Reclamation and Revegetation Research, 1 (1982) 123—160
Elsevier Scientific Publishing Company, Amsterdam — Printed in The Netherlands

RECLAMATION OF COAL MINED LANDS: THE ROLE OF *KOCHIA SCOPARIA* AND OTHER PIONEERS IN EARLY SUCCESSION

Louis R. Iverson and Mohan K. Wali

Department of Biology and Project Reclamation, The University of North Dakota, Grand Forks, ND 58202 (U.S.A.)

(Accepted for publication 4 March 1982)

Abstract

Iverson, L.R. and Wali, M.K., 1982. Reclamation of coal mined lands: the role of Kochia scoparia *and other pioneers in early succession.* Reclam. Reveg. Res., *1: 123—160.*

Keywords: early succession; pioneering species; coal mining; revegetation; North Dakota; autotoxicity; nutrients; Kochia scoparia*; allelochemics; competition.*

Patterns of colonization by pioneering species and their allelochemic and competitive relations were studied in 4 reclaimed areas in western North Dakota, ranging in age from 1 to 4 years after mining; a site from a native mixed grass prairie was used for comparison. Early changes in floristic composition revealed that despite seeding of agronomic species, initial colonization was by fugitive species. Of the 95 species recorded, Kochia scoparia *(Chenopodiaceae) dominated in the first 2 years after mining.* Kochia *had relatively low densities in the first year (50—80 plants m^{-2}), but was robust and attained heights of 88 cm, with a biomass of about 400 g m^{-2}. In the second year,* Kochia *densities increased to over 10 000 m^{-2}, but height and biomass were reduced to 15 cm and 90 g m^{-2}, respectively. During the third and fourth years,* Kochia *density declined, while the planted* Agropyron *grasses increased. Other pioneers like* Amaranthus retroflexus, Chenopodium album, Helianthus annuus, Salsola *spp. and* Setaria *spp. showed a less abrupt, but similar, decline. Chemical analyses of the soils over the same time-period showed decreases in electrical conductivity, and in the concentrations of Ca, Mg, Na, Li, Sr, and SO_4 (due to leaching), while total N and organic matter increased.*

Field studies were conducted on the interspecific relationships of the 2 dominant species, Kochia scoparia *and* Agropyron *spp., during early succession. It was found that* Kochia *acted as a "nurse crop" for several months during the first year of* Agropyron *spp. establishment, but then began to* *shade heavily by late July, which reduced grass tillering.*

Autotoxicity in Kochia *appears to be a major factor responsible for the decline in its growth. Results from a field experiment indicated that thinning dense second-year* Kochia *stands to the density of first-year stands did not alter the growth of* Kochia, *providing strong evidence for autotoxicity. Similarly, several growth-chamber experiments showed that small amounts of decaying* Kochia *leaves and (especially) roots were toxic to* Kochia, *but not to* Melilotus officinalis *or* Agropyron caninum. *Chemical analyses of the soils and plant tissues indicated that nutritional imbalances, as shown by P/Mn and P/Zn ratios, may be responsible for autotoxicity. A bioassay experiment indicated that allelochemic influences may be important for several colonizing species besides* Kochia. *Although our results indicate that later-stage species have greater toxicities than first-year colonizers, autotoxicity in the very initial stages seems to be accentuated by harsh habitat conditions.*

Introduction

Surface mining for coal and minerals is responsible for drastic disturbance to land surfaces throughout the world. In the United States alone, 1.3 million ha were disturbed from prehistoric times to 1965; an equivalent area, it is estimated, will have been disturbed between 1965 and 1985 (U.S. Department of the Interior, 1967; Morgan, 1973). Reclamation of mined lands has been one of the most intensely debated environmental issues of the 1970's. Of particular significance to this and future ecological studies is the recent legal requirement that principles of succession shall be incorporated in devising reclamation procedures for these disturbed areas (Imes and Wali, 1977, 1978).

Considerable knowledge of succession has come from studies of areas after glacial retreats (Crocker and Major, 1955; Stevens and Walker, 1970), mudflows (Dickson and Crocker, 1953a, b, 1954), alluvial deposits (Wright et al., 1959), and abandoned old fields (Whitman et al., 1943; Keever, 1950; Egler, 1954; Bazzaz, 1968; Rice, 1974; Jackson and Willemsen, 1976). These studies, together with the recent work on abandoned coal mine areas in the Great Plains region (Wali and Freeman, 1973; Glenn-Lewin, 1979; Jonescu, 1979; Schafer and Nielsen, 1979; Sindelar, 1979; Wali and Pemble, 1982), are important in understanding successional processes on mined lands. However, new regulatory controls require that land areas after coal mining (1) be shaped to "blend" with the prevailing topography of the area, (2) have topsoil re-spread on them (removed and stockpiled prior to mining), (3) be fertilized, and (4) be seeded with a mix of "desirable" agronomic species. Regardless of what is seeded, the pioneer (volunteer) species play an important role in the initial stages of succession in these areas.

Of the several pioneering species on newly reclaimed areas in North Dakota, *Kochia scoparia* (L.) Schrader (Chenopodiaceae) is the dominant colonizer. Several aspects of the ecology of this species have been studied;

its drought resistance (Erickson, 1947), halophytic attributes (Monk and Wiebe, 1961), weedy nature in agriculture (Weatherspoon and Schweizer, 1969; Bell et al., 1972), and its forage potential (Sherrod, 1971, 1973). Little is known, however, of its role in the revegetation of surface-mined areas.

In this paper, we document the changes in (1) plant species composition, and (2) physical and chemical properties of soils in the first 4 years after mining in areas that have been reclaimed (i.e. contoured, topsoil replaced, fertilized, and seeded). We discuss possible mechanisms by which these changes occur based on studies of (3) intraspecific competition in *Kochia*, (4) interspecific competition between *Kochia* and *Agropyron* spp., and (5) the role of allelochemics in the decline of *Kochia* and other pioneer species.

Study area

The study area is located in the mixed grass prairie ecogeographic region (Whitman and Wali, 1975), on a glaciated portion of the Missouri Plateau of the Great Plains Physiographic Province in western North Dakota. The 5 study areas, representing areas 1, 2, 3, and 4 years after reclamation and an unmined site, were located within 3 km of each other, 5—7 km south of Beulah. Each site consisted of 2—6 ha which had been treated similarly during reclamation (Appendix I). Topsoil for each site was obtained from lightly grazed prairie. Prior to mining, each site had a similar topography and fire history. The unmined site was an occasionally-grazed native prairie; data gathered from this site were used for comparison.

Climate

Western North Dakota has a semi-arid, continental climate with an annual mean precipitation of 44 cm, 74% of which falls during the growing season (Wali and Sandoval, 1975). Climatic data for the sites during the years 1975, 1976 and 1977 indicated a rainfall of 47, 36 and 51 cm, and 105, 130 and 159 frost-free days, respectively, compared to the 25-year averages of 44 cm and 120 frost-free days (National Oceanic and Atmospheric Administration, 1975—1977). The sites had a temperature range of —31 to 42°C, and an average wind speed of 21 km h^{-1}, predominantly from the west (Stearns-Rogers Inc., 1976—1978). For the months of June—August during the years 1975—1977, pan evaporation exceeded incoming precipitation by 16.5 cm.

Geology and soils

Parent materials in the study area belong to the Paleocene Sentinel Butte Formation of the Fort Union Group, which is characterized by a non-marine deltaic floodplain—floodbasin with natural levees of silt—clay—sand deposits (Jacob, 1973). The entire area was glaciated. Most soils are Typic

Haploborolls with an A horizon approximately 25 cm thick (Omodt et al., 1975). The topsoil has a low electrical conductivity (E.C. < 1 mmho cm^{-1}) and low sodium adsorption ratios (SAR < 1); subsoil typically has higher values, with E.C. of approximately 5 mmhos cm^{-1} and SAR of 11 (Wali and Sandoval, 1975).

Methods of study

Plant and soil sampling

Species composition data were obtained in 1977 using 50 randomly placed 0.5×0.5 m quadrats within each of the 5 study areas. Analyses of plant growth on the mined sites were made separately and included measurements of height, density and biomass from a total of 392 quadrats (0.25×0.25 m), sampled over 7 tri-weekly intervals. Taxonomic nomenclature follows Van Bruggen (1976).

Replicate soil samples were collected 4 times from the top 15 cm at each mined site at intervals of approximately 6 weeks through the 1977 growing season; the unmined site was sampled in August 1977.

Field competition experiments

To study the competitive aspects of *Kochia* and some planted grasses (predominantly *Agropyron caninum* with some *A. smithii*), experiments were established on first- and second-year areas in early May 1977. Five replicate plots were chosen in an area seeded in November 1976; each was subdivided into 3 sub-plots (1.5×1.5 m) for the following treatments: (1) *Kochia* alone at initial densities of 25 plants m^{-2}; (2) *Agropyron* spp. alone at initial densities of 6 plants m^{-2}; and (3) both species together at the same densities. All other species were removed by hand as they germinated.

Areas seeded in autumn 1975 (second growing season in 1977, having greatly elevated plant densities) had 5 replicate plots, each with three similar treatments as above: (1) *Kochia* alone at about 10 000 plants m^{-2}; (2) *Agropyron* spp. alone at about 50 plants m^{-2}; and (3) both together at the same densities. Measurements were taken at seven 3-week intervals throughout the summer of 1977. Assessments of biomass were made within the plots by measuring the height (*Kochia* and *Agropyron*) and number of stems (*Agropyron* only) of the plants. This method was found to correlate well with biomass estimates from harvest techniques on 1- and 2-year-old study sites.

Field autotoxicity experiment

To determine if allelopathy was involved in the stunting of *Kochia* plants in 2-year-old sites, a field study was conducted by thinning high-density second-year populations to approximate the density of first-year areas. Five replicate plots, each with 2 sub-plots (0.5 × 0.5 m), were established in areas seeded in autumn 1975. The following treatments were established at the beginning of the second growing season: (1) *Kochia* alone with about 10 000 plants m^{-2}, and (2) *Kochia* alone with densities thinned to first-year levels, about 50 plants m^{-2}. Height and number of leaf pairs in *Kochia* were determined at intervals of 3 weeks during the 1977 growing season.

Insect sampling

During the summer of 1977, small red cocklebur weevils, *Rhodobaenus tredecimpunctatus* (Illiger) (Curculionidae) (Borror et al., 1976), were noticed frequently on the soil surface in the first-year areas. Later in the season, a large number of pioneer species were found to be infested with weevil larvae. Stems of the 7 dominant pioneer species were examined for larvae to determine the selectivity of cocklebur weevils. A total of 161 stems, 50—80 cm tall, were randomly chosen over a 0.5-ha area.

Growth chamber experiments

To determine the relative contributions of competition and allelopathy in plant compositional changes, 6 growth chamber experiments were conducted with the following climatic conditions: 25°C day—15°C night temperature, 55—70% relative humidity, 14 h day/10 h dark photoperiod, and photosynthetic active radiation (PAR) at 100 microeinsteins m^{-2} s^{-1}. Plants were irrigated with distilled—deionized water. After a period of growth, the plants were harvested, washed, and dried at 70°C to constant weight. Plants from selected experiments were further analyzed for nutrients and trace elements. The experiments were as follows:

To test the nature and effect of intraspecific competition on growth, *Kochia* was seeded in 15-cm undrained polyethylene pots containing 2 kg of stockpiled topsoil from the mined sites where field observations were made. Pots were seeded with sufficient numbers to enable thinning to desired plants densities after 2 weeks. The following final densities were established: 2, 4, 8, 16, 32, 64, and 128 plants/pot. Three replicates of each density were grown in a growth chamber for 37 days, after which the plants were harvested, and their above- and and below-ground dry matter yield (DMY) determined.

A set of 5 experiments was conducted to evaluate autoallelopathy in *Kochia*. Experiment 1 was designed to test the effect of decaying *Kochia* leaves on the growth of *Kochia* and of 2 species commonly sown on mined lands, viz. *Agropyron caninum* and *Melilotus officinalis*. In half (18) of the pots, 15 g of dried, ground *Kochia* leaf material was mixed with 2 kg of topsoil obtained from the field sites. The amount of *Kochia* leaves added was roughly equivalent to the maximum amount of dry matter produced by first-year *Kochia* plants per unit area at the field sites. Eighteen control pots received no *Kochia* leaf material. Each undrained 6-inch polyethylene pot received NPK at rates of 30, 20 or 15 p.p.m. to ensure an adequate supply of these nutrients. The pots were incubated at room temperature for 2 weeks at 10—20% soil water content to allow decomposition of *Kochia* leaves. The pots were then seeded, and after 2 weeks were thinned to 2 densities: *Kochia*, 4 or 64 plants/pot; *Agropyron*, 12 or 50 plants/pot; and *Melilotus*, 10 or 54 plants/pot. Each treatment was replicated 3 times such that 36 pots were placed in the growth chamber for 37 days, after which plants were harvested and weighed. Plants and soils were then analyzed for nutrient and trace elements.

Experiment 2 was designed to test the growth of four species (*Kochia scoparia*, *Salsola collina*, *Agropyron caninum*, and *Melilotus officinalis*) with three *Kochia* treatments; decaying leaves (KL), decaying roots (KR), and *Kochia* leaf leachate (KS). Two kg of topsoil was placed in each of 64 (15-cm) polyethylene pots; 16 were used as controls and received 5 g of Canadian sphagnum peat, 16 received 5 g ground *Kochia* leaf material, 16 received 2.5 g ground *Kochia* root material, and the remaining 16 received 5 g peat and were irrigated with *Kochia* leachate. After 2 weeks incubation at room temperature with 15—20% soil water content, the pots were seeded with the 4 species; each species had 4 replicates of each treatment: control, KL, KR and KS. All pots were equally irrigated, with the KS pots receiving *Kochia* leachate and the remaining pots receiving deionized water. Leachate was obtained by passing deionized water over large quantities of fresh *Kochia* shoots obtained from the field. After four weeks of growth, the pots with *Kochia*, *Agropyron* and *Melilotus* seedlings were thinned to a density of 15 plants; *Salsola* pots were thinned to 12 plants. After 8 weeks, the shoots were harvested and their DMY determined.

Experiment 3 was initiated to determine whether phytotoxic materials persist in the soil long enough to be toxic on subsequent growth. Soils from 4 of the treatments from Experiment 2 were used for this experiment; these 4 treatments were (1) *Kochia* grown in pots containing 2 kg soil and 5 g peat (control), (2) *Kochia* grown in soil containing 5 g *Kochia* leaves, (3) *Kochia* grown in soil containing 2.5 g *Kochia* roots, and (4) *Agropyron* grown in soil containing 5 g peat (another control). Soil from the 4 replicates of each treatment was combined, ground and passed through a 2-mm screen to remove the majority of the root material; 3 replicate pots of each treatment were set up from the resulting soil, giving a total of 12 pots. No additional material was added to the soil at this time. Seeds were sown, the density was reduced to 20 plants/pot after 4 weeks, and after 51 days in the growth chamber, the shoots were harvested, weighed, and analyzed for nutrient and trace elements.

Experiment 4 was conducted to determine the effect of *Kochia* leaves and roots in combination; to ensure uniformity, separate leaf and root treatments were also used. Four treatments were used in 12 pots containing

2 kg soil each: a control treatment with 6 g peat/pot; (2) 6 g *Kochia* leaves/pot (KL); (3) 4 g *Kochia* roots/pot (KR); and (4) 6 g leaves + 4 g roots/pot (KL+R). The levels used were approximately equivalent to the average amount of leaves and roots found on 1-year-old sites. *Kochia* seeds were sown, and after 4 weeks were thinned to 20 seedlings/pot; after 51 days in the growth chamber, the plants were harvested, weighed, and analyzed for nutrient and trace elements.

Experiment 5 was conducted to study autotoxicity of *Kochia* under stress conditions. Four replicate pots were set up for each of the 3 treatments: (1) 5 g peat in 2 kg soil (low water control); (2) 5 g *Kochia* leaves in 2 kg soil; and (3) 5 g peat in 2 kg soil (control). Treatments 1 and 2 received only 1/3 of the irrigation of the control during the course of the experiment. *Kochia* seeds were sown and the seedlings were thinned to 15 plants/pot after 4 weeks; after 8 weeks of growth the plants were harvested.

Bioassay of plant extracts

Bioassays of pioneer plant extracts for allelochemic studies were conducted as follows: leaves of 15 species were collected from mined sites on 8 August 1977. Extracts were made by mixing 20 g dry leaf material with 200 ml deionized water for 90 s in a Waring blender. The mixture was vacuum filtered and then sterilized by filtering through 0.45-micron millipore filters. The growing medium of agar was prepared following Melrod (1977) for germination and seedling elongation experiments. A 4-part agar solution: 1 part extract or control solution was used; 50 ml of this solution was needed for each of the 64 (15-cm) petri plates (germination experiment), and 7.5 ml were needed for each of the 320 (15 × 100 mm) test tubes (elongation studies). All transfers were done aseptically. Sterility was maintained in the extracts by filtration rather than by heat, which might have broken down some organic compounds.

Two seed sources were used for the bioassay — radish (*Raphanus* sp.) and *Kochia*. Seeds were soaked for 15 min in 15% H_2O_2 to achieve surface sterility. Two plates divided into thirds were used for each seed source, and 25 seeds were added to each of the resulting 6 replicates for each species extract. Germination was carried out at room temperature in the dark. Germinated seeds were counted every 24 h for 3 days with radish and 4 days with *Kochia*. Two-day germinated seedlings were transferred from the plates to the corresponding tubes. Ten replicates for each seed source were established (one seedling per tube) and seedling elongation was monitored over the next 3 days. The values reported here are the rates of elongation per day from the time of seeding (5 days).

Soil analysis

Field water content of the samples was determined gravimetrically. Soils were air-dried, crushed and passed through a 2-mm sieve. Particle size was determined by the hydrometer method (Bouyoucos, 1951). Chemical characteristics of all soil samples were determined as follows. Saturation extracts were made using distilled—deionized water, from which E.C., pH, saturation percentages, and concentrations of chloride (Cl), sulfate (SO_4), calcium (Ca), magnesium (Mg), sodium (Na), potassium (K), manganese (Mn), iron (Fe), zinc (Zn), lithium (Li) and strontium (Sr) were determined. Replaceable (water soluble + exchangeable) Ca, Mg, K, Na, Mn, Zn, Li, and Sr were determined in 1:5 soil:1 N ammonium acetate extracts (Wali and Krajina, 1973). Chelated/complexed Fe, Mn, Zn, Cu, Sr, nickel (Ni), cadmium (Cd), lead (Pb), aluminum (Al), silicon (Si), and boron (B) were determined in 1:2.5 soil:0.02 M disodium-EDTA extracts. All cations, except B, were determined by atomic absorption spectrophotometry, using standard methods (Perkin-Elmer, 1973). Boron was determined using a carmine colorimetric technique (Chapman and Pratt, 1961). Soil phosphorus (P) was determined using Olsen's method, total nitrogen (N) by the Kjeldahl method, and percent organic matter (O.M.) was determined by the Walkley—Black method (Jackson, 1958). Carbon/nitrogen rates were calculated assuming 58% of organic matter is carbon (Jackson, 1958). Chloride was determined potentiometrically using an Orion specific ion probe, and SO_4 was determined turbidimetrically following Kollman and Wali (1976).

Plant analysis

For above-ground biomass determination, harvested plants were washed, segregated by species, and oven-dried at 70°C to constant weight. Dried plant material was analyzed for nutrient and trace elements by first grinding plants in a Wiley Mill with 2-mm mesh, and then digesting in a 5:1 nitric acid:perchloric acid mixture. Total P concentration was determined by vanadomolybdophosphoric yellow method (Jackson, 1958). Concentrations of Ca, Mg, K, Na, Zn, Fe, Li, Ni, Cu, and Sr in plants were determined by atomic absorption spectrophotometry. Nutrient uptake values were calculated from concentration and above-ground biomass (Munson and Nelson, 1973).

Results and discussion

Early succession

Floristic changes

A total of 30 species were found to invade during the first 4 years after reclamation (Table I). Species richness increased regularly with site age. Of the 11 species that invaded during the first year, *Kochia scoparia*, *Setaria viridis*, *Salsola collina*, *Polygonum convolvulus* and *Avena fatua* were the most important. Seven additional species were present in the second year,

TABLE I

Percentage frequency of occurrence of plants on the mined and unmined[1] sites (data based on 250 plots, each 0.5 × 0.5 m). Species seeded on the mined sites are marked with an asterisk (*)

Species	Years after mining				Unmined
	1	2	3	4	
Kochia scoparia	100	98	10	8	2
Setaria viridis	58	52	—	—	—
Salsola collina	54	10	—	2	18
Polygonum convolvulus	40	16	2	—	—
**Agropyron caninum*	38	94	96	56	—
Avena fatua	30	4	—	—	—
Helianthus annuus	18	2	—	—	—
**Agropyron smithii*	16	4	64	60	—
Salsola iberica	10	—	—	—	—
Chenopodium album	10	—	—	2	—
Amaranthus retroflexus	6	—	—	—	—
Polygonum ramosissimum	4	54	2	14	—
Echinochloa crusgalli	2	2	—	—	—
Hordeum jubatum	—	36	6	2	—
**Medicago sativa*	—	18	—	—	—
Lepidium densiflorum	—	12	6	38	—
Aster ericoides	—	4	14	4	8
Setaria glauca	—	4	—	—	—
Bromus inermis	—	2	28	30	—
Elymus canadensis	—	2	—	—	—
Xanthium strumarium	—	2	—	—	—
**Melilotus officinalis*	—	2	—	—	—
Conyza canadensis	—	—	8	4	—
Grindelia squarrosa	—	—	6	12	—
**Agropyron elongatum*	—	—	2	40	—
**Agropyron cristatum*	—	—	2	34	12
Lactuca serriola	—	—	2	16	—
Poa pratensis	—	—	—	38	—
Descurainia sophia	—	—	—	10	2
Artemisia ludoviciana	—	—	—	8	48
Artemisia absinthium	—	—	—	4	—
Sisymbrium altissimum	—	—	—	4	6
Thlapsi arvense	—	—	—	4	—
Hedeoma hispida	—	—	—	4	8
Tragopogon dubius	—	—	—	2	—
Artemisia frigida	—	—	—	2	18

[1]The following species were found only on the unmined site; % frequency values are in parentheses for species or groups of species: *Bouteloua gracilis* (82), *Rosa arkansana* (52), *Aristida longiseta* (32), *Stipa comata* (20), *Lygodesmia juncea*, *Sphaeralcea coccinea*, *Calamovilfa longifolia* (18), *Artemisia dracunculus*, *Chrysopsis villosa* (16), *Echinacea angustifolia*, *Aster oblongifolius* (14), *Glycyrrhiza lepidota*, *Chenopodium leptophyllum*, **Bouteloua curtipendula* (12), **Andropogon scoparius*, *Lotus purshianus* (10), *Psoralea argophylla* (8), *Opuntia polycantha*, **Stipa viridula*, *Koeleria pyramidata*, *Kuhnia eupatorioides*, *Stipa spartea*, *Lithospermum incisum*, *Liatris punctata*, *Solidago mollis* (4), *Helianthus petiolaris*, *Oxytropis lambertii*, *Symphoricarpos occidentalis*, *Linum rigidum*, *Solidago missouriensis*, *Euphorbia podperae*, *Gentiana puberulenta*, *Apocynum cannabinum*, *Arabis holboellii*, *Andropogon gerardi*, *Ratibida columnifera* (2).

with *Hordeum jubatum*, *Lepidium densiflorum* and *Aster ericoides* being the most frequent. Along with the latter, *Conyza canadensis*, *Grindelia squarrosa* and *Lactuca serriola* were found on the third-year site. Eight more species were established on the four-year site. Several of the fourth-year species, e.g. *Artemisia ludoviciana*, *A. frigida*, *Sisymbrium altissimum*, and *Hedeoma hispida*, were also found at higher frequencies on the unmined site. This indicates that after 4 years, conditions may become more hospitable for the establishment of native prairie species. Many species, however, were found only on the unmined site, e.g. *Bouteloua gracilis*, *Rosa arkansana*, *Aristida longiseta* and *Stipa comata*. Only one seeded species which became established on mined sites, *Agropyron cristatum*, was important on the unmined site (Table I). In general, the cool-season grasses were the most important elements on mined but not on unmined sites, whereas the warm-season grasses did not establish in the short term.

Changes in soil properties

Of the 36 soil properties investigated, 25 showed significant differences (using ANOVA) among sites of different ages (Table II). Significant decreases in concentration in relation to increasing site age were noted for E.C. and SO_4, water soluble and replaceable Ca, Mg, Sr and Li, and EDTA-extractable Cu, Fe and Ni. Several elements showed higher concentrations in the first year after mining, then decreased in subsequent years but were higher at unmined sites; these included water soluble and replaceable Mn, and EDTA-extractable Al, B, Mn, Pb, and Si. Total nitrogen increased significantly in the years following mining, although nitrogen fertilizer was initially added to the sites; organic matter also increased, although this was only significant at the 10% level. When the mined sites were compared as a group with the unmined sites, the latter showed significantly lower E.C., pH, SO_4, P, Ca, Mg, Na, Sr, and clay content, and higher K, Zn, Al, and B (Table II).

Discussion of initial successional trends

Surface-mined areas where topsoil has been replaced (as in our study areas) go through a process closely akin to old field succession, unlike abandoned mined lands which represent primary succession (Wali and Kollman, 1977). Replaced topsoil has some nutrient and organic matter accumulation, microbial activity, and seeds and propagules from the original vegetation.

Kochia scoparia was the dominant colonizer, followed by *Setaria viridis*, *Salsola collina* and *Polygonum convolvulus*. These species, as well as many of the other colonizing species, establish quickly and grow vigorously despite the harsh conditions commonly found on reclaimed sites, viz. high temperatures, low water infiltration, and high wind erosion. One reason for the success of the colonizers on harsh habitats may be their ability to utilize the C_4 metabolic pathway (Baker, 1974). Six out of the 11 first-year pioneer

TABLE II

Physical and chemical characteristics of soils sampled from mined sites aged 1—4 years and an unmined site

Property	Year after mining				Unmined	Significance	
	1	2	3	4		Among years	Mined vs. unmined
Saturation (%)	42.6	40.3	41.3	44.4	44.5	NS	NS
Particle size (S—Si—Cl)[1]	43—27—30	49—23—28	50—24—26	52—24—24	64—21—15	NS	*
O.M. (%)	2.41	2.37	2.95	3.71	3.45	NS	NS
Total N (%)	0.11 a[2]	0.12 a	0.13 ab	0.20 c	0.18 bc	**	NS
C/N ratio	12.9	12.7	11.7	10.9	11.5	NS	NS
E.C. (Mmhos/cm)	3.08 bc	2.05 ac	2.37 ac	1.23 ac	0.30 a	*	*
pH	7.82 ac	7.99 bc	7.55 ac	7.87 ac	7.44 a	*	*
SO_4 (p.p.m.)	2265	1273	1566	402	39	*	*
Cl (p.p.m.)	20.4	17.7	19.0	18.1	12.8	NS	NS
P (p.p.m.)	15.4	13.2	5.1	13.1	4.5	**	*
wCa[3] (meq/100 g)	1.63 bc	1.04 ac	1.10 ac	0.40 a	0.21 a	**	*
rCa (meq/100 g)	14.8 ac	15.6 bc	16.5 bc	15.6 ac	7.1 a	*	**
wMg (meq/100 g)	1.75 bc	0.84 a	0.88 ac	0.23 a	0.13 a	**	NS
rMg (meq/100 g)	6.7 bc	6.2 ac	6.2 ac	4.2 ac	2.4 a	*	**
wK (meq/100 g)	0.09	0.06	0.05	0.06	0.06	NS	NS
rK (meq/100 g)	0.10 b	0.10 bc	0.08 b	0.14 a	0.13 ac	**	*
wNa (meq/100 g)	1.32	0.92	1.42	0.84	0.02	NS	NS
rNa (meq/100 g)	1.24	1.06	1.59	1.19	0.16	NS	*
wSr (p.p.m.)	4.9 b	2.2 a	1.8 a	0.4 a	0.1 a	**	NS
rSr (p.p.m.)	32.9	31.8	25.6	19.3	8.9	NS	*
wMn (p.p.m.)	0.46 a	0.08 b	0.23 ab	0.02 ab	0.38 ab	*	NS
rMn (p.p.m.)	6.2 a	3.0 b	2.7 b	2.7 b	5.0 ab	**	NS
cMn (p.p.m.)	163 a	81 bc	89 bc	117 ac	174 a	**	NS
wZn (p.p.m.)	0.06	0.07	0.06	0.05	0.11	NS	*
rZn (p.p.m.)	8.3 a	3.1 b	1.2 b	2.5 ab	2.4 ab	**	NS
wLi (p.p.m.)	0.09 a	0.03 b	0.02 b	0.01 ab	0.01 ab	**	NS
rLi (p.p.m.)	0.21 a	0.13 b	0.13 ab	0.11 ab	0.08 ab	**	NS
wFe (p.p.m.)	0.06 a	0.06 a	0.08 a	0.26 b	0.11 a	**	NS
cFe (p.p.m.)	297 b	129 a	106 a	149 a	85 a	**	NS
cCu (p.p.m.)	9.0 bc	4.8 a	3.3 a	3.1 ac	2.7 ac	**	NS
cAl (p.p.m.)	53 cd	18 b	20 b	24 bd	118 a	**	**
cSi (p.p.m.)	56 bc	29 a	30 a	56 ac	69 ac	**	NS
cB (p.p.m.)	2.0 ac	1.6 bc	1.7 ac	2.3 ac	2.8 a	*	*
cCd (p.p.m.)	0.66	0.59	0.57	0.54	0.55	NS	NS
cPb (p.p.m.)	3.8 bc	2.5 a	2.5 a	3.0 ac	3.7 ac	**	NS
cNi (p.p.m.)	7.0 b	3.6 a	3.0 a	3.2 a	2.9 a	**	NS

*, $P < 0.05$; **, $P < 0.01$; NS = non-significant.

[1] S = sand; Si = silt; Cl = clay.

[2] Rows with significant F values are further compared using Tukey's HSD multicomparison test. Numbers followed by the same letters do not differ significantly.

[3] w = water soluble; r = replaceable; c = chelated and/or complexed.

species in this study utilize the C_4 pathway; *Kochia scoparia*, *Setaria viridis*, *Salsola collina*, *S. iberica*, *Amaranthus retroflexus*, and *Echinochloa crusgalli*. This represents a large C_4 component compared with the overall North Dakota flora, in which 1.5% dicotyledons, 8% sedges, and 31% grasses utilize the C_4 pathway (Teeri and Stowe, 1976; Stowe and Teeri, 1978; Teeri et al., 1980). Furthermore, virtually all biomass production during the first year comes from the C_4 species. However, the dominance of colonizers is short-lived, as nearly all of the first-year species decline in frequency to give way to new immigrants and planted species.

Concomitant with the decline of the pioneers is the rise of perennial species which make up later successional stages. The pioneer vegetation, especially *Kochia*, probably aids in the establishment of later-stage species in several ways. Rapid early growth of the colonizers protects the otherwise barren ground from erosion by wind and thunderstorms, and protects the seedlings of the seeded species from desiccation. Also, tall stems remaining from first-year colonizers increase snow retention, resulting in somewhat better moisture conditions in second-year areas (10.6% in the first year, 12% in the second year ($P \leqslant 0.1$). However, shading by tall *Kochia* and other colonizing species later in the first year is probably responsible for diminished tillerage by the planted grasses.

Rice et al. (1960) found that early species in old-field succession may increase the availability of N and P in the surface layers of soil, thus enabling species with higher nutrient demands to become established gradually (facilitation model of Connell and Slatyer, 1977). Total nitrogen did increase in the years after mining (although NPK was added initially to the sites), but for the most part, nutrient concentrations showed steady declines following reclamation (Table II). Although the time period for any discernible soil development was extremely short, leaching of soluble ions from the upper soil layers and a slight build-up of total N was noted. The E.C. dropped significantly each year after mining, as did some soluble ions, particularly SO_4, Ca, Mg, Sr, and Li. Although statistically non-significant, a decline in clay content could also be attributed to leaching from the upper 10 cm of newly replaced topsoil (see also Wright et al., 1959; Schafer and Nielsen, 1979); organic matter accumulation may be due to increased planted grass production, which was higher than that of the unmined site (see also Rice and Parenti, 1978).

Stepwise regressions of the 36 edaphic characteristics against the overall frequency of all colonizers revealed P, Cu, and replaceable Na to be the best "predictors"; pH, P, Cu and water-soluble Fe were the best "predictors" for *Kochia* frequency. These results seem to implicate P as a major limiting nutrient during the colonization and early succession process on surface-mined lands in North Dakota. Nutrient response studies conducted under glasshouse and growth-chamber conditions on mine spoil material (Sandoval et al., 1973; Safaya and Wali, 1979; Iverson and Wali, unpublished data) show that plant growth is adversely affected when P is in low supply; hence, regression analysis of the field data is consistent with these findings.

Competition studies

Population dynamics of *Kochia* and *Agropyron* during the first four years

Kochia attained a large size in the first year after mining, averaging 88 cm in height. Populations, about 50 plants m^{-2}, attained 410 g m^{-2} in above-ground biomass in the first year (Table III). In the following year, however, average density increased up to 10 500 plants m^{-2}, while biomass decreased by two-thirds and mean plant height was only 11 cm. These large differences in size and weight illustrate the plasticity of the species. By the third year, *Kochia* was practically non-existent, with only sporadic and very small plants remaining. On the other hand, above-ground biomass and density of *Agropyron* spp. increased in the first 4 years after mining (Table III). In addition to the large yearly changes in *Kochia* and *Agropyron* populations, several seasonal trends were apparent (Table III). (1) *Kochia* plant densities increased in first-year areas as new seedlings were established until the end of June, after which the density declined. (2) Second year *Kochia* attained

TABLE III

Density and biomass of *Kochia* and *Agropyron* from areas 1—4 years after reclamation. (Values represent means of 5 quadrats, 0.5 × 0.5 m, harvested during 1977)

Date	Density (stems m^{-2})				Biomass (g m^{-2})			
	Year 1	Year 2	Year 3	Year 4	Year 1	Year 2	Year 3	Year 4
Kochia scoparia[1]								
5/11	5 a[2]	15700 a			0	29		
5/31	25 ac	16200 a			17	45		
6/23	86 bc	11100 ac			172	69		
7/14	80 ac	10400 ac			270	95		
8/3	64 ac	8100 ac			411	79		
8/22	57 ac	6300 bc			307	92		
9/17	46 ac	5500 bc			380	87		
Mean	52	10500			223	71		
Agropyron spp.[3]								
5/11	3	72 a	460 a	702	0	14.4 a	27.7	47.6
5/31	20	116 a	492 ac	622	1.0	14.5 a	60.0	33.2
6/23	26	228 ac	524 ac	1116	2.6	37.0 ac	98.4	118.0
7/14	27	266 ac	712 ac	1136	2.4	47.8 ac	127.1	113.2
8/3	14	425 bc	661 ac	1084	0.7	51.4 bc	113.2	128.8
8/22	34	365 bc	641 ac	916	1.6	52.2 bc	107.2	125.2
9/17	45	400 bc	729 bc	964	5.8	33.4 ac	91.1	100.8
Mean	24	267	603	934	2.0	35.8	89.2	95.8

[1] *Kochia* existed only sporadically on the 3- and 4-year sites.
[2] Colums with significant F values ($P < 0.05$) are further compared using Tukey's HSD multicomparison test. Numbers followed by the same letters do not differ significantly.
[3] *Agropyron* group includes *A. smithii*, *A. caninum*, and *A. elongatum*.

maximum density in May, after which self-thinning set in. (3) *Kochia* height and biomass generally increased throughout the growing seasons in years 1 and 2 until senescence occurred. (4) *Agropyron* height, biomass, plant density and stem density were generally greatest at mid-season, the time of maturity of the cool-season wheatgrasses.

Field competition experiment with *Kochia* and *Agropyron*

Kochia, when grown with *Agropyron* in first-year field plots, caused a significant reduction in *Agropyron* tillering (from 3.8 to 1.8 stems/plant, Table IV). This effect may be the result of shading of *Agropyron* seedlings by the tall *Kochia* plants. However, despite the high density of *Kochia* in the second year, *Agropyron* growth did not seem to be affected, nor did the increasing growth of *Agropyron* affect *Kochia* (Table IV).

TABLE IV

Growth of *Agropyron* and *Kochia* plants from first sampling date to seasonal maximum in the field competition study. (Values based on means of 5 sub-plots and compared statistically using *t*-test)

Treatment	*Agropyron*		*Kochia*
	Growth, height (cm)	Growth, stems (stems/plant)	Growth, height (cm)
Year 1			
Agropyron only	14.4	3.8	—
Kochia only	—	—	66.2
Agropyron+Kochia	10.2	1.8	62.6
Significance	NS[1]	*	NS
Year 2			
Agropyron only	31.6	3.4	—
Kochia only	—	—	8.8
Agropyron+Kochia	29.2	3.0	9.2
Significance	NS	NS	NS

[1] NS = non-significant; *, $P < 0.05$.

Intraspecific competition in *Kochia*

To demonstrate the performance under varying density stress, *Kochia* was grown in the growth chamber at 7 densities; these densities were equivalent to a range of 100—7000 plants m^{-2} in the field. Biomass/pot increased linearly with increasing density up to 16 plants/pot, then began to level off to a constant production with increasing density (Fig. 1). The biomass per plant, on the other hand, showed a quadratic relationship, with decreasing DMY/plant as density increased. These data indicate that at increased densities, DMY/plant of *Kochia* is reduced, suggesting that increased density stress is a contributing factor in the decline of *Kochia* in the field.

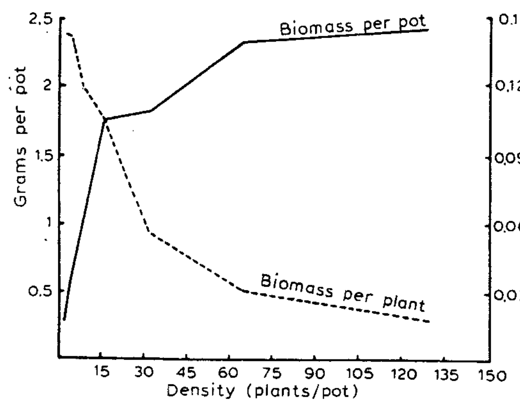

Fig. 1. The effect of increasing density on the above-ground biomass per pot and biomass per plant of *Kochia scoparia*.

Overall appraisal of competitive aspects

Studies of *Kochia* and *Agropyron* growth responses give some indications why *Kochia* succeeds on newly reclaimed sites. Possible explanations for this success are: (1) *Kochia* has an efficient seed dispersal mechanism. Becker (1978) found that decay caused by the fungus *Rhizoctonia*, together with anatomical, internal moisture and wind-loading factors, may be responsible for stem abscission at ground level in large, mature *Kochia* plants which produces "tumbleweeds". The numerous small seeds (up to 50 000 seeds/plant) have also been shown to be dispersed widely in dust storms (King, 1966). (2) *Kochia* is capable of producing large quantities of seed when sufficient moisture is present; some seeds are produced even under extreme conditions of high density and low water availability. (3) *Kochia* seeds germinate very early in spring and are extremely resistant to injury from freezing (Erickson, 1947); thus, they are established even before other plants emerge. (4) Seedling growth of *Kochia* is extremely rapid (Table III). (5) *Kochia* is drought resistant. In one experiment, when small *Kochia* plants were left unirrigated for over one month in pots containing soil, *Kochia* remained alive and became vigorous within one day after irrigation. (6) *Kochia* fixes carbon by the C_4 mechanism, a probable advantage in drought resistance and productivity on hot, dry North Dakota mined areas. (7) *Kochia* is halophytic (Monk and Wiebe, 1961), and high Na-containing areas are common in North Dakota. (8) *Kochia* may have some chemical resistance to insect predators (see allelochemic section of this paper). (9) *Kochia* has the ability to take up more nutrients, especially P, from deficient substrates than many range species (Safaya et al., 1979).

Many of these characteristics are shared with other colonizing species, but *Kochia* is the major colonizer of North Dakota mined areas. Yet *Kochia* declined abruptly 1—2 years after reclamation, prompting investigation of intraspecific crowding responses as well as interspecific relations between *Kochia* and *Agropyron* spp., the main planted species. Plant populations growing in pure stands may respond to density stress by decreasing individual plant size as they adjust to share limiting resources, increasing mortality, or increasing size differentials causing a hierarchy of exploitation (Harper, 1967; Risser, 1969). All 3 effects were observed in *Kochia*; the first 2, in particular, are shown here to fit closely with models developed by other workers. That *Kochia* can adjust its individual plant size with increasing density is shown by its conformity to the reciprocal yield law (Shinozaki and Kira, 1956; de Wit, 1960; Harper, 1967) in the growth-chamber experiment. The relationship of reciprocal yield to density conformed to the expected straight line (Fig. 2). This indicates that *Kochia* adjusts to density stress by decreasing plant size. In addition, *Kochia* further exhibited plasticity in the field, producing seeds when plant heights ranged from 4 to 200 cm.

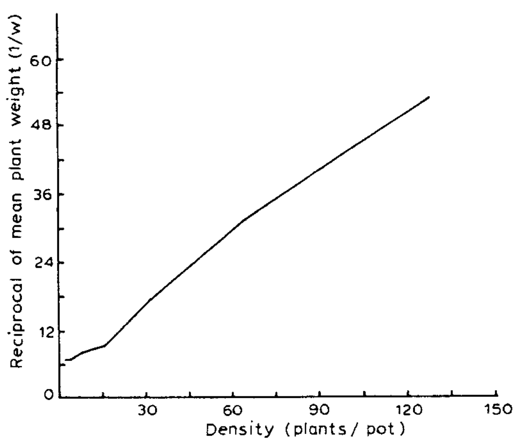

Fig. 2. Reciprocal yield law effect of increasing density on the above-ground biomass of *Kochia scoparia*; the 7 densities investigated ranged from 2 to 128.

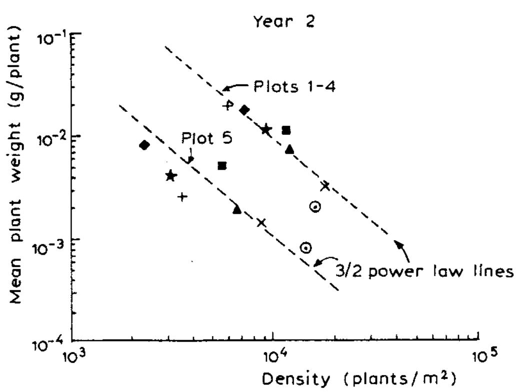

Fig. 3. Second year *Kochia scoparia* growth in the field illustrating the 3/2 power law of self-thinning (symbols represent sample dates: ⊙, 5/11/77; X, 5/31/77; ▲, 6/22/77; ■, 7/13/77; ★, 8/2/77; ◆, 8/22/77; +, 9/17/77).

In the field, 2 years after mining, *Kochia* was overcrowded and conditions were harsh, and density-dependent mortality occurred (Table III). In this case, the 3/2 power law of self-thinning in overcrowded stands (Yoda et al., 1963) fitted well; data from second-year sites closely matched the expected —3/2 slope (Fig. 3). Those of our study sites (Plots 1—4) which were similar in soil and plant conditions conformed closely to one line (regression coefficient of —1.58), whereas an area with a greater proportion of plants other than *Kochia*, and more compacted soils (Plot 5), had its line shifted downward to lower *Kochia* biomass per plant (regression coefficient of —1.08). Yoda et al. (1963) observed that wild Japanese populations of *Amaranthus retroflexus*, *Chenopodium album*, and *Erigeron (Conyza) canadensis*, three pioneer species which also occur on North Dakota mined lands, conformed to the 3/2 law of self-thinning in spite of the differences in age, stage of growth, locality, fertility, and microhabitat conditions (as for *Kochia*). Also shown is the seasonal pattern in *Kochia*, with points from each successive date rising to the left on the line, implying self-thinning and growth of surviving plants (Fig. 3). Thus, for *Kochia*, (1) the chance of a seedling producing a mature plant decreases with increasing density, (2) there is a maximum population size produced (regardless of the number of seeds available), and (3) densities tend to converge with time irrespective of initial density, with population size adjusting in relation to increasing plant size.

Along with the intraspecific relations of *Kochia* discussed above, field experiments on the interspecific competitive relationships between *Kochia* and *Agropyron* spp. were undertaken on first- and second-year areas. On first-year areas, the number of tillers produced per *Agropyron* plant was significantly reduced when grown with *Kochia*; however, grass height was not affected (Fig. 4). The most probable explanation for the reduction in tillerage is competition for light. Competition for nutrients would not be expected to be intense here, as the areas were fertilized and this was the first season of growth. Roots of the large first-year *Kochia* plants extended to a depth of 25 cm, whereas the grass roots only extended 10 cm; thus, there may have been avoidance of competition by differing rooting depth, as reported by Berendse (1979). Competition for water was rejected as a reason for reduced tillerage, because water levels were observed to be higher near the surface under tall *Kochia* plants than in the *Agropyron*-only plots, which received more intense solar irradiation at the surface. Light levels beneath first-year *Kochia* stands were found to be very low, with only 2.3% of photosynthetic active radiation (PAR) reaching the ground surface. In comparison with North Dakota prairie communities, the *Stipa—Bouteloua* stands had 68%, *Andropogon scoparius* stands 37%, and *A. gerardi* stands 4.2% of PAR at ground level. Monsi and Saeki (1953), comparing light values beneath several forest communities to those of herbaceous communities, found that 28% of daylight penetrated in *Pinus* communities but only 4.5% in *Helianthus* and 1.2% in *Phragmites* communities. Donald (1961) and

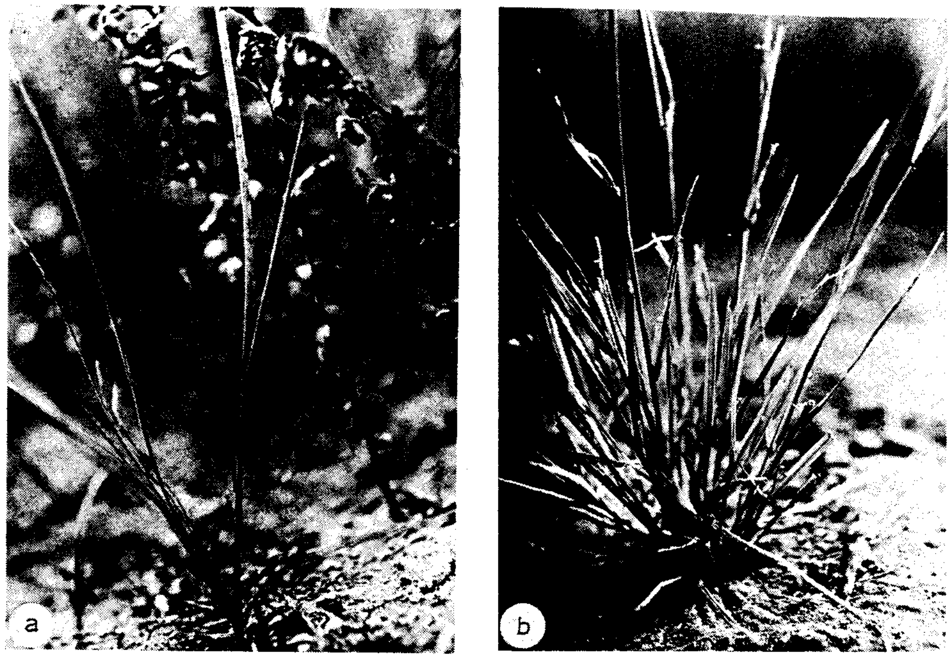

Fig. 4. Effect of (a) shading by *Kochia scoparia* on the tillering of *Agropyron caninum*, (b) *Agropyron* growing under full sunlight.

Grime (1966) showed that competition for light can be very important, even when nutrients or water are limited. Williams (1964) and Milthorpe (1961) recognized the importance of timing of emergence in competition. Weedy species, including *Kochia*, emerge early, become established before grasses on first-year areas, and begin shading early in the season. Thus, light is probably responsible for the depression of tillerage in *Agropyron* spp. (Fig. 4). This is an important consideration in the management plans for mined areas.

The second-year competition experiments revealed that interspecific competition between the planted *Agropyron* grasses (now quite well established) and *Kochia* (very small in size but large in number) was not very intense and neither species seemed to be much affected by the other (Table IV). This may be due to spatial separation of their roots; *Agropyron* rooted to an average depth of 12 cm, while *Kochia* rooted only half as deeply.

The role of allelochemics

Bioassay of pioneer plant extracts

Results obtained from this experiment indicated that each of the pioneering species investigated was toxic to radish and *Kochia* seedlings. Radish germination after 3 days showed significant reductions with the extracts of *Conyza canadense*, *Helianthis annuus*, and *Xanthium strumarium* — all

TABLE V

Effect of plant extracts on the germination and seedling growth of radish (used as a control). Plants are listed in order of the increasing toxicity of their extracts, i.e. *Avena* extract was the least toxic, *Chenopodium* the most toxic

Species	Germination		Mean daily growth		Year of maximum frequency
	Final (%)[1]	Rank[3]	Growth/day (cm)	Rank	
Control	100.0	1	1.37[4]	1	—
Avena fatua	100.0	3	0.86	3	1
Amaranthus retroflexus	100.0	6	0.67	5	1
Polygonum convolvulus	100.0	2	0.54	9	1
Echinochloa crusgalli	99.3	4	0.62	7	1,2
Setaria viridis	99.3	6	0.57	8	1
Xanthium strumarium	91.1[2]	14	0.87	2	2
Kochia scoparia	99.4	4	0.52	12	1
Conyza canadense	60.1[2]	16	0.72	4	3
Helianthus annuus	88.7[2]	15	0.65	6	1
Lactuca serriola	95.3	12	0.54	9	4
Salsola iberica	97.9	11	—	—	1
Grindelia squarrosa	98.7	13	0.54	9	4
Aster ericoides	97.3	9	0.48	13	3
Setaria glauca	96.7	8	0.23	15	2
Chenopodium album	98.6	10	0.32	14	1

[1] Percent germination after 3 days.
[2] Significantly different ($P < 0.01$) from control using Dunnett's test.
[3] Rank based on percent germination after each of 3 days.
[4] All comparisons to the control were significant ($P < 0.01$) using Dunnett's test.

shown to be allelopathic by previous workers (Table V). Extracts of several other species — *Chenopodium album*, *Grindelia squarrosa*, *Lactuca serriola*, and *Salsola iberica* — significantly slowed the radish germination rate after one day. The slowing of the germination rate may influence the resulting plant composition if competition is occurring during seedling establishment. Seedling elongation of radish was inhibited by every extract (Table V). All extracts caused severe reductions of germination and elongation of *Kochia* seeds (Table VI).

Field evidence for *Kochia* autotoxicity

Kochia plants growing on two-year-old sites did not have better growth when the population was thinned to densities of one-year-old sites. The growth of *Kochia* plants from 11 May to 17 September 1977 averaged 8.8 cm when at densities of about 10 000 plants m^{-2}, and 8.6 cm for the thinned population of about 50 plants m^{-2} (n.s., *t*-test). Similarly, the growth of leaf pairs did not differ significantly; 5.4 leaf pairs/plant for high density *Kochia* and 7.2 for thinned *Kochia* plants (*t*-test). Whereas *Kochia* on the first-year

TABLE VI

Effect of plant extracts on the germination and seedling growth of *Kochia*. Plants are listed in order of the increasing toxicity of their extracts, i.e. *Setaria viridis* extract was the least toxic and the *Conyza* extract the most toxic

Species	Germination		Mean daily growth		Year of maximum frequency
	Final (%)[1]	Rank[3]	Growth/day (cm)	Rank	
Control	50.0[2]	1	0.52[2]	1	—
Setaria viridis	25.5	2	0.24	3	1
Salsola iberica	23.2	3	—	—	1
Aster ericoides	22.0	4	—	—	3
Kochia scoparia	19.2	6	0.33	2	1
Chenopodium album	15.7	5	0.09	8	1
Avena fatua	15.3	7	0.11	6	1
Echinochloa crusgalli	16.2	8	0.10	7	1,2
Polygonum convolvulus	12.6	12	0.17	4	1
Amaranthus retroflexus	11.6	11	0.13	5	1
Setaria glauca	17.2	9	0.08	9	2
Grindelia squarrosa	15.1	10	0.06	10	4
Helianthus annuus	10.3	14	0.05	11	1
Xanthium strumarium	13.4	15	0.05	11	2
Lactuca serriola	9.6	16	0.05	11	4
Conyza canadensis	10.4	13	0.03	14	3

[1] Percent germination after 4 days.
[2] All comparisons to the control were significant ($P < 0.01$) using Dunnett's test.
[3] Rank based on percent germination after each of 3 days.

areas at a density of about 50 plants m^{-2} normally attained heights of over 80 cm and exhibited large biomass (Table III), *Kochia* from second-year areas, when thinned to a density equal to that on first-year areas, reached heights of only 10 cm, with very low biomass. This growth suppression on second-year areas provides field evidence for autotoxicity occurring in *Kochia*.

Evidence from laboratory investigations

Experiment 1. Effects of decaying *Kochia* leaves on the growth of *Kochia*, *Agropyron*, and *Melilotus*. The growth of *Kochia* was severely inhibited by decaying *Kochia* leaves in soil (hereafter referred to as KL), whereas *Agropyron* was only slightly affected and *Melilotus* was not inhibited at all (Fig. 5a, Table VII). An attempt to understand the inhibitions in terms of nutritional imbalances was made using chemical analyses of plants and soils. In general, plant nutrient concentrations (Table VIII), but not the nutrient uptake values (Fig. 6), were greater in the KL treatment than controls. This was mostly attributable to the presence of leaf material in the soil prior to seeding of plants and a concentration effect in *Kochia*.

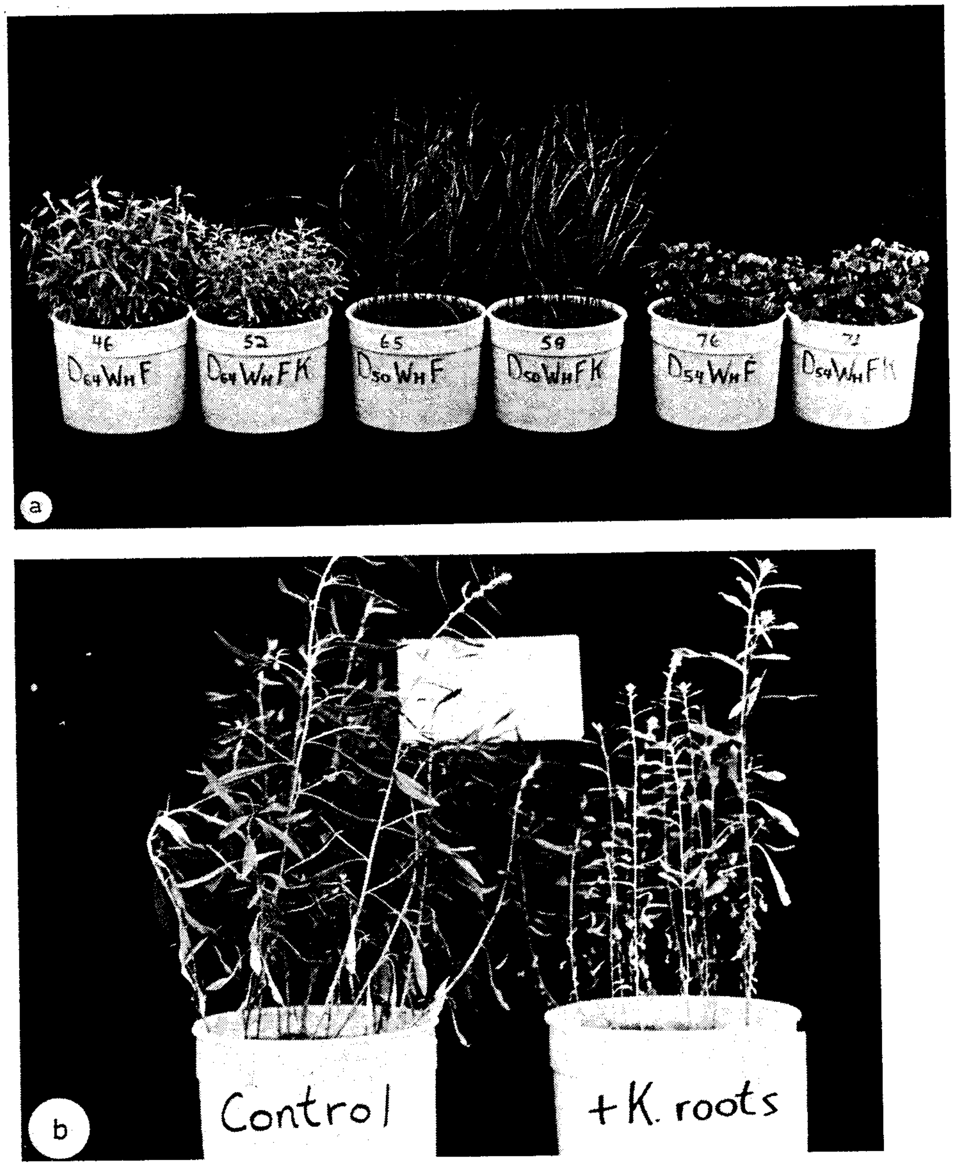

Fig. 5. Allelochemic effects. (a) *Kochia scoparia* (left), *Agropyron caninum* (middle) and *Melilotus officinalis* (right) grown with *Kochia* leaves added to the growth medium (pots marked with "K"). Pots on the left in each species are the controls. Note the depression in growth in *Kochia* due to the effects of autotoxicity. (b) Growth of *Kochia* was even more depressed by the addition of *Kochia* root material.

Significant increases in concentration under the KL treatment were noted for Ca, K, Na, P and Sr in *Kochia*, Mg, Mn and Sr in *Agropyron*, and Mg and Na in *Melilotus* (Table VIII). However, in spite of the larger nutrient

TABLE VII

Dry matter yield of plants in Experiment 1. Data given are means of 3 replicates (KL = 7.5 g *Kochia* leaves per kg soil)

Density	Treatment	*Kochia*		*Agropyron*		*Melilotus*	
		g/plant	g/pot	g/plant	g/pot	g/plant	g/pot
Low	Control	0.90	3.59	0.13	1.62	0.16	1.56
High	Control	0.07	4.32	0.04	1.94	0.05	2.45
Low	KL	0.54	2.14	0.13	1.52	0.16	1.55
High	KL	0.05	3.12	0.03	1.58	0.05	2.44
Kochia lvs. significance[1]		**	**	NS	*	NS	NS
Density significance		**	**	**	NS	**	**

[1] Significant at 0.01 (**) or 0.05 (*) level using 2-way analysis of variance; NS = non-significant.

pool in the KL-treatment pots, *Kochia* plants had reduced concentrations of Mn and Zn, and *Agropyron* showed a reduction in Zn and Fe.

Soil analysis showed that increasing the organic matter by adding *Kochia* leaves resulted in increased concentration of nearly every ion (see pre-incubation samples, Table IX). For example, prior to plant growth, electrical conductivity in the KL-treatment pots was twice that in controls. The pre-incubation samples also showed much higher levels of P, Zn and Mn in the KL-treatment pots. This is important when considering that *Kochia* had reduced plant concentration (Table VIII) and uptake (Fig. 6) of Mn and Zn, even when more was available. On the other hand, P uptake (Fig. 6) was as great in the KL pots as in the controls, even though *Kochia* plants were severely stunted by the KL treatment. Thus, the relative absorption of P was hastened and the absorption of Mn and Zn was reduced in the KL plants, a possible explanation for the autotoxic effect shown in *Kochia*.

At the termination of the experiment, the increased nutrient pool in the KL pots was again evidenced by the significantly greater soil concentrations of water-soluble Ca, Mg, Na, K, Mn, Sr, Cl, and SO_4, and replaceable Mg, K, Na and Mn after the growth of all 3 species (Table IX). However, after the growth of at least 2 of the 3 species, the soil concentrations of EDTA-extractable Fe, Mn, Al, Ni and Mo were decreased in the KL pots, possibly due to complexing of these ions by organic compounds present in *Kochia* material. It should also be noted that (1) the pH of *Melilotus* soils was higher than soils of the other 2 species, and as a result, (2) Ca and Sr in *Melilotus* soils were higher (Table IX), even after the uptake of these two elements by *Melilotus* was much higher compared to the other 2 species (Fig. 6).

Experiment 2. Effect of decaying *Kochia* leaves and roots and *Kochia* leachate. *Kochia* root material (KR), when added at a rate of only 2.5 g

TABLE VIII

Concentrations of major and trace elements in the shoots of *Kochia*, *Agropyron*, and *Melilotus* in autotoxicity Experiment 1. Each value is the mean of 3 replicates (K = *Kochia* leaves added, D = density)

Nutrient	Control		KL treatment		F (KL)[1]	F (D)
	Low density	High density	Low density	High density		
Kochia scoparia						
Ca (%)	0.87	0.89	1.22	0.96	**	*
Mg (%)	0.79	0.76	0.81	0.74	—	—
K (%)	5.47	4.43	7.20	4.60	**	**
Na (%)	0.09	0.07	0.18	0.11	**	**
P (%)	0.34	0.34	0.58	0.57	**	**
Mn (p.p.m.)	74	100	61	81	**	**
Zn (p.p.m.)	39	42	37	34	**	—
Fe (p.p.m.)	76	76	86	59	—	*
Sr (p.p.m.)	21	25	32	27	**	—
Agropyron caninum						
Ca (%)	0.44	0.53	0.50	0.61	—	*
Mg (%)	0.22	0.23	0.23	0.25	**	**
K (%)	3.40	3.19	3.21	3.08	—	—
Na (%)	0.01	0.01	0.01	0.02	—	—
P (%)	0.25	0.18	0.25	0.22	—	**
Mn (p.p.m.)	56	69	71	93	**	**
Zn (p.p.m.)	23	24	16	17	**	—
Fe (p.p.m.)	80	78	75	68	**	*
Sr (p.p.m.)	13	18	14	20	*	**
Melilotus officinalis						
Ca (%)	2.84	2.85	2.70	2.99	—	—
Mg (%)	0.80	0.81	0.85	0.92	**	*
K (%)	2.98	2.78	2.74	3.07	—	—
Na (%)	0.01	0.01	0.01	0.02	*	—
P (%)	0.24	0.19	0.24	0.19	—	**
Mn (p.p.m.)	72	80	72	87	—	**
Zn (p.p.m.)	20	23	20	24	—	**
Fe (p.p.m.)	101	98	94	99	—	—
Sr (p.p.m.)	134	139	127	144	—	**

[1] **, $P < 0.01$; *, $P < 0.05$; —, $P > 0.05$; using 2-way analysis of variance.

per kg of soil, significantly inhibited the growth of *Kochia* (Fig. 5b), *Salsola* and *Agropyron*, but not *Melilotus* (Table X). *Kochia* leaves added at 5 g/pot did not cause any significant effect, nor did irrigation with *Kochia* leachate. These results indicate that even at low *Kochia* root levels, the organic compounds released upon degradation inhibited the growth of *Kochia*, whereas for the *Kochia* leaves, an application rate of 15 g/pot caused significant reductions in *Kochia* growth (previous experiment) but the rate of 5 g/pot

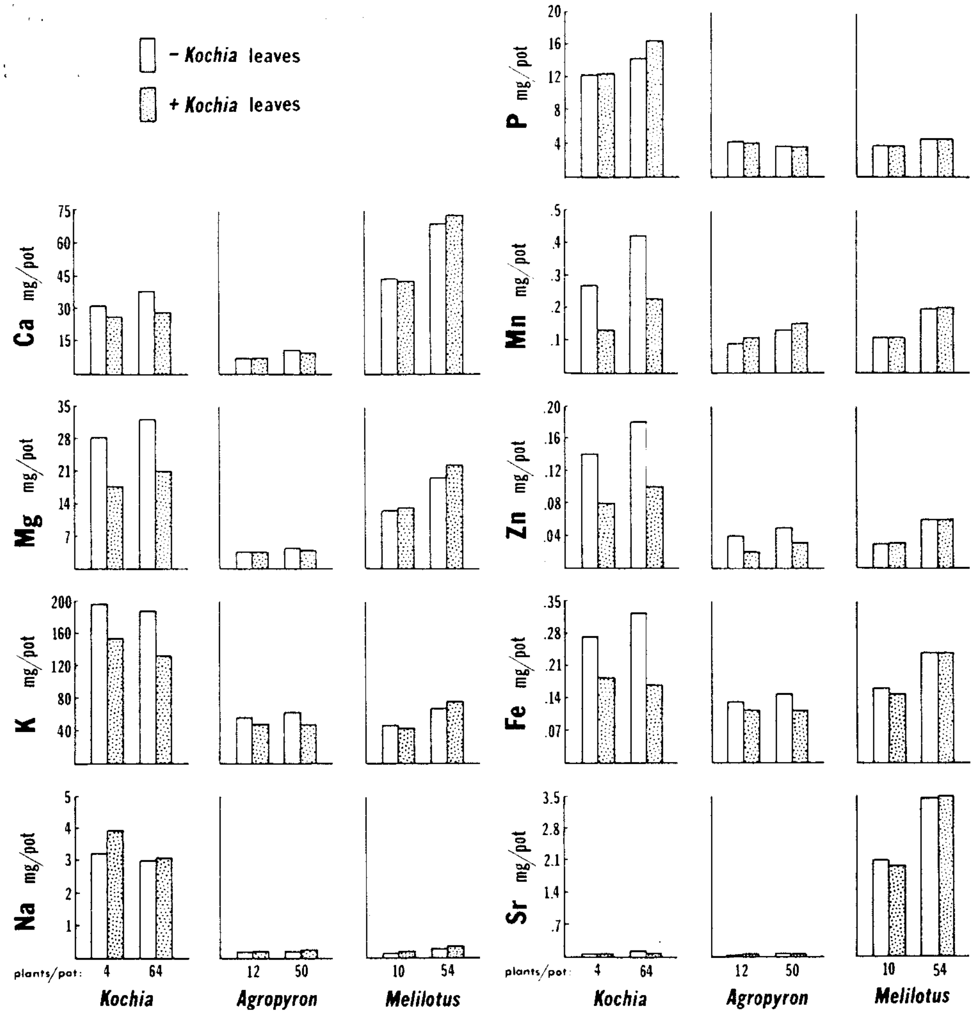

Fig. 6. Nutrient removal by the above-ground biomass by 3 plant species.

caused no significant effect. There seems to be a threshold effect somewhere between 5 and 15 g *Kochia* leaves/pot on the growth of *Kochia*.

Experiment 3. Residual effects on subsequent plant growth. When plants were grown a second time in the same soil without any additional treatment, there was a significant stimulation in the KL treatment and a slight, but non-significant, inhibition in the KR treatment when compared to the controls (Table XI). There was no growth difference between the two controls. The results can hence be interpreted as a residual effect of treatments from the previous experiment. In the previous experiment, there was a 22% (though non-significant) stimulation of *Kochia* due to the addition of *Kochia* leaves and a significant inhibition of 24% from *Kochia* roots (Table X). In this experiment, the regrowth of *Kochia* in these same soils showed a significant stimulation of 82% from *Kochia* leaves and a 22% inhibition (nonsignificant) from *Kochia* roots (Table XI). Apparently there is a gradient, with allelochemics involved. At low concentrations, the allelochemics are stimulatory, as with less than 5 g *Kochia* leaves per 2 kg soil. At higher concentrations, the allelochemics are inhibitory, as with greater than 2.5 g *Kochia* roots per 2 kg soil. These compounds are broken down in time; the present experiment showed a shifting of the gradient such that the allelochemics became less inhibitory and more stimulatory during the regrowth of *Kochia*. Thus, it appears that active compounds remain in the soil for some time, gradually losing their activity.

In analysis of nutrients, P concentration was significantly higher in the KR plants, although Mn and Zn showed no difference. Uptake of Ca, Mg, Na, and Mn was less in the KR plants, probably due to smaller root systems. The stimulated KL plants showed significantly higher uptake values for all elements, but no differences in concentration (Table XI).

Experiment 4. Effects of decaying *Kochia* leaves and roots and both together on *Kochia* growth. Dry matter yield (DMY) in *Kochia* was depressed by the addition of *Kochia* roots but was increased by the addition of *Kochia* leaves (Table XII), even though the levels of plant material added were quite low. The addition of both roots and leaves (KL+R), however, caused a significant stimulation in the growth of *Kochia*, possibly the result of an interaction between various compounds.

Several interesting features emerged from plant mineral analysis. For example, P concentration over all treatments was negatively correlated with DMY ($r = -0.82$, $P < 0.01$ level); there was a significant increase in P in KR treatment and a decrease in KL+R treatment as compared to control. This cannot be interpreted solely as a dilution effect, because the uptake values for P show that, although KR plants had only one-fourth the DMY of controls, they had one-half the total uptake. Therefore, the rate of P uptake by KR plants was twice that of the controls. Similarly, the KR plants had P uptake rates about 3.5 times those of KL or KL+R plants. Zinc and Cu concentration and uptake were significantly reduced in KR plants (Table XII). The reduction in concentration of Zn and Cu in the stunted KR plants indicated an inhibition of Zn and Cu absorption, as uptake cannot keep pace with growth. The disruptions in nutrient absorption may be responsible for the significant DMY changes demonstrated by the experiment.

Experiment 5. Autotoxicity of *Kochia* under stress conditions. Final DMY values from this experiment were: (1) low water + peat = 0.315 g/pot; (2) low water + *Kochia* leaves = 0.318 g/pot; and (3) control = 2.525 g/pot (significantly different from (1) and (2) at 0.01 level). Thus, the effect of low water had a severe effect on the growth of *Kochia*, the DMY of stressed plants being only 13% of the controls. Although there was no difference in DMY between the two low-water treatments, there were visual

TABLE IX

Properties of soils in which *Kochia*, *Agropyron*, and *Melilotus* were grown at 2 densities with or without the addition of *Kochia* leaves. Analyses of soils prior to the growing of plants are also included. (K = *Kochia*, D = density, F = significance test, C = control)

Properties	*Kochia scoparia*						*Agropyron caninum*		
	C	C	KL	KL	F(K)	F(D)	C	C	KL
Density (plants/pot)	4	64	4	64			12	50	12
pH	8.18	8.03	8.18	8.15	—[1]	*	8.02	8.05	8.16
E.C. (Mmhos/cm)	0.43	0.31	0.94	0.97	*	—	0.36	0.54	1.02
Saturation (%)	36.1	34.5	38.3	37.5	*	*	35.9	37.4	38.0
P (p.p.m.)	10.7	10.9	13.3	10.9	*	—	13.1	13.4	12.5
SO_4 (p.p.m.)	123	72	233	235	**	—	137	115	177
Cl (p.p.m.)	7.4	8.4	102.2	109.7	**	—	8.4	8.9	118.3
wCa (meq/100 g)[2]	0.11	0.07	0.21	0.22	**	—	0.08	0.13	0.23
rCa (meq/100 g)	10.32	9.96	10.24	9.85	—	—	9.79	9.49	10.36
wMg (meq/100 g)	0.07	0.04	0.15	0.16	**	—	0.06	0.09	0.16
rMg (meq/100 g)	4.67	4.57	5.18	5.02	**	—	4.69	4.62	5.14
wK (meq/100 g)	0.01	0.01	0.03	0.03	**	—	0.01	0.02	0.04
rK (meq/100 g)	0.40	0.39	0.65	0.67	**	—	0.48	0.48	0.78
wNa (meq/100 g)	0.01	0.01	0.03	0.03	**	—	0.01	0.02	0.04
rNa (meq/100 g)	0.08	0.08	0.14	0.14	**	—	0.08	0.08	0.15
wZn (p.p.m.)	0.014	0.020	0.011	0.042	—	—	0.024	0.016	0.018
cZn (p.p.m.)	1.05	1.00	1.10	1.21	*	—	1.08	1.01	1.07
wFe (p.p.m.)	0.036	0.052	0.027	0.038	—	—	0.057	0.045	0.038
cFe (p.p.m.)	110	118	105	102	**	—	112	110	99
wMn (p.p.m.)	0.011	0.014	0.118	0.149	**	**	0.007	0.040	0.118
rMn (p.p.m.)	2.9	2.9	6.0	6.0	**	—	2.6	3.6	5.4
cMn (p.p.m.)	197	216	192	195	**	**	208	201	183
wSr (p.p.m.)	0.08	0.05	0.17	0.18	**	—	0.06	0.11	0.18
rSr (p.p.m.)	11.8	11.6	11.3	11.4	—	—	11.7	11.6	11.6
cSr (p.p.m.)	0.99	0.94	1.02	1.03	**	—	0.99	0.99	1.07
wLi (p.p.m.)	0.004	0.004	0.004	0.005	—	—	0.004	0.004	0.005
rLi (p.p.m.)	0.10	0.10	0.10	0.10	—	—	0.10	0.10	0.10
cMo (p.p.m.)	0.021	0.023	0.017	0.017	*	—	0.019	0.015	0.013
cCu (p.p.m.)	2.22	2.34	2.24	2.45	—	—	2.88	2.45	2.32
cNi (p.p.m.)	4.59	4.88	4.34	4.45	**	**	4.77	4.65	4.35
cPb (p.p.m.)	1.98	1.96	1.75	1.78	**	—	2.03	2.19	2.07
cCd (p.p.m.)	0.22	0.24	0.23	0.23	—	—	0.19	0.30	0.17
cB (p.p.m.)	2.3	2.1	2.7	2.6	—	—	2.0	1.7	2.6
cAl (p.p.m.)	111	123	111	99	**	—	117	113	103
cSi (p.p.m.)	88	83	80	81	—	—	79	73	79

[1] Indicates significance (—, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$) using 2-way analysis of variance.

[2] Indicates soil extraction (w = water soluble, r = replaceable (ammonium acetate), c = chelated/complexed (EDTA)).

			Melilotus officinalis						Pre-incubation samples	
KL	F(K)	F(D)	C	C	KL	KL	F(K)	F(D)	C	KL
50			10	54	10	54				
8.24	**	—	8.40	8.38	8.35	8.49	—	*	8.01	8.24
1.05	**	*	0.63	0.71	1.08	1.24	**	*	1.02	1.93
40.2	**	*	36.7	38.1	38.9	39.4	*	—	37.4	40.6
11.8	*	—	13.3	14.7	13.1	13.9	—	*	18.6	27.7
223	*	—	183	82	230	290	**	—	250	545
105.7	**	—	14.3	11.6	116.3	121.7	**	—	11.4	96.2
0.26	**	**	0.17	0.19	0.24	0.31	**	*	0.24	0.47
10.68	**	—	11.03	11.16	10.07	11.02	—	—	9.63	9.99
0.18	**	**	0.09	0.12	0.17	0.22	**	**	0.16	0.37
5.35	**	—	4.80	4.88	5.24	5.52	**	*	4.58	5.20
0.04	**	—	0.02	0.02	0.04	0.04	**	—	0.02	0.08
0.75	**	—	0.51	0.47	0.73	0.73	**	—	0.58	0.92
0.04	**	—	0.02	0.02	0.04	0.05	**	*	0.02	0.14
0.18	**	—	0.11	0.13	0.15	0.23	**	*	0.07	0.31
0.016	—	—	0.018	0.012	0.015	0.014	—	—	0.018	0.027
1.08	—	—	0.99	1.03	1.05	1.19	**	**	1.08	1.23
0.035	—	—	0.029	0.039	0.023	0.027	*	—	0.040	0.129
98	**	—	95	95	100	97	—	—	117	116
0.222	**	*	0.005	0.043	0.148	0.302	**	**	0.050	0.949
6.5	**	**	2.8	3.7	5.9	7.1	**	**	4.7	13.5
185	**	—	182	187	186	185	—	—	209	198
0.21	**	**	0.11	0.14	0.19	0.23	**	*	0.17	0.34
12.1	—	—	12.4	12.4	11.5	12.0	**	*	11.2	11.1
1.11	**	—	1.17	1.14	1.14	1.20	—	—	0.98	1.05
0.006	*	—	0.004	0.004	0.007	0.008	**	—	0.007	0.019
0.11	—	—	0.10	0.10	0.10	0.10	—	—	0.13	0.15
0.014	—	—	0.015	0.017	0.012	0.13	*	—	0.059	0.21
2.34	—	—	2.40	2.48	2.28	2.27	—	—	2.30	2.23
4.43	**	—	4.51	4.56	4.48	4.46	—	—	4.72	4.61
2.19	—	—	2.28	2.13	2.07	2.07	**	—	2.04	2.00
0.20	*	**	0.20	0.21	0.20	0.20	—	—	0.26	0.25
2.7	**	—	1.7	1.8	2.0	2.6	*	—	1.0	2.8
105	**	—	105	107	106	104	—	—	126	120
78	—	—	75	75	75	80	—	—	77	77

TABLE X

Effects of *Kochia* leachate, *Kochia* leaves and *Kochia* roots on DMY of 4 species in Experiment 2 (mean of 4 replicates)

Species	Control (2.5 g peat kg^{-1})	+*K*. leachate (irrigation)	+*K*. leaves (2.5 g kg^{-1})	+*K*. roots (1.25 g kg^{-1})
Kochia scoparia	2.52	2.44	3.07	2.04*
Salsola collina	1.96	1.99	2.00	1.38*
Agropyron caninum	2.48	2.44	2.72	1.72*
Melilotus officinalis	2.42	2.31	2.58	2.44

*Indicates significant ($P \leqslant 0.05$) reduction from the control, using Dunnett's test after the ANOVA.

differences throughout the course of the experiment. Those plants treated with *Kochia* leaves were smaller than the low-water controls, thereby requiring less moisture for maintenance. After one month, the low-water control plants began showing signs of severe water stress — drying of the lower leaves and a very spindly appearance. The small KL plants, on the other hand, did not show these drought characteristics and remained healthy and green; at the time of the harvest, the DMY of the KL plants equalled that of the water-stress controls. The apparent advantage of the KL plants under conditions of low water or deficit may be important when considering the evolutionary aspects of autotoxicity.

General assessment of allelochemics

While we realize the limitations of bioassay experiments (see Greig-Smith, 1979; Stowe, 1979), our study provides evidence that allelopathy may be playing an important role in compositional changes of early successional species. The bioassay is a test for allotoxicity among the colonizers, which provides a means of comparing the relative toxicities of the extracts. A ranking of allelopathic tendency for each extract was devised by averaging the germination and elongation ranks for each seed source (species in Tables V—VI are ranked by this scheme). When the rankings were compared to the year of maximum frequency for each species in the field, a general trend was apparent. The first-year colonizers were the least toxic (Tables V—VI). Spearman's rank correlation coefficient (r_s) between rank of allelopathic tendency and year of maximum frequency was found to be significant at the 0.05% level for both seed sources. Based on this correlation, we speculate that species invading after the initial colonizers may be aided by allelopathy, since allelochemics inhibit germination and/or growth of the initial colonizers and, in effect, reduce interspecific competition (inhibition model of Connell and Slatyer, 1977). It should be pointed out that all extracts showed some toxicity when compared to the controls (Tables V—VI). Although the initial colonizers had relatively lower toxicity than

TABLE XI

Tissue concentrations, elemental uptakes and dry matter yield in *Kochia* plants in Experiment 3[1] (KL = *Kochia* leaves added, KR = *Kochia* roots added) (mean of 3 replicates)

Grown previously (and residual treatment)	Tissue concentrations (p.p.m.) and Dry Matter Yield (g/pot)											
	P	Ca	Mg	K	Na	Mn	Zn	Fe	Cu	Sr	Li	DMY
Kochia (control)	6800 a	7743 a	9964 a	23061 a	5211 a	72.4 ab	39.5 a	87 a	5.5 a	69 a	2.8 a	0.79 a
Kochia (KL)	6583 a	7322 a	9486 a	25139 a	4100 ac	92.8 b	39.4 a	105 a	5.5 a	68 a	2.5 a	1.44 b
Kochia (KR)	9458 b	7551 a	9793 a	26607 ac	4228 ac	70.1 a	44.3 ac	78 a	6.0 ac	68 a	2.7 a	0.65 a
Agropyron (control)	10333 b	6960 b	9321 a	31250 bc	3811 bc	83.9 ab	53.5 bc	76 a	6.7 bc	51 b	2.2 a	0.86 a

	Nutrient uptake (mg/pot)										
	P	Ca	Mg	K	Na	Mn	Zn	Fe	Cu	Sr	Li
Kochia (control)	5.40 a	6.15 a	7.91 a	18.31 a	4.14 a	0.06 a	0.03 a	0.07 a	0.004 a	0.05 a	0.002 a
Kochia (KL)	9.46 b	10.55 b	13.66 b	36.34 b	5.88 b	0.13 b	0.06 b	0.15 b	0.008 b	0.10 b	0.004 b
Kochia (KR)	6.09 a	4.89 c	6.33 c	17.21 a	2.74 c	0.05 c	0.03 a	0.05 a	0.004 a	0.04 ac	0.002 a
Agropyron (control)	8.83 b	5.70 ac	8.01 ac	26.70 b	3.23 c	0.07 a	0.05 b	0.06 a	0.006 c	0.04 c	0.002 a

[1] Numbers followed by the same letter within a column have a significant *F* value and do not differ at the 95% confidence level (Tukey's HSD test).

TABLE XII

Tissue concentrations, elemental uptakes, and dry matter yield of *Kochia* plants in Experiment 4[1] (KL = *Kochia* leaves added, KR = *Kochia* roots added, and KL + R = both leaves and roots added)

Treatment	Tissue concentrations (p.p.m.) and Dry Matter Yield (g/pot)											
	P	Ca	Mg	K	Na	Mn	Zn	Fe	Cu	Sr	Li	DMY
Control	1233 a	11574 a	16706 ab	26617 a	5789 a	162 a	48.5 a	148 a	8.6 a	145 ab	3.1 a	0.82 a
KL	933 ac	15735 a	20367 a	28639 a	11166 b	146 a	39.9 ac	121 a	7.4 ac	195 b	3.4 a	1.40 b
KR	2399 b	12250 a	12486 b	22055 a	7353 ab	162 a	26.0 b	111 a	5.2 b	122 a	5.3 a	0.20 c
KL + R	667 c	11773 a	16933 ab	25228 a	9674 b	117 a	30.6 bc	98 a	5.8 bc	173 ab	3.2 a	1.34 b
	Nutrient uptake (mg pot^{-1})											
	P	Ca	Mg	K	Na	Mn	Zn	Fe	Cu	Sr	Li	
Control	1.01 a	9.50 a	13.72 a	21.86 a	4.73 a	0.13 a	0.04 a	0.12 a	0.007 a	0.12 a	0.003 a	
KL	1.32 a	22.02 b	28.63 b	40.37 a	15.47 b	0.21 a	0.06 a	0.17 a	0.011 a	0.27 b	0.005 b	
KR	0.48 b	2.45 c	2.52 c	4.42 b	1.47 c	0.03 b	0.01 b	0.02 b	0.001 b	0.02 c	0.001 c	
KL + R	0.90 a	15.88 ab	22.76 ab	21.96 a	12.96 b	0.16 a	0.04 a	0.13 a	0.008 a	0.23 ab	0.004 ab	

[1] Numbers followed by the same letter within a column have a significant F value and do not differ at the 95% confidence level (Tukey's HSD test).

later colonizers, the fact remains that the initial colonizers not only produced maximum biomass after invading a harsh system, but also produced toxins which may have afforded protection against predators.

Along with the preceding study of allotoxic phenomena, extensive experimentation on the autotoxic behavior of *Kochia scoparia* was conducted. Since *Kochia* plants in second-year field plots did not grow any larger when the density was reduced, growth suppression can be attributed, at least in part, to allelopathy. Growth-chamber experiments also indicate that decaying *Kochia* material from first-year plants can be inhibitory to *Kochia* seedlings. The identification of known inhibitors, viz. chlorogenic, caffeic and ferulic acids, myricetin and quercitin in *Kochia* extracts reported from our laboratory (Lodhi, 1979), provides further evidence for this autotoxicity.

For some growth-chamber experiments reported here, the results may initially seem contradictory. Leaf material caused a depression in growth in Experiment 1 (applied at 15 g/pot) but did not do so in Experiments 2 and 4 (applied at 5 and 6 g/pot). The allelochemics apparently act like some plant hormones, stimulating at low levels and inhibiting at high levels. Such observations have also been made by Tukey (1966) and Grodzinsky (1971). Experiments 2 and 4 show the differential allelopathic tendencies between *Kochia* root and leaf material. Root material is strongly toxic even at low levels, whereas leaf material becomes inhibitory only when present in larger quantities. The stimulation arising from the addition of both leaf and root material (Table XII) is puzzling, as one would expect cumulative effects; evidently, there is an interaction in which inhibitory properties of root material are negated by the stimulatory properties of the leaf material, or the inhibitor is simply deactivated.

It has been shown that phytotoxicity is most effective when the plant is under stress (Rice, 1974); in such cases, a smaller quantity of phytotoxin produces the inhibitory effect. This was confirmed by Experiment 5, where *Kochia* plants treated with *Kochia* leaf material (at a level which was stimulatory under high-water conditions) and grown under low water were initially stunted but finally attained similar yields as controls after the controls began to senesce prematurely.

An effort was made to understand the mechanism of toxicity by studying the nutrient relations and noting the deviations of inhibited plants from controls. Most evident were the increases of P and decreases of Zn and Mn in the inhibited plants. Phosphorus-induced Zn or Mn deficiencies have been reported (Boawn and Brown, 1968; Safaya, 1976). Although no visual symptoms of Zn or Mn deficiencies were observed in the growth-chamber experiments, the P/Zn and P/Mn ratios were greatly increased in those plants showing significant reductions in growth (Table XIII). Plants which were not affected or stimulated by *Kochia* material did not show such great increases of their P/Zn or P/Mn ratios. The nutrient imbalances could have a deleterious effect on the plant and could be a reason for the depres-

TABLE XIII

Dry matter yield and P/Zn and P/Mn ratios for plant tissue elemental concentration and uptake in Experiments 1, 3 and 4[1] (KL = *Kochia* leaves added, KR = *Kochia* roots, KL + R = both added)

	DMY (g/plant)	Concentration		Uptake	
		P/Zn	P/Mn	P/Zn	P/Mn
Experiment 1 (6 reps.)					
Kochia control	0.49	82	39	83	38
Kochia KL	0.30	160	81	168	80
Significance[2]	**	**	**	**	**
Agropyron control	0.09	91	35	94	35
Agropyron KL	0.08	139	29	144	28
Significance	NS	**	NS	**	NS
Melilotus control	0.16	97	28	102	26
Melilotus KL	0.16	98	27	98	26
Significance	NS	NS	NS	NS	NS
Experiment 3 (3 reps.)					
Kochia regrowth on:					
Kochia control	0.79 a	172 ac	94 a	172 ac	94 a
Kochia KL	1.44 b	167 a	72 b	167 a	72 b
Kochia KR	0.65 a	213 b	135 c	213 b	135 c
Agropyron control	0.86 a	193 bc	123 c	194 bc	123 c
Significance	**	**	**	**	**
Experiment 4 (3 reps.)					
Kochia control	0.82 a	25 a	8 a	25 a	8 a
Kochia KL	1.40 b	23 a	6 a	22 a	6 a
Kochia KR	0.20 c	92 b	15 b	92 c	15 b
Kochia KL + R	1.34 b	22 a	6 a	23 a	6 a
Significance	**	**	**	**	**

[1] Numbers followed by the same letter within a column do not differ at the 95% confidence level.
[2] **, $P \leqslant 0.01$; NS = non-significant.

sion in growth; the phytotoxins presumably change the permeability of the cell membrane or alter active transport mechanisms. Buckholtz (1971) and Rice (1974, 1979) have also reported disturbances in nutrient uptakes due to phytotoxin effects.

In dealing with the autotoxic phenomenon in *Kochia*, a question arises: Is this adverse characteristic of autotoxicity advantageous to the species and therefore selected for during evolutionary development? Some interpretations can be presented:

1. Autotoxicity may be neither advantageous nor disadvantageous if the species is a fugitive (Whittaker and Feeny, 1971). *Kochia* is a pioneering species, as its fecundity and dispersal mechanisms allow it to continually colonize newly disturbed areas.

2. There may be a relationship between plants and weather, as high density *Kochia* plants stunted by autotoxicity seem to be affected less severely by drought conditions. Stunted plants may be able to produce greater numbers of viable seed for subsequent years, while taller, uninhibited plants, especially those growing at high densities, use a greater proportion of their available water for maintenance, and seed production is less. Experiment 5, as well as field observations of first- and second-year areas during a drought, support this hypothesis.

3. There may be a greater selective advantage in producing these compounds as a defensive mechanism than the selective disadvantage from the effects of the substances on short-lived populations of the species itself (Whittaker, 1975). The autotoxic compounds may have arisen primarily as a defense mechanism. To obtain evidence for this defense hypothesis, we examined several pioneering species in the field for insect infestation (see Methods of Study). Infestation by cocklebur weevil larvae was 100% for *Salsola collina*, *Helianthus annuus*, and *Chenopodium album*, 96% for *Amaranthus retroflexus*, 80% for *Salsola iberica*, but only 40% for *Kochia*. Analysis of a 6 (species) $\times$ 2 (presence/absence of larvae) contingency table indicated a highly significant association ($P \leqslant 0.01$), with *Kochia scoparia* responsible for nearly all the variation. Therefore, there is some evidence of an "aversion" of the weevil to *Kochia* plants. There were noticeable reductions in seed production for any plant infested with the larvae; therefore, infestation may curtail reproduction. Certain secondary products stored in first-year *Kochia* plants may in some way make *Kochia* tissue less palatable to the weevil. Todd et al. (1976) reported that quercetin, chlorogenic acid, caffeic acid, and ferulic acids present in barley may account for its resistance to *Schizaphis graminum* (greenbugs); all of these compounds, as mentioned earlier, have been reported in *Kochia* from our study sites (Lodhi, 1979). Swain (1979) pointed out that hundreds of secondary plant substances may be utilized for such defenses. The importance of the role of herbivores initially in succession has been emphasized by Connell and Slatyer (1977). It appears that *Kochia* is an exception to the general belief that early successional species are less resistant to grazing by insects.

4. The autotoxic behavior of such pioneer plants may simply be a mechanism preventing overgrowth on the soils which they invade (Pickett and Baskin, 1973). Reduction in size and self-thinning of *Kochia* in the second-year areas allow for seed production which would not otherwise occur. Field observations of dense, 6-cm tall, second-year *Kochia* stands producing about 5 seeds/plant compared with occasionally dense, 80 cm tall, first-year *Kochia* stands which had died prior to seed set, are evidence for this hypothesis. Seed production by a large number of plants, though low per plant, also maintains high genetic variability in the species.

The rapid elimination of *Kochia* may be attributed at least partially to autotoxicity whereby toxic substances are released by decaying roots and leaves. There is also preliminary evidence that species such as *Conyza canad-*

ensis, *Lactuca serriola* and *Grindelia squarrosa* are allelopathic to *Kochia* and other pioneers (bioassay experiment). Inhibition by either process is then magnified by the competitive, nutritive, water, and light stress conditions encountered later, resulting in the exclusion of *Kochia*. Our study implicates allelopathy as being partially responsible for determining the fate of species during the early successional stages after disturbance.

It should be pointed out that drastically disturbed ecosystems, such as the mined areas, afford numerous opportunities for the study of ecosystem development and its rate processes. Only after these processes are quantified and understood can the long-term rehabilitation of these ecosystems be realized.

Acknowledgements

We are grateful to Dr. P.G. Risser of the Illinois Natural History Survey, Dr. P.L. Marks of Cornell University, and to Dr. N.M. Safaya, Dr. S.A. Nicholson, Dr. N. Malakondaiah, R.H. Bares, A.L. Kollman, and D. Schimmelpfennig, of the University of North Dakota, for critical reviews of the manuscript, and M. Iverson and L. Brophy for technical assistance. This study was a part of the project "A Systems Approach to the Reclamation of Strip-mined Areas in North Dakota" funded by the U.S. Department of the Interior — Bureau of Mines, Grant No. G0264001 and Contract No. J0292015 to M.K.W.; support was also provided by the National Science Foundation through an Energy-Related Needs Fellowship to L.R.I.

References

Baker, H.G., 1974. The evolution of weeds. Annu. Rev. Ecol. Syst., 5: 1—24.

Bazzaz, F.A., 1968. Succession on abandoned fields in Shawnee Hills, southern Illinois. Ecology, 49: 924—936.

Becker, D.A., 1978. Stem abscission in tumbleweeds of the Chenopodiaceae: *Kochia*. Am. J. Bot., 65: 375—383.

Bell, A.R., Nalewaja, J.D. and Schooler, A.B., 1972. Light period, temperature and *Kochia* flowering. Weed Sci., 20: 462—464.

Berendse, F., 1979. Competition between plant populations with differing rooting depths. Oecologia (Berlin), 43: 19—26.

Boawn, L.C. and Brown, J.C., 1968. Further evidence of a P—Zn imbalance in plants. Soil Sci. Soc. Am. Proc., 32: 94—97.

Borror, D.J., Delong, D.M. and Triplehorn, A., 1976. An Introduction to the Study of Insects. Holt, Rinehart and Winston, New York.

Bouyoucos, D.J., 1951. A recalibration of the hydrometer method for making mechanical analysis of soils. Agron. J., 43: 434—438.

Buckholtz, K.P., 1971. The influence of allelopathy on mineral nutrition. In: U.S. National Committee for International Biological Program (Editors), Biochemical Interaction among Plants. National Academy of Sciences, Washington, DC, pp. 86—89.

Chapman, H.D. and Pratt, P.F., 1961. Methods of Analysis for Soils, Plants and Water. Division of Agricultural Sciences, University of California, Berkeley, CA.

Connell, J.H. and Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat., 111: 1119—1144.

Crocker, R.L. and Major, J., 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J. Ecol., 43: 427—448.

Dickson, B.A. and Crocker, R.L., 1953a. A chronosequence of soils and vegetation near Mt. Shasta, California. I. Definition of the ecosystem investigated and features of the plant succession. J. Soil Sci., 4: 123—141.

Dickson, B.A. and Crocker, R.L., 1953b. A chronosequence of soils and vegetation near Mt. Shasta, California. II. The development of the forest floors and the carbon and nitrogen profiles of the soils. J. Soil Sci., 4: 142—152.

Dickson, B.A. and Crocker, R.L., 1954. A chronosequence of soils and vegetation near Mt. Shasta, California. III. Some properties of the mineral soils. J. Soil Sci., 5: 173—191.

Donald, C.M., 1961. Competition for light in crops and pastures. Symp. Soc. Exp. Biol., 15: 282—313.

Egler, F.E., 1954. Vegetation science concepts. I. Initial floristic composition — a factor in old-field vegetation development. Vegetatio, 4: 412—417.

Erickson, E.L., 1947. Forage from *Kochia*. S. D. Agric. Exp. Stn., 384: 1—27.

Glenn-Lewin, D.C., 1979. Natural revegetation of acid coal spoils in southeast Iowa. In: M.K. Wali (Editor), Ecology and Coal Resource Development, Vol. 2. Pergamon, New York, pp. 568—575.

Greig-Smith, P., 1979. Presidential address 1979: Pattern in vegetation. J. Ecol., 67: 755—779.

Grime, J.P., 1966. Shade avoidance and shade tolerance in flowering plants. In: R. Bainbridge, G.C. Evans and O. Rackham (Editors), Light as an Ecological Factor. Blackwell Scientific, Oxford, pp. 187—207.

Grodzinsky, A.M., 1971. Problems and results of allelopathy in the work of Soviet scientists. In: U.S. National Committee for International Biological Program (Editors), Biochemical Interaction among Plants. National Academy of Sciences, Washington, DC, pp. 44—51.

Harper, J.L., 1967. A Darwinian approach to plant ecology. J. Ecol., 55: 247—270.

Imes, A.C. and Wali, M.K., 1977. An ecological—legal assessment of mined land reclamation laws. N. D. Law Rev., 53: 359—399.

Imes, A.C. and Wali, M.K., 1978. Governmental regulation of reclamation in the western United States: an ecological perspective. Reclam. Rev., 1: 75—88.

Jackson, M.L., 1958. Soil Chemical Analysis. Prentice Hall, New Jersey.

Jackson, J.R. and Willemsen, R., 1976. Allelopathy in the first stages of secondary succession on the Piedmont of New Jersey. Am. J. Bot., 63: 1015—1023.

Jacob, A.F., 1973. Depositional environments of Paleocene Tongue River Formation, western North Dakota. Am. Assoc. Pet. Geol. Bull., 57: 1038—1052.

Jonescu, M.E., 1979. Natural revegetation of strip-mined land in the lignite coalfields of southeastern Saskatchewan. In: M.K. Wali (Editor), Ecology and Coal Resource Development, Vol. 2. Pergamon, New York, pp. 592—608.

Keever, C., 1950. Causes of succession on old-fields of the Piedmont, North Carolina. Ecol. Monogr., 20: 229—250.

King, L.J., 1966. Weeds of the World. Interscience Publishers, New York.

Kollman, A.L. and Wali, M.K., 1976. Intraseasonal variations in environmental and productivity relations of *Potamogeton pectinatus* communities. Arch. Hydrobiol., Monogr. Beitrage, Suppl., 50: 439—472.

Lodhi, M.A.K., 1979. Germination and decreased growth of *Kochia scoparia* in relation to its autoallelopathy. Can. J. Bot., 57: 1083—1088.

Melrod, D.M., 1977. Allelopathy. A methodological approach into root exudations. M. S. Thesis, Cornell University, Ithaca, NY.

Milthorpe, F.L., 1961. The nature and analysis of competition between plants of different species. Symp. Soc. Exp. Biol., 15: 330—355.

Monk, R.W. and Wiebe, H.H., 1961. Salt tolerance and protoplasmic hardiness of various woody and herbaceous ornamental plants. Plant Physiol., 36: 478—482.

Monsi, M. and Saeki, T., 1953. Uber den Lichtfaktor in den Pflanzengesell-schaften und seine Bedeutung fur die Stoffproduktion. Jpn. J. Bot., 14: 22—52.

Morgan, R.L., 1973. Environmental inpact of surface mining; the biologist's viewpoint. In: M.K. Wali (Editor), Some Environmental Aspects of Strip Mining in North Dakota. Educational Series 5, North Dakota Geological Survey, Grand Forks, ND, pp. 61—71.

Munson, R.D. and Nelson, W.L., 1973. Principles and practices in plant analysis. In: L.M. Walsh and J.D. Beaton (Editors), Soil Testing and Plant Analysis. Soil Sci. Soc. Am. Madison, WI, pp. 223—248.

National Oceanic and Atmospheric Administration, 1975—1977. Annual Summaries. North Dakota Climatological Data, 84—86; 1—12.

Omodt, H.W., Schroer, F.W. and Patterson, D.D., 1975. The properties of important agricultural soils as criteria for mined land reclamation. N. D. Agric. Exp. Stn. Bull., 492: 1—52.

Perkin-Elmer Manual, 1973. Analytical Methods for Atomic Absorption Spectrophotometry. Perkin-Elmer, Norwalk, CT.

Pickett, S.T. and Baskin, J.M., 1973. Allelopathy and its role in the ecology of higher plants. Biologist, 55: 49—73.

Rice, E.L., 1974. Allelopathy. Academic Press, New York.

Rice, E.L., 1979. Allelopathy — an update. Bot. Rev., 45: 15—109.

Rice, E.L. and Parenti, R.L., 1978. Causes of decreases in productivity in undisturbed tall grass prairie. Am. J. Bot., 65: 1091—1097.

Rice, E.L., Penfound, W.T. and Rohrbough, L.M., 1960. Seed dispersal and mineral nutrition in succession in abandoned fields in central Oklahoma. Ecology, 41: 224—228.

Risser, P.G., 1969. Competitive relationships among herbaceous grassland plants. Bot. Rev., 35: 251—284.

Safaya, N.M., 1976. Phosphorus—zinc interaction in relation to absorption rates of phosphorus, zinc, copper, manganese, and iron in corn. Soil Sci. Soc. Am. J., 40: 719—722.

Safaya, N.M. and Wali, M.K., 1979. Growth and nutrient relations of a grass—legume mixture on sodic coal-mine spoil as affected by some amendments. Soil Sci. Soc. Am. J., 43: 747—753.

Safaya, N.M., Malakondaiah, N. and Wali, M.K., 1979. Relevance of flow culture studies in identifying P-efficient species for mine spoils. Agron. Abstr., p. 180.

Sandoval, F.M., Bond, J.J., Power, J.F. and Willis, W.O., 1973. Lignite mine spoils in the northern Great Plains — characteristics and potential for reclamation. In: M.K. Wali (Editor), Some Environmental Aspects of Strip Mining in North Dakota. Educational Series 5, North Dakota Geological Survey, Grand Forks, ND, pp. 1—24.

Schafer, W.M. and Nielsen, G.A., 1979. Soil development and plant succession on 1- to 50-year-old strip mine spoils in southeastern Montana. In: M.K. Wali (Editor), Ecology and Coal Resource Development. Pergamon, New York, pp. 541—549.

Sherrod, L.B., 1971. Nutritive value of *Kochia scoparia*. I. Yield and chemical composition at 3 stages of maturity. Agronomy Journal, 63: 343—344.

Sherrod, L.B., 1973. Nutritive value of *Kochia scoparia*. III. Digestibility of *Kochia* hay compared with alfalfa hay. J. Dairy Sci., 56: 923—926.

Shinozaki, K. and Kira, T., 1956. Intraspecific competition among higher plants. VII. Logistic theory of the C—D effect. Osaka City University. J. Inst. Polytech., D 7: 35—72.

Sindelar, B.W., 1979. Successional development of vegetation of surface mined land in Montana. In: M.K. Wali (Editor), Ecology and Coal Resource Development. Pergamon, New York, pp. 550—556.

Stearns-Rogers, Inc., 1976—1978. Meteorological and Air Quality Observations. Annu. Rep. 1, 2 and 3, Project C-15480, Coyote Station, Beulah, ND.

Stevens, P.R. and Walker, T.W., 1970. The chronosequences concept and soil formation. Q. Rev. Biol., 45: 333—350.

Stowe, L.G., 1979. Allelopathy and its influence on the distribution of plants in an Illinois old-field. J. Ecol., 67: 1065—1085.

Stowe, L.G. and Teeri, J.A., 1978. The geographical distribution of C_4 species of the Dicotyledonae in relation to climate. Am. Nat., 112: 609—623.

Swain, T., 1977. Secondary compounds as protective agents. Annu. Rev. Plant Physiol., 28: 479—501.

Teeri, J.A. and Stowe, L.G., 1976. Climate patterns and the distribution of C_4 grasses in North America. Oecologia (Berlin), 23: 1—12.

Teeri, J.A., Stowe, L.G. and Livingstone, D.A., 1980. The distribution of C_4 species of the Cyperaceae in North America in relation to climate. Oecologia (Berlin), 47: 307—310.

Todd, G.W., Getchum, A. and Cress, D.C., 1976. Resistance in barley to greenbug, *Schizaphis graminum* L., toxicity of the phenolic and flavonoid compounds and related substances. Entomol. Soc. Am. Ann., 64: 718—722.

Tukey, H.B., 1966. Leaching of metabolites from aboveground plant parts and its implications. Bull. Torrey Bot. Club, 93: 385—401.

United States Department of the Interior, 1967. Surface Mining and our Environment. A Special Report to the Nation, Washington, DC, 124 pp.

Van Bruggen, T., 1976. The Vascular Plants of South Dakota. Iowa State University Press, Ames, IA.

Wali, M.K. and Freeman, P.G., 1973. Ecology of some mined areas in North Dakota. In: M.K. Wali (Editor), Some Environmental Aspects of Strip Mining in North Dakota. Educational Series 5, North Dakota Geological Survey, Grand Forks, ND, pp. 25—47.

Wali, M.K. and Kollman, A.L., 1977. Ecology and mining or mining ecology? In: J.L. Thames (Editor), Disturbed Land Reclamation and Use in the Southwest. University of Arizona Press, Tucson, AZ, pp. 108—115.

Wali, M.K. and Krajina, V.J., 1973. Vegetation—environment relationships of some sub-boreal spruce zone ecosystems in British Columbia. Vegetatio, 26: 237—381.

Wali, M.K. and Pemble, R.H., 1982. Ecological studies on the revegetation process of surface coal mined areas in North Dakota. 3. Vegetation and soil development on abandoned mines. Rep. U.S. Dep. Interior, Bureau of Mines, 83 pp.

Wali, M.K. and Sandoval, F.M., 1975. Regional site factors and revegetation studies in western North Dakota. In: M.K. Wali (Editor), Practices and Problems of Land Reclamation in Western North America. University of North Dakota Press, Grand Forks, ND, pp. 133—153.

Weatherspoon, D.M. and Schweizer, E.E., 1969. Competition between *Kochia* and sugarbeets. Weed Sci., 17: 464—467.

Whitman, W.C. and Wali, M.K., 1975. Grasslands of North Dakota. In: M.K. Wali (Editor), Prairie: a Multiple View. University of North Dakota Press, Grand Forks, ND, pp. 53—73.

Whitman, W.C., Hanson, H.T. and Loder, G., 1943. Natural revegetation of abandoned fields in western North Dakota. N. D. Agric. Exp. Stn. Bull., 321: 2—18.

Whittaker, R.H., 1975. Communities and ecosystems. Macmillan, New York.

Whittaker, R.H. and Feeny, P.P., 1971. Allelochemics: chemical interactions between species. Science, 171: 757—770.

Williams, J.T., 1964. Studies on the biology of weeds with special references to the genus *Chenopodium* L. Ph.D. Thesis, University of Wales, U.K.

Wit, C.T. de, 1960. On competition. Versl. Landbouwkd. Onderz., 66: 1—82.
Wright, J.R., Leakey, A. and Rice, H.M., 1959. Chemical, morphological and mineralogical characteristics of a chronosequence of soils on alluvial deposits in the Northwest Territories. Can. J. Soil Sci., 39: 32—43.
Yoda, K., Kira, T., Ogawa, H. and Hozumi, K., 1963. Intraspecific competition among higher plants. XI. Self-thinning in overcrowded pure stands under cultivated and natural conditions. Osaka City University, J. Biol., 14: 107—129.

Appendix I

Species seeded by the Knife River Coal Mining Company at the study sites

Species	Rate of application (kg ha^{-1})	Date seeded*
Secale cereale (cover)	22.5	3
Avena sativa (cover)	20.2	1, 2, 4
Agropyron smithii	6.7	1, 2, 3, 4
Stipa viridula	5.6	1, 2, 3, 4
Agropyron caninum	4.5	1, 2, 3, 4
A. elongatum	2.3	1, 2, 4
A. trichophorum	2.3	1, 2, 4
A. cristatum	2.3	4
Bouteloua curtipendula	2.3	2, 3
Andropogon scoparius	2.3	2, 3
Melilotus officinalis	1.1	1, 2, 3, 4
Coronilla varia var. *emerald*	1.1	4
Medicago sativa	1.1	1

*1 = November 1976; 2 = September 1975; 3 = September 1974; 4 = September 1973.

Site information

1. All areas had 13—20 cm topsoil replaced after contouring. Topsoil was taken from closely located, similar, lightly grazed prairie and stockpiled for 1—2 years (which drastically reduces viable seed populations). Seed populations are, therefore, assumed to be roughly equivalent in numbers and kind for each site.
2. Areas were fertilized with 225 kg ha^{-1} of NPK as $N_{14}P_{10}K_{10}$ at the time of sowing.
3. All areas had approximately the same slope angles, position and aspects.
4. All areas were located 0.1—0.5 km from lightly grazed prairie.
5. Winter annuals do not occur in this region due to the severity of winters. Therefore, if the area is sown after early September, it will remain unvegetated through the winter and establishment will begin in the spring.