DEMOGRAPHIC PROFILES OF POPULATIONS OF COTTON RATS IN A CONTINUUM OF HABITAT TYPES

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We examined temporal relationships between characteristics of populations of cotton rats (*Sigmodon hispidus*) and vegetative characteristics of habitats following secondary succession of post oak (*Quercus stellata*)–blackjack (*Q. marilandica*) savannas in central Oklahoma. Successional changes in vegetation were induced on manipulated habitats by one of two herbicides (tebuthiuron, triclopyr) applied in 1983 and used in combination with or without annual prescribed burning during 1985 to 1988. Relative population density (animals caught per 100 trapnights) and percentage of reproductively active adult females (lactating or pregnant) were significantly greater on manipulated habitats dominated by monocots (grasses) than on habitats with monocots and dicots or undisturbed controls. Herbaceous dicots also influenced the density of cotton rats, especially in 1986; relative density peaked on all manipulated habitats following a peak in production of herbaceous dicots in 1985. Nutritional quality of herbaceous vegetation may have been enhanced by annual burning; relative densities and proportions of juveniles in the trapable population were higher in burned than in unburned habitats. This observation was most pronounced in 1986, when herbaceous dicots comprised a greater proportion of the primary production, than in 1987 or 1988.

Key words: *Sigmodon hispidus,* herbicide, fire, population dynamics, monocots, dicots

Cotton rats (*Sigmodon hispidus*) occupy a wide variety of habitats throughout their range (Cameron and Spencer, 1981). Nonetheless, their distribution within any particular type of habitat is not random (Kincaid et al., 1983). In the coastal prairie of Texas, habitat variation is the dominant environmental factor influencing the dynamics of populations of cotton rats (Cameron, 1977; Kincaid and Cameron, 1982, 1985; Kincaid et al., 1983). In this case, cotton rats show a strong association with monocot-dominated (grass) patches (with some shrub overstory) and little or no affinity for dicot-dominated patches of habitat. These observations generally are supported by food-habit studies that typically show monocots comprising >80% of the diet of cotton rats (Kincaid and Cameron, 1982). Characterization of preferred habitat is complicated by seasonal, sex-related, and density-related shifts in habitat use by cotton rats (Kincaid and Cameron, 1985; Kincaid et al., 1983; Lidicker et al., 1992).

Although there is general agreement that habitat use and preference by cotton rats depends on density of monocots, other studies have been equivocal in demonstrating the role of other life forms of vegetation (Fleharty and Mares, 1973; Goertz, 1964;

Guthery et al., 1979; Kaufman and Fleharty, 1974; Senzota, 1985). Part of this discrepancy is due to strong interactions between the composition of vegetation (proportion of monocots versus dicots) and structural (density and height of vegetation; cover) attributes of the habitat (Fleharty and Mares, 1973; Goertz, 1964; Phillips, 1936). Cotton rats may respond favorably to high proportions of dicots in the habitat if cover remains optimal. For example, Guthery (1977) and Guthery et al. (1979) observed an irruption of cotton rats on root-plowed prairie that experienced an increase in diversity and biomass of early-successional forbs (i.e., *Sida*) and members of the Abrosiaceae. Similar irruptions in density of cotton rats have occurred on drained lakebeds in central Oklahoma after latent seed stores germinated and produced dense standing crops of herbaceous dicots (R. L. Lochmiller, pers. comm.). Our objective was to assess relationships between population and physiological characteristics of cotton rats and vegetative characteristics of habitats following secondary succession of post oak (*Quercus stellata*)–blackjack (*Q. marilandica*) savannas in central Oklahoma.

Materials and Methods

Research was conducted on the Cross Timbers Experimental Range, located ca. 11 km southwest of Stillwater, Oklahoma (36°02′40″ to 36°04′20″N, 97°09′30″ to 97°11′39″W). The Cross Timbers Experimental Range provided an opportunity to monitor demographic changes in populations of cotton rats on 648 ha of rangeland undergoing secondary succession and representing a continuum of habitats, ranging from monocot- to dicot-dominated sites. The Cross Timbers Experimental Range originally represented upland forest with interspersed grassland-cedar savannas. Prior to treatment, this area was representative of the cross-timbers vegetational type (Ewing et al., 1984), which accounts for nearly 5 × 10^6 ha of rangeland in Oklahoma, Kansas, and Texas (Soil Conservation Service, 1981).

Upland-forest habitats in the Cross Timbers Experimental Range are dominated by post oak (*Quercus stellata*) and black-jack oak (*Q. marilandica*) in the overstory and eastern redcedar (*Juniperus virginiana*), rough-leaf dogwood (*Cornus drummondii*), redbud (*Cercis canadensis*), American elm (*Ulmus americana*), and coralberry (*Symphoricarpos orbiculatus*) in the understory. Herbaceous ground cover is dominated by little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), rosette panicgrass (*Panicum oligosanthes*), and western ragweed (*Ambrosia psilostachya*).

The Cross Timbers Experimental Range was divided into 20 fenced experimental plots (32.4 ha) representing four replications each of five experimental treatments of brush control in a randomized-block design. Plots were assigned to respective blocks according to their similarity in total cover of woody canopy and soils. The experimental treatments were: 1) tebuthiuron, a soil applied herbicide (Dow Elanco, Indianapolis, IN), applied aerially at 2.2 kg/ha in March 1983; 2) tebuthiuron (as with treatment 1) with annual prescribed burning beginning April 1985; 3) triclopyr, a foliage applied herbicide (Dow Elanco), applied aerially at 2.2 kg/ha in June 1983; 4) triclopyr (as with treatment 3) with annual prescribed burning beginning in April 1985; 5) control plots receiving no herbicide or burning. All plots were moderately grazed by yearling cattle from April to September of each year.

Current standing crop of understory vegetation was sampled in late July and early August each year. Vegetation was sampled within movable wire cages (50- by 50-cm ground surface area) in March to prevent grazing. In March, each of seven cages were randomly placed in densely wooded (>80% woody-over-story canopy cover), shallow, and sandy savanna sites. Growth from the current year was clipped to ground level and separated into monocots (grasses), woody dicots, or herbaceous dicots and dried at 70°C to determine dry weight. Growth of woody dicots included leaves and production of twigs of all woody species growing ≤1.5 m above ground level.

Populations of cotton rats were censused on 10 occasions; March, June, September, and December of 1986 and 1987, and June and December of 1988. During the first sampling period, two of the four replicates of each treatment were selected randomly and censused using removal trapping on a 1.1-ha grid (8 by 8 with 15-m spacing) that was randomly placed in upland-forest habitat. Trapping grids were relocated before each sampling period so that no area within an experimental pasture was trapped more than once. Replications were alternated after every 2 successive sampling periods. Two Museum Special traps per station and one Victor rat trap at every other station (equals three traps at every other station) were placed adjacent to available woody or herbaceous structures within a 1-m radius of the grid point. One Museum Special trap per station and all Victor rat traps were baited with a mixture of peanut butter and rolled oats, whereas the second Museum Special trap was baited with sliced apples. Each grid was trapped for 3 consecutive nights, with daily removal of all captured individuals. Relative density was estimated as the number of animals caught per 100 trapnights (a trapnight was defined as one trap set for a single 24-h period). Catch per unit effort was calculated as the mean of the replications within each treatment, with corrections made for traps sprung by all causes (Nelson and Clark, 1973). Collected animals were returned to the laboratory, and lengths of body, tail, and hind foot (±1 mm), as well as body mass (±0.1 g) were determined. Animals ≥60.0 g were classified as adults; those <60.0 g were classified as juveniles (Odum, 1955).

Reproductive status of each male was determined by scoring the relative abundance of sperm in the epididymides and weights of the testes and seminal vesicle gland. Presence of spermatozoa in the epididymis was ascertained by cutting the caudal pole, extruding its contents, and smearing them across a glass microscope slide. Slides were examined microscopically, and sperm abundance was ranked as 0 (none), 1 (trace), 2 (moderate), or 3 (abundant). Females that were pregnant or lactating were considered reproductively active. Females were classified as pregnant, and embryos were counted when visible upon necropsy. Females were considered lactating if mammary tissue was conspicuous with hair-free areas surrounding the nipples.

Condition of both sexes was assessed by examining weights (±0.1 g for body, ±0.1 mg for others) of liver, spleen, adrenal glands (Christian et al., 1965), body, and oven-dried stomach contents. Contents of each stomach were removed and dried to constant weight at 55°C. A general condition score was calculated for each animal as 100 times body weight divided by length of body.

Catch per unit effort estimates were arcsine transformed (Sokal and Rohlf, 1981), and differences among treatments and seasons tested by two-way analysis of variance (PROC GLM—SAS Institute, Inc., 1985). Differences in age ratios, sex ratios, sperm abundance, and female reproductive status among treatments and seasons were tested using chi-square analysis (Koopmans, 1981). Body mass, organ and gland masses, and condition scores were rank transformed, and then main and interactive effects of treatment, season, and sex were examined using analysis of variance (Conover and Iman, 1981). Specific contrasts and Duncan's multiple range tests were used in all analysis-of-variance procedures to evaluate differences between major brush-treatment components (tebuthiuron versus triclopyr, burned versus unburned, brush treated versus untreated controls). Statistical significance was $P \leq 0.05$ for all tests.

Results

Habitat characteristics.—Manipulated habitats, regardless of herbicide or fire regime, exhibited a substantial increase in production of herbaceous monocots and dicots compared to control sites (Fig. 1). Overall, peak productivity of herbaceous dicots (1985) and monocots (1986) was 81 and 46 times greater, respectively, on manipulated habitats than on controls. A peak in productivity of woody dicots was not apparent, although overall productivity in 1986 on habitats manipulated with triclopyr (burned and unburned) was two times that of controls. However, burned and unburned tebuthiuron-treated habitats were essentially equal (14% greater) to controls (Fig. 1). Productivity of herbaceous dicots steadily declined from 1986 through 1988; nonetheless, monocots and woody dicots exhibited only marginal fluctuations in productivity.

Population characteristics.—Based on the capture of 707 cotton rats, relative densities (Fig. 2) differed among seasons (two-way ANOVA, $P < 0.001$) and experimental treatments ($P < 0.001$). Specific contrasts revealed that relative population density of cotton rats from modified habitats were significantly ($P < 0.001$) greater than those from controls. Relative population density also was significantly greater on habitats modified with tebuthiuron ($P < 0.001$) compared to those treated with triclopyr and on burned habitats ($P < 0.025$) compared to unburned habitats. Overall, relative population densities of cotton rats were greatest on tebuthiuron-treated habitats that were burned annually. Populations on all modified habitats peaked during winter 1986; the greatest density was 8.29 animals/100 trap-nights on pastures that were burned and treated with tebuthiuron representing an eight-fold increase from spring. Cotton rats were captured on control pastures only in summer and autumn 1986, and relative density never exceeded 0.92 animals/100 trap-nights.

Males composed 55.0% of the total sample, with no significant relationship of sex ratio to season or experimental modifications ($P > 0.05$). Juveniles were collected in all sampling periods; however, the percentage of juveniles fluctuated greatly among pooled seasons ($\chi^2 = 28.9$, $d.f. = 3$, $P < 0.001$). Proportion of juveniles was greater in summer (56%) and autumn (54%) than in spring (28%) and winter (38%). Proportion of juveniles differed significantly among experimental treatments (all years pooled; $\chi^2 = 12.1$, $d.f. = 4$, $P < 0.025$), with a greater proportion in burned than unburned habitats ($\chi^2 = 10.5$, $d.f. = 1$, $P < 0.005$; Fig. 3). Differences in percentage of juveniles between burned and unburned habitats were most pronounced in 1986 ($\chi^2 = 9.6$, $d.f. = 1$, $P < 0.005$) and 1988 ($\chi^2 = 5.5$, $d.f. = 1$, $P < 0.025$).

Reproductive activity.—Peaks of reproductive activity by adult females occurred in autumn 1986 and 1987, when 93% and 100% of adult females, respectively, were reproductively active (Fig. 4). Percentage of reproductively active adult females was higher than expected in autumn and less than expected in winter and spring (years pooled; $\chi^2 = 96.1$, $d.f. = 3$, $P < 0.001$). Percentage of adult females that were reproductively active (all seasons and years

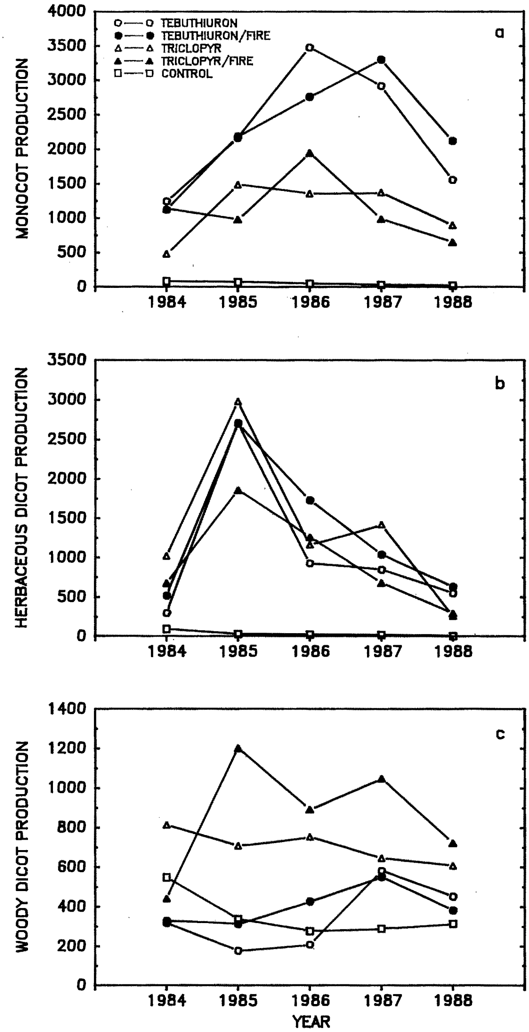

FIG. 1.—Current standing crop (kg/ha) of (a) monocots, (b) herbaceous dicots, and (c) woody dicots on five experimental treatments from 1984 to 1988.

pooled) was lower than expected on triclopyr-modified habitats compared to those modified with tebuthiuron ($\chi^2 = 3.9$, $d.f. = 1$, $P < 0.05$; Fig. 4). Litter size ranged from three to 12 individuals ($\bar{X} = 6.55$; $SE = 0.23$; $n = 63$), and no differences among seasons or experimental treatments were observed.

Mean mass of testes as well as mean mass of seminal vesicles differed significantly ($P < 0.001$) among seasons. Multiple-range tests showed that mass ($\bar{X} \pm SE$) of testes

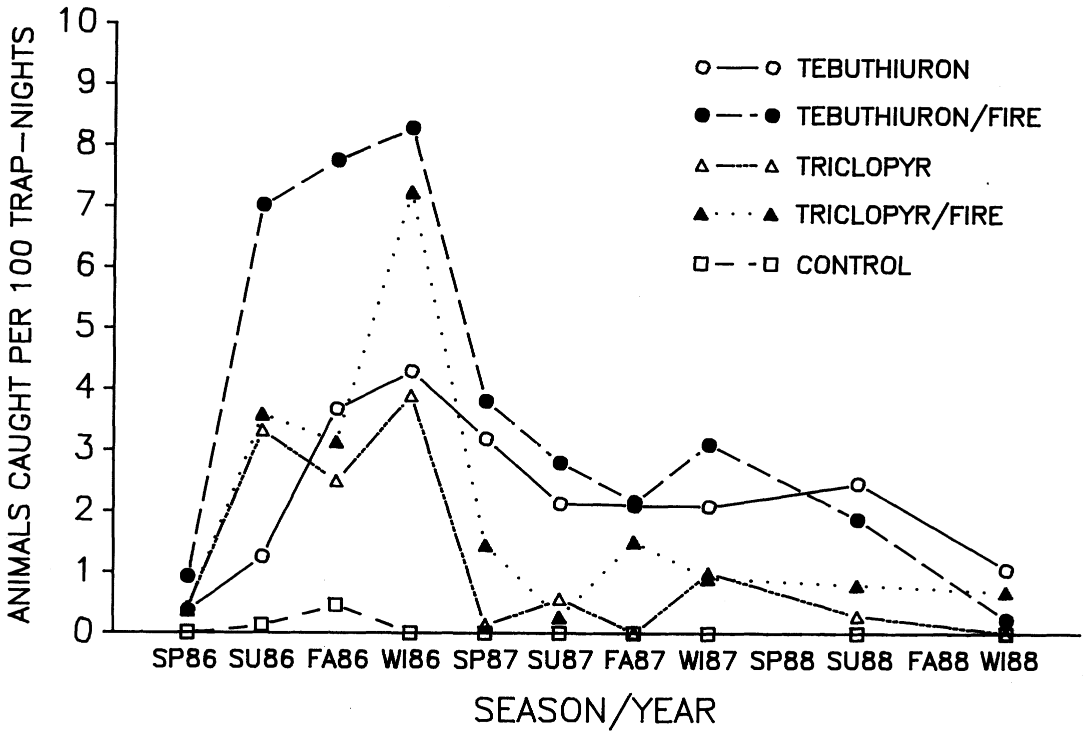

FIG. 2.—Total catch per unit effort of cotton rats on five experimental treatments from spring 1986 to winter 1988. First two letters of each label on X axis represent season (SP, SU, FA, and WI = spring, summer, fall, and winter, respectively), and last two numbers represent year.

and seminal vesicles for each season differed from those in all others and that testes and seminal vesicles were heaviest in summer and lightest in winter (testes, 1.53 ± 0.11 g versus 0.13 ± 0.01 g; seminal veiscles, 0.80 ± 0.11 g versus 0.02 ± 0.002 g). Additionally, season influenced percentage of adult males with relative sperm abundance scores ≥2 (all years pooled), with greater than expected percentages in summer (95.2%) and autumn (78.8%) compared to spring (50.0%) and winter (3.4%) (χ^2 = 120.4, *d.f.* = 3, $P < 0.001$). Significant differences in mean mass of testes, mass of seminal vesicles, or relative sperm abundance scores ≥2 did not exist among experimental treatments ($P > 0.10$). However, specific contrasts indicated that mass of seminal vesicles from adult cotton rats from triclopyr-treated habitats were significantly ($P < 0.02$) heavier than those from cotton rats from tebuthiuron-treated habitats.

Condition.—Body mass of females was corrected for pregnancy prior to analysis by subtracting uterine mass from body mass. Mean ranked body mass as well as condition differed significantly among seasons ($P < 0.001$), with a significant season by sex interaction ($P < 0.006$). Multiple-range tests indicated that adult body mass and condition in autumn and summer (mass, 111.4 ± 3.1 g; condition score, 71.0 ± 1.5) were greater than in spring and winter (mass, 87.8 ± 1.6 g; condition score, 60.3 ± 0.8), due primarily to higher body mass of females. Habitat modifications had no influence ($P > 0.10$) on body mass or condition score of adult cotton rats.

Mass of stomach contents differed ($P < 0.024$) between sexes and was analyzed separately for males and females. Mass of dried stomach contents of males collected from undisturbed habitats (1.53 ± 0.14 g, $n = 4$) was greater than that of males from modi-

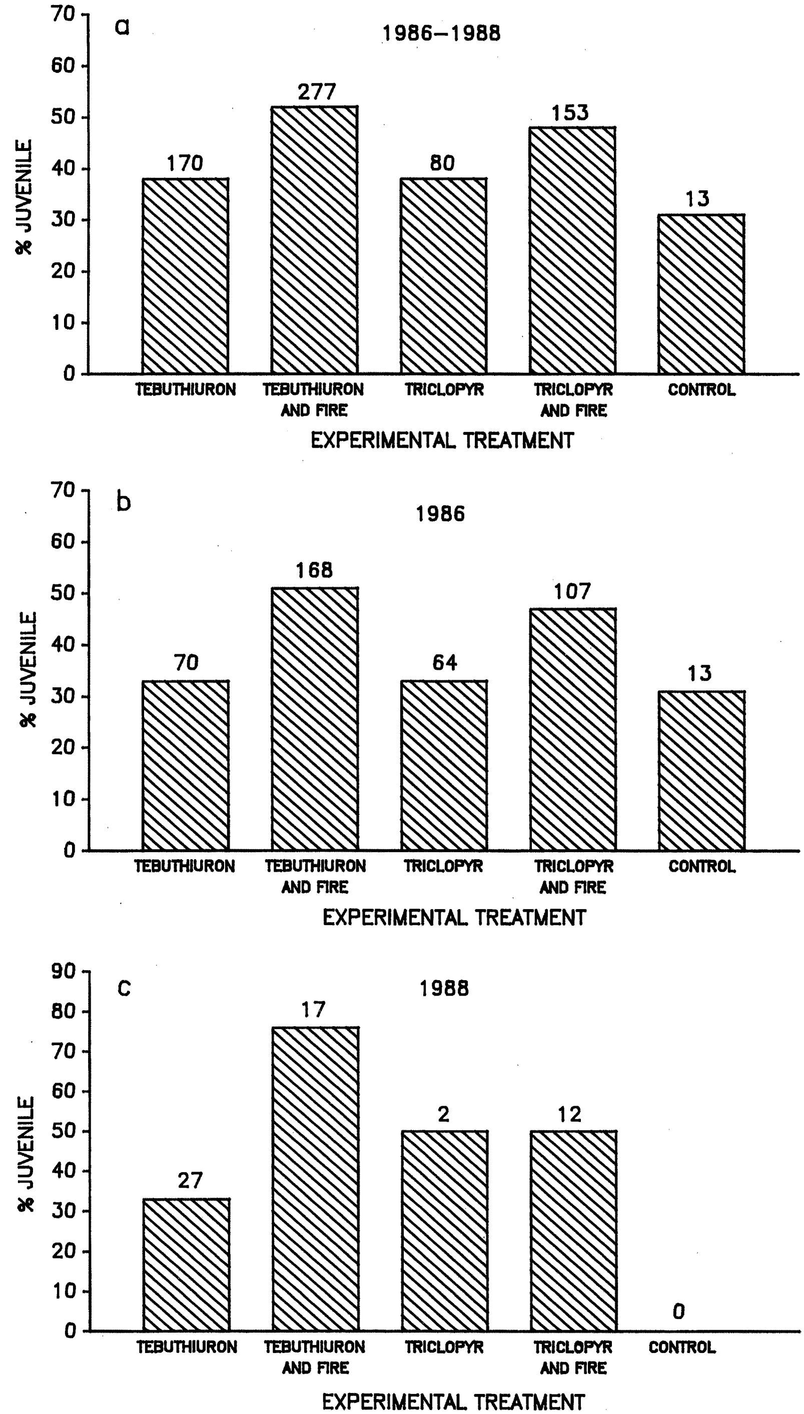

FIG. 3.—Differences in percent juvenile cotton rats among five experimental treatments for (a) pooled years and seasons and for pooled seasons in 1986 (b) and 1988 (c). Values above bars represent sample size.

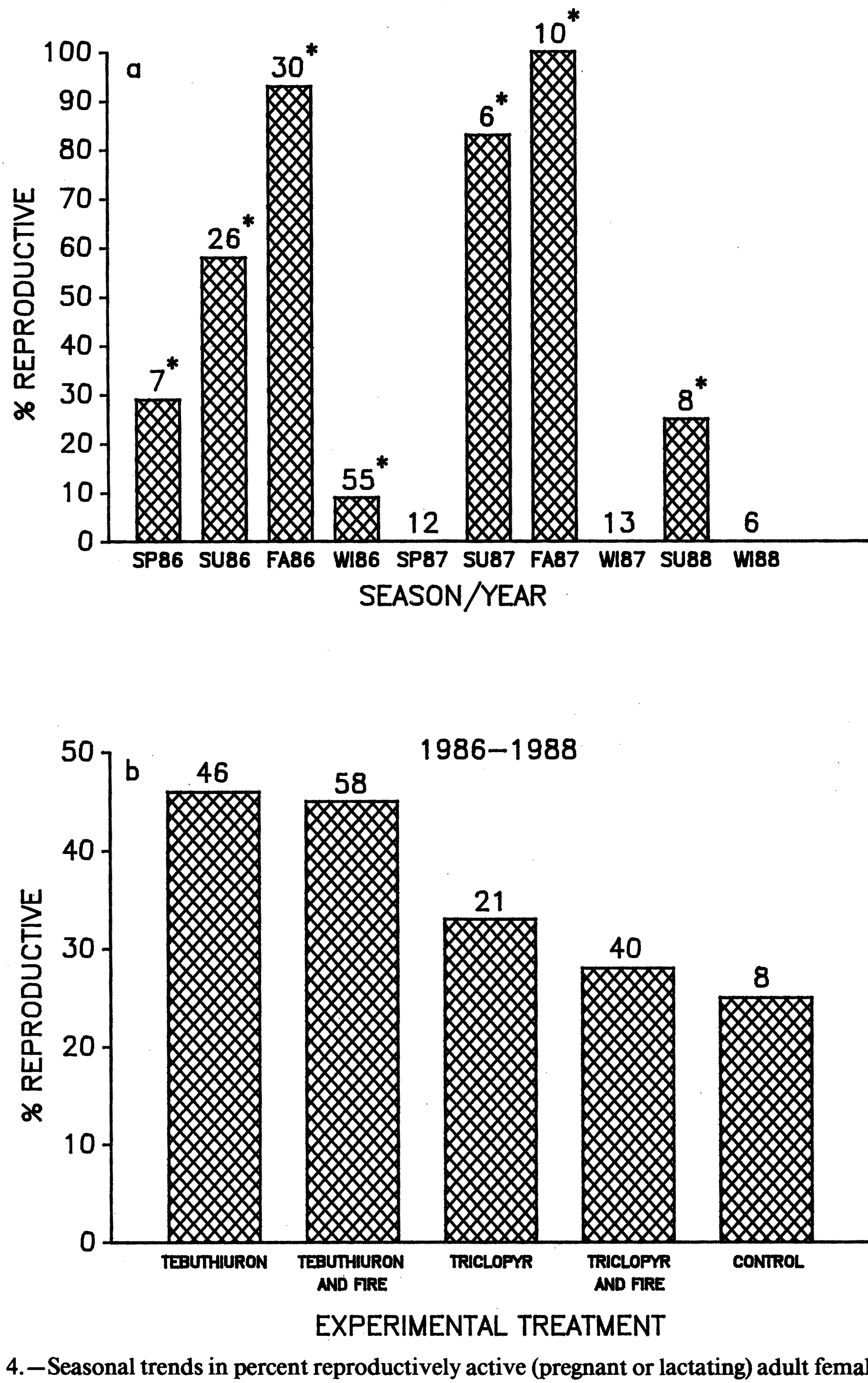

FIG. 4.—Seasonal trends in percent reproductively active (pregnant or lactating) adult female cotton rats from spring 1986 to winter 1988 (a) and differences among experimental treatments for which years and seasons were pooled (b). First two letters of each label on X axis represent season (SP, SU, FA, and WI = spring, summer, fall, and winter, respectively), and last two numbers represent year. Values above bars represent sample size and asterisks above bars denote seasons in which pregnant females were caught.

fied habitats (0.82 ± 0.06 g, $n = 117$, $P < 0.05$); for females, no differences in mean mass of dried stomach contents occurred among treatments. Seasonal differences in mass of stomach contents were apparent for females ($P < 0.001$), but not males ($P > 0.10$). Mass of stomach contents of females collected in summer (1.10 ± 0.11 g) and autumn (1.37 ± 0.15 g) was greater than that of females collected in winter (0.78 ± 0.09 g).

Ranked masses of liver and spleen of adults did not differ ($P > 0.10$) among experimental treatments, but seasonal differences were apparent ($P < 0.028$ and $P < 0.001$, respectively), and there was a significant season by sex interaction ($P < 0.001$). Mean liver mass and spleen mass were highest in summer (4.53 ± 0.35 g and 0.21 ± 0.02 g, respectively) and autumn (4.35 ± 0.31 g and 0.22 ± 0.02 g, respectively) for females, and in spring (4.67 ± 0.22 g and 0.30 ± 0.04 g, respectively) for males. Paired adrenal gland mass differed between sexes ($P < 0.001$), but was not influenced by experimental treatments ($P > 0.10$). Seasonal differences were significant for both males and females ($P < 0.001$ and $P < 0.006$, respectively). Adrenal mass of males was heavier in spring (0.033 ± 0.002 g) and winter (0.030 ± 0.001 g) than in autumn (0.021 ± 0.002), and adrenal mass of females was heavier in summer (0.045 ± 0.004 g) than in winter (0.031 ± 0.002 g).

Discussion

A previous study in the vicinity of the present experimental area documented a strong relationship between density of cotton rats and production of monocots in the cross-timbers vegetational type (Goertz, 1964). Later studies in tallgrass prairie of Kansas (Fleharty and Mares, 1973) and coastal prairie of Texas (Kincaid and Cameron, 1985) provided further support for the premise that cotton rats have a strong preference for monocot-dominated habitats. However, no study has explored adequately the responses of populations of cotton rats to experimental manipulations of habitat that induce secondary succession, altering the availability of monocots and dicots (both herbaceous and woody). We hypothesized that indices of reproductive activity, condition, and density should increase on modified habitats in which production of monocots was elevated compared to undisturbed controls, be greater on monocot-dominated areas that were treated with tebuthiuron than on comparable areas treated with triclopyr, and be greater on burned than unburned habitats because of improved quality of forage. We further expected that population responses on modified habitats should be proportional to successional changes in primary production of monocots.

Demographic responses of populations of cotton rats to changes in production of monocots and dicots were in general agreement with these hypotheses. Removal of savanna overstory resulted in increased production by monocots, which peaked in 1986 and remained high through 1987. Relative densities of cotton rats ostensibly increased in response to increased production of monocots, although this effect was restricted primarily to 1986. The positive association between density of cotton rats and production of monocots also was supported by the observation that peak densities were lowest in 1988, when production of monocots declined from 1987 levels on all habitats. Relative densities of cotton rats also were higher on tebuthiuron-treated habitats, which supported greater biomass of monocots in all years compared to those modified with triclopyr. Efficient control of woody resprouts by tebuthiuron resulted in 89% and 164% more average monocot-biomass on tebuthiuron-modified habitats compared to triclopyr-treated habitats in 1986 and 1987, respectively. Production of woody dicots was two to three times greater on triclopyr-treated pastures than on tebuthiuron-treated areas, and, thus, triclopyr treatments may have been avoided by cotton rats (Kincaid and Cameron, 1985; Kincaid et al., 1983). Reproductive activity of females paralleled differences in density between tebuthiuron-and triclopyr-treated habitats.

A positive association between relative density of cotton rats and production of monocots was apparent; however, production of monocots alone did not completely account for observed demographic responses. This was evident in 1987, when despite no appreciable change in production of monocots, relative density of cotton rats declined in manipulated sites and remained low through 1988. After the 1985 growing season, all modified habitats were characteristic of early secondary succession on disturbed sites and were dominated by a variety of herbaceous dicots. Although populations of cotton rats were not censused until the following spring, we suspect densities in 1985 were high and over-winter survival was a contributing factor to the high density observed in 1986 (Cole and Batzli, 1979; Fleharty et al., 1972). Production of herbaceous dicots declined in 1987 and 1988, corresponding to declines in relative densities of cotton rats on all modified habitats.

Monocots provided necessary cover and forage requirements to permit colonization of habitats, but selected species of herbaceous dicots probably provided important nutritional resources to stimulate recruitment during early secondary succession (Randolf et al., 1991). Male cotton rats on undisturbed sites consumed about two times more dry matter than did cotton rats from treated sites. Consumption of more forage on control sites may have been an attempt to meet nutritional requirements on poor-quality forage. In general, however, indices of condition indicated that trapable cotton rats were indistinguishable among treatments. Monocots compose a major component of the diet of cotton rats (Fleharty and Olson, 1969); herbaceous dicots also are important, especially in spring (Kincaid and Cameron, 1985). Use of herbaceous dicots was not quantified through dietary analyses in our study, but cursory examination of stomach contents revealed consumption of pokeweed (*Phytolacca americana*), which was a dominant species in all modified habitats in 1986, but declined substantially in abundance in 1987 and 1988.

Burning of habitats had a positive influence on populations of cotton rats, as indicated by greater relative densities and percentage of juveniles in the trapable population. Litter size was not different between burned and unburned treatments, indicating that increased survival of neonates may have been the primary contributing factor to increased numbers of juveniles on burned sites. Burning effects were most pronounced in 1986, when overall population density of cotton rats was highest and dicots constituted the greatest proportion of the herbaceous vegetation compared to 1987 and 1988. Standing biomass of herbaceous dicots on burned habitats that were treated with tebuthiuron or triclopyr exceeded their unburned counterparts by 87 and 9%, respectively. Additionally, spring burning of rangeland can increase the nutritive quality of several species of plants (Allen et al., 1976), thereby further enhancing the benefits of increased production by herbaceous dicots.

Responses of populations of cotton rats to experimental manipulations support the concept that herbaceous dicots are an important and necessary resource. A limited number of controlled studies are available that examine the demographic responses of cotton rats to secondary succession on disturbed habitats. Kaufman et al. (1990) observed that cotton rats preferred disturbed over undisturbed habitats and suggested that cotton rats would be less affected than other species of rodents by destruction of native-grassland habitat. Similar associations of cotton rats with disturbed, forb-dominated agricultural habitats have been described by Fleharty and Navo (1983).

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