.7 | 33.0 | 29.7 | 28.3 | 37.3 | 27.1 | 25.8 | 24.8 | 34.9 | 30.2 | 28.7 | 27.8 |
| 15 Aug. 75 | 33.1 | 26.1 | 25.2 | 24.2 | 38.3 | 32.1 | 30.9 | 28.3 | 39.9 | 26.9 | 26.3 | 25.4 | 37.4 | 28.6 | 27.3 | 26.4 |
| 22 Aug. 75 | 29.4 | 24.1 | 23.9 | 23.6 | 39.2 | 31.8 | 30.3 | 28.7 | 40.0 | 28.1 | 27.8 | 27.0 | 38.1 | 32.7 | 30.6 | 29.0 |
| 30 Aug. 75 | 34.6 | 24.7 | 24.1 | 23.2 | 39.2 | 31.0 | 30.2 | 28.9 | 41.6 | 28.8 | 28.1 | 26.7 | 39.4 | 35.6 | 32.6 | 30.5 |
| 04 Sept. 75 | 35.3 | 25.5 | 24.2 | 23.6 | 41.3 | 32.9 | 30.9 | 30.2 | 41.6 | 32.6 | 30.7 | 29.6 | 40.4 | 35.7 | 32.4 | 31.1 |
| 09 Sept. 75 | 34.5 | 25.1 | 24.4 | 22.6 | 39.9 | 30.5 | 28.5 | 27.0 | 39.6 | 30.5 | 28.6 | 27.3 | 38.4 | 35.2 | 32.3 | 20.8 |
| 16 Sept. 75 | 27.6 | 20.0 | 19.9 | 19.5 | 29.3 | 24.4 | 23.2 | 21.7 | 29.3 | 22.8 | 21.8 | 21.3 | 30.4 | 24.3 | 23.2 | 22.5 |
| 10 May 76 | 28.5 | 19.3 | 18.4 | 17.1 | 23.9 | 19.0 | 17.9 | 17.3 | 28.9 | 24.2 | 20.9 | 20.4 | 26.4 | 20.7 | 19.5 | 19.0 |
| 15 May 76 | 28.8 | 20.0 | 19.0 | 17.6 | 24.4 | 19.6 | 18.4 | 17.9 | 29.2 | 24.7 | 21.8 | 20.5 | 26.5 | 20.9 | 19.7 | 18.9 |
| 22 May 76 | 30.1 | 21.3 | 19.8 | 18.7 | 27.5 | 21.8 | 21.7 | 20.7 | 27.9 | 23.6 | 22.5 | 21.7 | 29.2 | 24.8 | 23.4 | 22.8 |
| 30 May 76 | 29.6 | 21.0 | 20.2 | 19.5 | 25.8 | 22.6 | 21.9 | 20.9 | 27.8 | 25.1 | 23.3 | 22.1 | 27.6 | 26.0 | 25.2 | 23.8 |
| 04 June 76 | 30.5 | 21.7 | 20.2 | 19.7 | 28.4 | 22.9 | 21.6 | 21.1 | 28.5 | 23.7 | 22.9 | 22.3 | 29.7 | 25.5 | 24.2 | 23.6 |

# APPENDIX E

# MEAN PERCENT FULL LIGHT VALUES AND NUMBER OF READINGS PER LIGHT CLASS FOR ALL TRANSECTS SAMPLED IN THE MODERATELY GRAZED AND SEVERELY GRAZED PRAIRIE SITES

Values for a.m. are readings taken between 7:00-9:00 a.m.; p.m. values are readings taken between 12:00 noon - 2:00 p.m.

| Site | Collection Month | Transect Number | Number of Values Per Light Class <br> <26% FL am | <26% FL pm | 26-50% FL am | 26-50% FL pm | 51-76% FL am | 51-76% FL pm | >76% FL am | >76% FL pm | mean of all values % am | mean of all values % pm |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Moderately Grazed Prairie | May 76 | 1 | 43 | 21 | 7 | 11 | | 11 | | 7 | 11.0 | 40.9 |
| | | 2 | 49 | 16 | 1 | 8 | | 12 | | 14 | 7.8 | 51.2 |
| | | 3 | 50 | 19 | | 6 | | 9 | | 16 | 9.0 | 50.3 |
| | June 76 | 1 | 34 | 17 | 12 | 13 | 2 | 14 | 2 | 6 | 20.3 | 45.8 |
| | | 2 | 29 | 18 | 14 | 15 | 7 | 12 | | 5 | 22.5 | 43.9 |
| | | 3 | 37 | 15 | 13 | 15 | | 11 | | 9 | 19.2 | 46.1 |
| | July 75 | 1 | 29 | 18 | 14 | 14 | 6 | 12 | 1 | 6 | 25.6 | 41.9 |
| | | 2 | 32 | 19 | 18 | 15 | | 12 | | 4 | 22.5 | 39.8 |
| | | 3 | 29 | 16 | 21 | 12 | | 13 | | 9 | 20.3 | 47.9 |
| | Aug. 75 | 1 | 38 | 22 | 10 | 16 | 2 | 8 | | 4 | 17.1 | 34.2 |
| | | 2 | 38 | 30 | 11 | 9 | 1 | 8 | | 3 | 16.2 | 27.5 |
| | | 3 | 35 | 16 | 15 | 20 | | 12 | | 2 | 18.6 | 36.1 |
| | Sept. 75 | 1 | 39 | 22 | 11 | 14 | | 8 | | 6 | 17.9 | 36.6 |
| | | 2 | 40 | 37 | 10 | 7 | | 5 | | 1 | 13.8 | 19.4 |
| | | 3 | 33 | 17 | 16 | 19 | 1 | 13 | | 1 | 18.6 | 36.0 |
| Severely Grazed Prairie | May 76 | 1 | 35 | 2 | 15 | 6 | | 14 | | 28 | 22.7 | 73.2 |
| | | 2 | 23 | | 27 | 5 | | 11 | | 34 | 27.9 | 82.8 |
| | | 3 | 31 | 5 | 19 | 10 | | 13 | | 22 | 22.1 | 62.8 |
| | June 76 | 1 | 37 | 4 | 13 | 8 | | 13 | | 25 | 20.1 | 65.9 |
| | | 2 | 28 | 2 | 22 | 5 | | 12 | | 31 | 25.3 | 80.3 |
| | | 3 | 34 | 6 | 16 | 9 | | 14 | | 21 | 20.8 | 59.6 |
| | July 75 | 1 | 49 | 11 | 1 | 8 | | 13 | | 18 | 15.4 | 58.8 |
| | | 2 | 32 | 1 | 18 | 3 | | 16 | | 30 | 24.6 | 79.0 |
| | | 3 | 35 | 14 | 15 | 11 | | 11 | | 14 | 19.1 | 52.0 |
| | Aug. 75 | 1 | 42 | 6 | 8 | 20 | | 14 | | 10 | 19.0 | 53.2 |
| | | 2 | 37 | 2 | 13 | 13 | | 15 | | 20 | 20.4 | 64.4 |
| | | 3 | 47 | 10 | 3 | 20 | | 14 | | 6 | 12.5 | 47.5 |
| | Sept. 75 | 1 | 22 | 7 | 28 | 16 | | 16 | | 11 | 27.1 | 55.6 |
| | | 2 | 26 | 1 | 23 | 14 | 1 | 14 | | 21 | 29.4 | 64.7 |
| | | 3 | 37 | 14 | 13 | 17 | | 11 | | 8 | 19.0 | 43.4 |

# APPENDIX F

# MEAN PERCENT FULL LIGHT VALUES AND NUMBER OF READINGS PER LIGHT CLASS FOR ALL TRANSECTS SAMPLED IN THE CLIMAX PRAIRIE AND HAY MEADOW SITES

Values for a.m. are readings taken between 7:00-9:00 a.m.; p.m. values are readings taken between 12:00 noon - 2:00 p.m.

| Site | Collection Month | Transect Number | Number of Values Per Light Class |  |  |  |  |  |  |  | Mean of all values % |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  | <26% FL |  | 26-50% FL |  | 51-76% FL |  | >76% FL |  |  |  |
|  |  |  | am | pm | am | pm | am | pm | am | pm | am | pm |
| Climax Prairie | May 76 | 1 | 50 | 33 |  | 15 |  | 2 |  |  | 2.6 | 21.8 |
|  |  | 2 | 49 | 24 | 1 | 14 |  | 7 |  | 5 | 6.1 | 34.1 |
|  |  | 3 | 50 | 26 |  | 16 |  | 7 |  | 1 | 4.4 | 26.0 |
|  | June 76 | 1 | 50 | 35 |  | 13 |  | 2 |  |  | 2.8 | 21.3 |
|  |  | 2 | 50 | 33 |  | 12 |  | 3 |  | 2 | 4.3 | 19.7 |
|  |  | 3 | 50 | 36 |  | 9 |  | 4 |  | 1 | 4.1 | 20.2 |
|  | July 75 | 1 | 50 | 34 |  | 14 |  | 2 |  |  | 2.7 | 18.6 |
|  |  | 2 | 50 | 38 |  | 10 |  | 1 |  | 1 | 2.3 | 16.4 |
|  |  | 3 | 50 | 37 |  | 9 |  | 3 |  | 1 | 3.0 | 19.4 |
|  | Aug. 75 | 1 | 50 | 44 |  | 6 |  |  |  |  | 3.3 | 13.1 |
|  |  | 2 | 50 | 39 |  | 9 |  | 2 |  |  | 3.6 | 14.8 |
|  |  | 3 | 50 | 40 |  | 10 |  |  |  |  | 5.3 | 14.8 |
|  | Sept. 75 | 1 | 50 | 45 |  | 5 |  |  |  |  | 2.7 | 10.8 |
|  |  | 2 | 50 | 41 |  | 6 |  | 3 |  |  | 3.8 | 14.7 |
|  |  | 3 | 50 | 46 |  | 3 |  | 1 |  |  | 3.2 | 11.0 |
| Hay Meadow | May 76 | 1 | 50 | 35 |  | 11 |  | 4 |  |  | 3.8 | 19.8 |
|  |  | 2 | 50 | 24 |  | 13 |  | 9 |  | 4 | 2.5 | 35.1 |
|  |  | 3 | 50 | 38 |  | 10 |  | 2 |  |  | 1.3 | 16.5 |
|  | June 76 | 1 | 50 | 42 |  | 5 |  | 2 |  | 1 | 4.1 | 16.8 |
|  |  | 2 | 50 | 40 |  | 7 |  | 1 |  | 2 | 2.1 | 12.7 |
|  |  | 3 | 50 | 43 |  | 5 |  | 2 |  |  | 2.3 | 15.9 |
|  | July 75 | 1 | 50 | 47 |  | 3 |  |  |  |  | 4.2 | 10.4 |
|  |  | 2 | 50 | 47 |  | 3 |  |  |  |  | 1.6 | 6.6 |
|  |  | 3 | 50 | 41 |  | 7 |  | 2 |  |  | 2.9 | 14.4 |
|  | Aug. 75 | 1 | 20 | 2 | 30 | 16 |  | 21 |  | 11 | 27.7 | 57.7 |
|  |  | 2 | 33 | 5 | 17 | 12 |  | 21 |  | 12 | 23.2 | 57.4 |
|  |  | 3 | 34 | 11 | 16 | 22 |  | 9 |  | 8 | 22.6 | 44.8 |
|  | Sept. 75 | 1 | 48 | 21 | 2 | 21 |  | 8 |  |  | 15.6 | 31.7 |
|  |  | 2 | 46 | 21 | 4 | 21 |  | 7 |  | 1 | 14.4 | 33.3 |
|  |  | 3 | 50 | 21 |  | 17 |  | 12 |  |  | 12.6 | 34.5 |

# APPENDIX G

# EFFECTS OF *ANDROPOGON SCOPARIUS* LEAF LEACHATE ON GERMINATION AND RADICLE GROWTH OF 15 TEST SPECIES

Values represent percent of control (n = 30).

| Test Species | Month | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Jan.[a] | | Feb. | | Mar. | | Apr. | | May | | June | | July | | Aug. | | Sept. | | Oct. | | Nov. | | Dec. | |
| | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R |
| Achillea lanulosa | 20* | 122 | 71 | 73 | 88 | 150 | 100 | 78* | 88 | 70* | 11* | 61* | 33* | 62* | 117 | 74* | 133 | 107 | 100 | 33 | 100 | 97 | 100 | 97 |
| Chrysopsis pilosa | 100 | 105 | 125 | 71 | 100 | 91 | 75 | 47* | 125 | 48* | 75 | 25* | 100 | 59 | 60 | 81 | 75 | 59 | 100 | 86 | 125 | 98 | 100 | 97 |
| Desmodium sessilifolium | 80 | 36* | 100 | 59* | 71* | 74* | 62* | 56* | 83 | 63* | 114 | 60* | 67 | 55 | 114 | 68 | 100 | 131 | 80 | 51 | 80 | 67 | 80 | 43* |
| Elymus canadensis | 100 | 87 | 200 | 102 | 100 | 88 | 25* | 69 | 62* | 106 | 33 | 66 | 100 | 83 | 112 | 79 | 100 | 97 | 75 | 70* | 100 | 87* | 100 | 92 |
| Hieracium longipilum | 100 | 104 | 100 | 80 | 100 | 89 | 50 | 54 | 100 | 62* | 50* | 36* | 75 | 44* | 60 | 50* | 100 | 59 | 200 | 77* | 50 | 115 | 100 | 92 |
| Plantago purshii | 90 | 104 | 90 | 106 | 112 | 80* | 112 | 86* | 112 | 94 | 100 | 54* | 125 | 67* | 100 | 69* | 100 | 91 | 89 | 88 | 100 | 92 | 100 | 102 |
| Rumex crispus | 71 | 89 | 86 | 106 | 100 | 89 | 88 | 61* | 100 | 80 | 100 | 91 | 100 | 105 | 89 | 71* | 90 | 92 | 100 | 81 | 78 | 89 | 112* | 94 |
| Datura stramonium | 150* | 84 | 67 | 106 | 88 | 94 | 86 | 123 | 86 | 79 | 100 | 76 | 100 | 83 | 117 | 90 | 88 | 86 | 114 | 119 | 86 | 87 | 86 | 88 |
| Lolium perenne | 111 | 88* | 100 | 88 | 100 | 92 | 111 | 88* | 100 | 101 | 100 | 86 | 100 | 104 | 100 | 92 | 111 | 104 | 111* | 90 | 100 | 113 | 100 | 91 |
| Chenopodium album | 100 | 108 | 300* | 64 | 100 | 94 | 200* | 111 | 50* | 93 | 100 | 58 | 60 | 64* | 40 | 130 | 100 | 50* | 50 | 107 | 100 | 88 | 100 | 75 |
| Amaranthus retroflexus | 100 | 88 | 60 | 104 | 100 | 109 | 100 | 112 | 117 | 86 | 75 | 103 | 50 | 111 | 60 | 114 | 100 | 44 | 67 | 167 | 100 | 86 | 100 | 94 |
| Bromus secalinus | 125 | 92 | 100 | 102 | 100 | 83* | 50 | 79 | 50 | 67 | 60 | 90 | 150 | 129 | 75 | 92 | 125 | 118 | 133 | 84 | 100 | 97 | 167 | 71 |
| Bromus japonicus | 100 | 52* | 100 | 80 | 100 | 89 | 100 | 53* | 89 | 34* | 60* | 27* | 89 | 40* | 89 | 34* | 80 | 57* | 78 | 22* | 100 | 58* | 100 | 57* |
| Bromus tectorum | 100 | 88* | 111 | 95 | 100 | 107 | 100 | 76* | 100 | 77* | 120 | 71* | 71 | 93 | 117 | 82* | 100 | 86 | 117 | 92 | 100 | 95 | 100 | 91 |
| Eragrostis trichiodes | 100 | 86 | 100 | 50* | 100 | 106 | 100 | 46* | 90 | 37* | 90* | 32* | 90 | 34* | 90 | 18* | 100 | 51* | 100 | 35* | 111 | 97 | 80* | 105 |

*Significant difference at $p < 0.05$ by t-test.

[a] G = germination
R = radicle length

# APPENDIX H

# EFFECTS OF *ANDROPOGON GERARDI* LEAF LEACHATE ON GERMINATION AND RADICLE GROWTH OF 12 TEST SPECIES

Values represent percent of control (n = 30).

| Test Species | Month | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Jan.[a] | | Feb. | | Mar. | | Apr. | | May | | June | | July | | Aug. | | Sept. | | Oct. | | Nov. | | Dec. | |
| | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R |
| Achillea lanulosa | 100 | 99 | 33* | 48* | 100 | 89* | 89 | 80* | 100 | 78* | 88 | 90 | 75 | 104 | 78 | 98 | 200 | 110 | 140 | 121 | 114 | 95 | 67 | 108 |
| Chrysopsis pilosa | 133 | 73 | 83 | 95 | 100 | 93 | 133 | 63* | 80 | 93 | 80 | 79 | 100 | 91 | 175* | 118 | 100 | 27* | 75 | 98 | 133 | 82 | 80 | 88 |
| Desmodium sessilifolium | 125 | 86 | 100 | 71 | 67* | 106 | 86 | 157* | 200 | 49* | 78 | 64 | 44* | 49 | 75 | 85 | 71 | 61 | 100 | 73 | 50 | 100 | 67 | 57* |
| Elymus canadensis | 100 | 69 | 100 | 102 | 100 | 97 | 67* | 88 | 100 | 100 | 50 | 77 | 56 | 76* | 90 | 101 | 50* | 110 | 88 | 95 | 140 | 114 | 100 | 117 |
| Hieracium longipilum | 200 | 52 | 100 | 97 | 100 | 95 | 200 | 82 | 100 | 108 | 80 | 87 | 50 | 91 | 67 | 80 | 200 | 115 | 67 | 90 | 100 | 95 | 133 | 97 |
| Plantago purshii | 90 | 100 | 111 | 82* | 100 | 92* | 112 | 78* | 90 | 83* | 125* | 93* | 114 | 79* | 100 | 65* | 111 | 111 | 89 | 98 | 100 | 92 | 111 | 92 |
| Rumex crispus | 117 | 94 | 114 | 82 | 86 | 95 | 88 | 105 | 88 | 90 | 129 | 107 | 100 | 114 | 90 | 105 | 117 | 103 | 120 | 96 | 133 | 108 | 100 | 81* |
| Datura stramonium | 88 | 85 | 117 | 80 | 117 | 157* | 111 | 83 | 133 | 72 | 100 | 103 | 150* | 82 | 86 | 81 | 86 | 92 | 100 | 85 | 100 | 111 | 116 | 83 |
| Lolium perenne | 90 | 103 | 111 | 100 | 100 | 95 | 111 | 85* | 90 | 80* | 100 | 93 | 100 | 103 | 90 | 85* | 111 | 98 | 100 | 99 | 100 | 114* | 100 | 100 |
| Chenopodium album | 100 | 89 | 100 | 95 | 50 | 97 | 100 | 109 | 50 | 100 | 60 | 87 | 300 | 145 | 133 | 141 | 100 | 182 | 50 | 90 | 150 | 80 | 50 | 91 |
| Amaranthus retroflexus | 100 | 92 | 167 | 106 | 117 | 97 | 175 | 88* | 129* | 85 | 167 | 143 | 33* | 165* | 75 | 110 | 100 | 93 | 100 | 39 | 112 | 76 | 57* | 106 |
| Bromus secalinus | 57 | 103 | 133 | 106 | 80 | 94 | 80 | 130 | 100 | 91 | 80 | 89 | 60 | 102 | 71 | 112 | 100 | 73 | 117 | 120* | 100 | 118* | 71 | 95 |

*Significant difference at $p < 0.05$ by t-test.

[a] G = germination; R = radicle length

# APPENDIX I

# EFFECTS OF *PANICUM VIRGATUM* LEAF LEACHATE ON GERMINATION AND RADICLE GROWTH OF 12 TEST SPECIES

Values represent percent of control (n = 30).

| Test Species | Month | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Jan.[a] | | Feb. | | Mar. | | Apr. | | May | | June | | July | | Aug. | | Sept. | | Oct. | | Nov. | | Dec. | |
| | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R |
| Achillea lanulosa | 57 | 116 | 75 | 103 | 86 | 92 | 89 | 98 | 112 | 54* | 133 | 80* | 80 | 73* | 67* | 91 | 67 | 76 | 100 | 93 | 100 | 98 | 100 | 89 |
| Chrysopsis pilosa | 67 | 93 | 100 | 72 | 75 | 84 | 75 | 56 | 133 | 52* | 167 | 38* | 200* | 114 | 200* | 116 | 133 | 53* | 100 | 79 | 200 | 88 | 75 | 85 |
| Desmodium sessilifolium | 38* | 48* | 43* | 38* | 67 | 56* | 29* | 61 | 86 | 52* | 75 | 57 | 44* | 34* | 56 | 64 | 38* | 44 | 60 | 58 | 25* | 33* | 71 | 44* |
| Elymus canadensis | 150 | 59* | 100 | 89 | 140 | 90 | 175 | 58 | 117 | 102 | 40 | 67* | 78 | 83* | 100 | 91 | 75 | 126 | 100 | 86* | 100 | 104 | 133 | 93 |
| Hieracium longipilum | 150 | 80 | 67 | 146* | 100 | 81 | 100 | 118 | 250 | 82 | 40* | 38* | 57* | 50* | 83 | 69* | 200 | 134 | 50 | 86 | 175* | 66 | 67 | 97 |
| Plantago purshii | 90 | 92 | 112 | 102 | 100 | 108 | 90 | 82* | 111 | 77* | 89 | 51* | 90 | 88* | 100 | 94 | 89 | 93 | 100 | 98 | 90 | 93 | 89 | 103 |
| Rumex crispus | 133 | 102 | 88 | 97 | 100 | 135 | 100 | 124 | 114 | 87 | 100 | 99 | 111 | 87 | 111 | 112 | 114 | 95 | 70 | 105 | 100 | 91 | 100 | 97 |
| Datura stramonium | 117 | 138 | 100 | 101 | 100 | 92 | 100 | 101 | 120 | 95 | 89 | 71* | 78 | 85 | 74 | 72 | 86 | 72* | 100 | 107 | 100 | 83 | 88 | 96 |
| Lolium perenne | 90 | 94 | 100 | 94 | 90 | 99 | 100 | 87* | 100 | 76* | 100 | 108 | 111 | 91 | 90* | 78* | 100 | 80* | 100 | 97 | 100 | 85* | 100 | 90* |
| Chenopodium album | 100 | 95 | 100 | 96 | 200 | 106 | 100 | 60 | 100 | 87 | 50 | 70 | 67 | 82 | 133 | 135 | 100 | 45 | 100 | 83 | 100 | 94 | 150 | 95 |
| Amaranthus retroflexus | 125 | 135 | 114 | 76 | 100 | 90 | 100 | 96 | 88 | 89 | 80 | 117 | 100 | 89 | 74 | 151 | 50 | 111* | 233 | 127 | 100 | 84 | 62 | 83 |
| Bromus secalinus | 120 | 74* | 100 | 105 | 100 | 102 | 120 | 64* | 75 | 98 | 88 | 100 | 140 | 86 | 80 | 92 | 150 | 54* | 167 | 124* | 133 | 99 | 67 | 107 |

*Significant difference at $p < 0.05$ by t-test.

[a] G = germination
R = radicle length

# APPENDIX J

# EFFECTS OF *SORGHASTRUM NUTANS* LEAF LEACHATE ON GERMINATION AND RADICLE GROWTH OF 12 TEST SPECIES

Values represent percent of control (n = 30).

| Test Species | Month | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Jan.[a] | | Feb. | | Mar. | | Apr. | | May | | June | | July | | Aug. | | Sept. | | Oct. | | Nov. | | Dec. | |
| | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R |
| Achillea lanulosa | 83 | 86 | 117 | 90* | 150 | 86* | 133 | 170* | 67 | 78* | 75 | 81* | 67* | 112 | 78* | 90 | 100 | 82 | 125 | 115 | 100 | 91 | 83 | 88 |
| Chrysopsis pilosa | 75 | 29* | 75 | 110 | 80 | 1 8 | 80 | 75* | 60 | 101 | 60* | 110 | 83 | 88 | 100 | 90 | 100 | 136 | 100 | 88 | 100 | 58* | 80 | 100 |
| Desmodium sessilifolium | 83 | 109 | 100 | 114 | 83* | 113 | 67 | 107 | 100 | 115 | 100 | 109 | 71 | 60* | 78 | 76 | 100 | 132 | 66 | 167 | 83 | 100 | 67* | 78 |
| Elymus canadensis | 167 | 97 | 100 | 90 | 71 | 101 | 100 | 90 | 150 | 99 | 100 | 107 | 90 | 95 | 100 | 88 | 150 | 89 | 90 | 95 | 90 | 111 | 86 | 105 |
| Hieracium longipilum | 67 | 76 | 75 | 86 | 100 | 98 | 100 | 123* | 33 | 105 | 75 | 110 | 80 | 83 | 67 | 79* | 200 | 33* | 100 | 48* | 83 | 75 | 100 | 90 |
| Plantago purshii | 100 | 97 | 100 | 91 | 100 | 110* | 100 | 126* | 100 | 94 | 100 | 66* | 100 | 78* | 100 | 98 | 100 | 111 | 89 | 100 | 100 | 97 | 100 | 114* |
| Rumex crispus | 100 | 108 | 133* | 84 | 80 | 142 | 129 | 121 | 88 | 85 | 100 | 97 | 100 | 121* | 89 | 86 | 114 | 110 | 100 | 98 | 100 | 92 | 100 | 84 |
| Datura stramonium | 75* | 117 | 120 | 95 | 125 | 102 | 100 | 90 | 129 | 110 | 120 | 79 | 78 | 93 | 80 | 111 | 117 | 81 | 114 | 80 | 88 | 82 | 100 | 88 |
| Lolium perenne | 100 | 97 | 100 | 100 | 100 | 82* | 100 | 79* | 112 | 93 | 90 | 91 | 100 | 80* | 111 | 110 | 100 | 83* | 100 | 105 | 100 | 107 | 100 | 92 |
| Chenopodium album | 100 | 103 | 100 | 91 | 100 | 107 | 200 | 140 | 100 | 87 | 140 | 88 | 67 | 134 | 100 | 100 | 100 | 100 | 200 | 73 | 100 | 85 | 200 | 89 |
| Amaranthus retroflexus | 150 | 72 | 100 | 97 | 160* | 103 | 88 | 81 | 83 | 75 | 100 | 117 | 75 | 107 | 167 | 155* | 167 | 134 | 67 | 104 | 100 | 115 | 65 | 96 |
| Bromus secalinus | 140 | 91 | 100 | 108 | 83 | 92 | 200* | 66 | 83 | 82 | 100 | 134 | 100 | 107 | 33 | 51 | 100 | 150 | 80 | 96 | 100 | 89 | 150 | 92 |

*Significant difference at $p < 0.05$ by t-test.

[a] G = germination; R = radicle length

# APPENDIX K

## EFFECTS OF <u>ANDROPOGON</u> <u>SACCHAROIDES</u> LEAF LEACHATE ON GERMINATION AND RADICLE GROWTH OF 12 TEST SPECIES

Values represent percent of control (n = 30).

| Test Species | Month | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Jan.[a] | | Feb. | | Mar. | | Apr. | | May | | June | | July | | Aug. | | Sept. | | Oct. | | Nov. | | Dec. | |
| | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R |
| Achillea lanulosa | 60 | 94 | 67* | 89* | 83 | 96 | 71 | 76* | 80 | 100 | 100 | 94 | 75 | 92 | 100 | 100 | 60 | 95 | 50 | 93 | 100 | 99 | 80 | 104 |
| Chrysopsis pilosa | 100 | 63 | 100 | 100 | 75 | 87 | 125 | 60* | 125 | 81 | 100 | 144 | 125 | 61* | 150 | 93 | 167 | 60 | 75 | 76 | 100 | 69* | 100 | 113 |
| Desmodium sessilifolium | 83 | 82 | 117 | 107 | 100 | 90 | 100 | 106 | 100 | 95 | 111* | 111 | 133 | 86 | 117 | 83 | 83 | 140 | 150 | 97 | 60* | 126 | 100 | 59 |
| Elymus canadensis | 67 | 76 | 75 | 91 | 80 | 94 | 100 | 95 | 100 | 66* | 86 | 89 | 143 | 76* | 50 | 102 | 50* | 77 | 89* | 93 | 100 | 88* | 75 | 91 |
| Hieracium longipilum | 100 | 81 | 100 | 64* | 100 | 107 | 111 | 112 | 80 | 43 | 50* | 84 | 100 | 114 | 50* | 58* | 100 | 178 | 100 | 74 | 120 | 92 | 67 | 104 |
| Plantago purshii | 90 | 78* | 100 | 89* | 90 | 94 | 89 | 108 | 112 | 69* | 112 | 55* | 80 | 75* | 100 | 81* | 100 | 96 | 89 | 92 | 89 | 99 | 89 | 93 |
| Rumex crispus | 114 | 69 | 114 | 97 | 111 | 89 | 100 | 94 | 89 | 97 | 89 | 118 | 100 | 113 | 111 | 72* | 100 | 77 | 86* | 104 | 88 | 98 | 125* | 88 |
| Datura stramonium | 88 | 134* | 117 | 99 | 100 | 88 | 100 | 119 | 100 | 157* | 140 | 70 | 86 | 109 | 150 | 106 | 78 | 83 | 86 | 90 | 114 | 110 | 100 | 86 |
| Lolium perenne | 100 | 86* | 100 | 103 | 100 | 93 | 100 | 79* | 112 | 99 | 111 | 88 | 100 | 76 | 100 | 98 | 100 | 81* | 100 | 96 | 100 | 101 | 100 | 91 |
| Chenopodium album | 50 | 126 | 100 | 84 | 100 | 96 | 300* | 109 | 100 | 77 | 50 | 111 | 75 | 86 | 100 | 100 | 100 | 88 | 50 | 82 | 100 | 98 | 100 | 87 |
| Amaranthus retroflexus | 125 | 93 | 80 | 87 | 88 | 73 | 80 | 148* | 40 | 71 | 80 | 103 | 83 | 131 | 100 | 88 | 100 | 158* | 112 | 86 | 100 | 91 | 100 | 91 |
| Bromus secalinus | 120 | 112 | 88 | 99 | 100 | 89 | 50 | 81 | 67 | 73 | 80 | 99 | 120 | 102 | 60 | 118 | 100 | 101 | 100 | 96 | 120 | 87 | 133 | 85 |

*Significant difference at $p < 0.05$ by t-test.

[a] G = germination
R = radicle length

# APPENDIX L

# EFFECTS OF ANDROPOGON SCOPARIUS LEAF LEACHATE ON GERMINATION AND RADICLE GROWTH OF FIVE WEEDY SPECIES COMMON TO DISTURBED TALL GRASS PRAIRIES

Values are given as percent of controls (n = 30).

| | Collection Date | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | May, 1974 | | | | | | | | | | June, 1974 | | | | | | | | | | | | | |
| Assay Species | April[a] 1974 | | 09 | | 13 | | 20 | | 25 | | 31 | | 06 | | 13 | | 20 | | 27 | | June 1973 | | July 1973 | | Aug. 1973 | |
| | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R | G | R |
| Achillea lanulosa | 100 | 78* | 83 | 90 | 88 | 70* | 62 | 89 | 100 | 74* | 44* | 41* | 44* | 48* | 44* | 53* | 40* | 58* | 33* | 49* | 11* | 61* | 33* | 62* | 117 | 74* |
| Chrysopsis pilosa | 75 | 47* | 100 | 55* | 125 | 48* | 100 | 64 | 100 | 71 | 100 | 52* | 100 | 75* | 50* | 29* | 50* | 49* | 60* | 67* | 75 | 25* | 100 | 59 | 60 | 81 |
| Hieracium longipilum | 50 | 54 | 50 | 46 | 100 | 62* | 12* | 62 | 17* | 71 | 100 | 68* | 50* | 39* | 29* | 30* | 75 | 39* | 14* | 44* | 50* | 36* | 75 | 44* | 60 | 50* |
| Plantago purshii | 112 | 86* | 100 | 93 | 112 | 94 | 90 | 74* | 80 | 67* | 86 | 66* | 100 | 67* | 89 | 50* | 90 | 67* | 89 | 69* | 100 | 54* | 125 | 67* | 100 | 69* |
| Bromus tectorum | 100 | 76* | 100 | 89 | 100 | 77* | 100 | 88 | 100 | 82* | 100 | 47* | 100 | 69* | 100 | 71* | 100 | 90 | 111 | 110 | 120 | 71* | 71 | 93 | 117 | 82* |

*Significant difference at $p < 0.05$ by t-test.

[a] G = germination
R = radicle length

# APPENDIX M

# $R_f$ VALUES OF TWO SOLVENT SYSTEMS, FLUORESCENCE UNDER UV AND COLOR RESPONSE TO TWO SPRAY REAGENTS ON TWELVE COMMERCIAL (SIGMA CHEMICAL CO.) PHENOLIC COMPOUNDS

Values based upon at least five replications.

| Compound | $R_f$ Values[a] |  | Fluorescence |  | Reagent Colors[b,c] |  |
|---|---|---|---|---|---|---|
|  | BAW | 6% AA | Long UV | Short UV | DPN | DSA |
| Vanillic acid | .90 | .55 | * | dk. bl. abs. | pi | lt. br. |
| Arbutin | .97 | .77 | * | ft. bl. abs. | bl. vio. | yel. |
| Gallic acid | .66 | .49 | * | dk. bl. abs. | ft. br. | ft. tan |
| Phloridizen | .80 | .42 | * | * | or. yel. | yel. br. |
| p-coumaric acid | .91 | .48 | dk. bl. abs. | dk. bl. abs. | dk. bl. | red. br. |
| Chlorogenic acid | .66 | .59 | S. bt. abs. | S. bt. abs. | yel. br. | yel. tan |
| Scopoletin | .87 | .44 | V. S. bt. abs. | V. S. bt. abs. | red. br. | pi |
| Gentisic acid | .89 | .57 | V. S. bt. abs. | V. S. bt. abs. | yel. or. | ft. tan |
| Caffeic acid | .82 | .28/.59 | S. bt. abs. | S. bt. abs. | red. br. | pl. yel. |
| p-hydroxy-benzoic acid | .90 | .61 | * | dk. bl. abs. | red | yel. tan |
| Ferulic acid | .88 | .34/.64 | S. bt. abs. | S. bt. abs. | br. bk. | ft. or. |
| Hydroquinone | .86 | .71 | dk. bl. abs. | dk. bl. abs. | dk. br. | pl. yel. |

[a] Solvent systems: BAW: n-Butanol : Acetic acid : water (63:10:27, v./v./v.)
6% AA: 6% acetic acid in aqueous solution

[b] Spraying reagents: DPN: Diazotized p-nitroaniline, overspray with 10% $Na_2CO_3$ (Bray, et al., 1950).
DSA: Diazotized sulfanilic acid, overspray with 10% $Na_2CO_3$ (Bray, et al., 1950).

[c] Symbols:
abs - absorption
* - not detected
dk - dark
bl - blue
ft - faint
S - strong
bt - bright
V - very
pi - pink
lt - light
br - brown
vio - biolet
yel - yellow
tan - tan
or - orange
red - red
pl - pale
bk - black

# VITA

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Doctor of Philosophy

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