LIFE HISTORY TRAITS AND THE EFFECTS OF DISTURBANCE ON THE ASHY DOGWEED (THYMOPHYLLA TEPHROLEUCA), A NARROW TEXAS ENDEMIC

THESIS

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ABSTRACT

Thymophylla tephroleuca, a federal and state endangered plant species, was monitored in an attempt to document certain reproductive and population level traits. The study was conducted from September 1999 to June 2001 on three populations in Webb and Zapata Counties, Texas. Life history traits examined were breeding system, phenology, pollen viability, floral insect visitors and achene viability. In addition, population level attributes such as recruitment, density and size structure of individuals were examined. Precipitation and temperature were obtained from the National Climatic Data Center. Plant species associated with *T. tephroleuca* habitat were collected. GPS mapping was performed to determine population area of the study sites. Achenes were collected for a genetic reserve of *T. tephroleuca*. A controlled, replicated experiment was also conducted documenting the effects of anthropogenic disturbances on *T. tephroleuca* recruitment and growth. The disturbances included root-plow, blade and root-plow seeded with buffelgrass (to document competitive effects).

Insects of the orders Coleoptera, Diptera, Hymenoptera and Lepidoptera were observed and captured on *T. tephroleuca* flowers. Fruit set mainly occurred in xenogamous crosses, with 88.8% achene set. Peak flowering months for field plants were from May to November. However, flowering appears to be initiated by rainfall events, as individuals will flower all year long with sufficient watering. Pollen viability in field plants averaged 82.5% in 2000 and 86% in 2001. Achene viability averaged 36.5% in 1999 and 8.3% in 2000. Density, recruitment and size of individuals varied significantly between two populations. In one population (previously disturbed), plants

were small and density at the end of monitoring was 4.1 plants/m^2. Recruitment was observed at 21 plants for the year. In a second population (not previously disturbed), individuals were larger and density was lower throughout the study period at 0.6 plants/m^2. No recruitment was observed in this population. In addition to the results obtained from these two populations, the controlled field experiment suggested that soil disturbance increases plant density. A significantly higher number of individuals were recruited into the root-plow plots than in root-plow seeded with buffelgrass or control plots. No significant difference was observed between root-plow and bladed plots. Aboveground and belowground biomass accumulation was also significantly greater in the root-plow plots than in bladed or control plots.

Results indicate that *T. tephroleuca* is an outcrossing species with a variety of potential pollinators. Pollen viability was consistently high, while achene viability was low and variable depending on the year. Density, recruitment, and size structure of individuals was variable between the two monitored populations, presumably due to site characteristics. Results of the disturbance experiment indicate that root-plowing increases density of plants. Landowners can now make informed decisions about the effects of certain land management practices on Ashy dogweed populations that reside on their ranches.

INTRODUCTION

Thymophylla is a genus consisting of 17 species distributed throughout the southwestern United States and Mexico (Karis and Ryding, 1994). Ashy dogweed, *Thymophylla tephroleuca* (S. F. Blake) Strother, was first collected in Starr County, Texas in 1932. It was listed as a federally endangered species on July 19, 1984 by the US Fish and Wildlife Service and soon thereafter by the State of Texas. The U.S. Fish and Wildlife Service (1984) has designated the recovery of *T. tephroleuca* priority number 5, indicating it is a full species with a high degree of threat. Currently, there are no other members of the genus listed as threatened or endangered.

The plant is an herbaceous perennial in the family Asteraceae. It has a semi-woody taproot, densely pubescent leaves and a capitulum composed of ray and disk florets in a campanulate cup (Turner, 1980). The species is endemic to the ceniza-blackbrush-creosotobush brush community (McMahan et al., 1984) within the South Texas Plains vegetation area (Gould, 1975). Historically this region was thought to have been a grassland. Grazing by introduced livestock and fire suppression are thought to have been the driving forces behind the historic changes in vegetation (Archer, 1995). Plants grow in open areas on fine sandy-loam soils of the Hebbronville and Aguilares series with little or no slope (Turner. 1980; Poole, 1987). Currently, six populations are reportedly known to exist in Webb and Zapata Counties, Texas (Poole, 1987). The type locality in adjacent Starr County was never rediscovered and the species has not been collected in Mexico (Turner, 1996). While all populations exist on privately owned land, one extends onto the US Highway 83 right-of-way between Laredo and Zapata.

The *T. tephroleuca* recovery plan (Poole, 1987) indicates that practices by the ranching industry, gas and oil companies and the Texas Department of Transportation present the greatest threats to its survival and have had the most impact on ashy dogweed. Habitats have been modified by the introduction of buffelgrass (*Cenchrus ciliaris*), an exotic, invasive species used for cattle forage. Pipeline installation and resource exploration by oil and gas companies, as well as road construction by the Texas Department of Transportation have the effect of fragmenting populations. This leads to reduced gene flow and ultimately less genetic variability within a population (Steinberg and Jordan, 1998). The Texas Department of Transportation has plans to widen US Highway 83 (personal comm.), further fragmenting that population.

Prior to this study, documented work on *T. tephroleuca* included the species description (as *Dyssodia tephroleuca*; Blake, 1935), a description of morphology, systematics, and habitat requirements by Turner (1980), and a chromosome count by Strother (1967). Strother (1986) also redefined the genus *Dyssodia* and transferred *D. tephroleuca* to *Thymophylla*. In addition, Poole (1992) reported on achene viability and germination requirements. Nothing, however, has been documented about the population biology or population ecology of the species (Poole, 1987). The objectives of this study were to examine the life history traits in an attempt to answer questions about the rarity (inherent or man-induced) of this species. In addition, the hypothesis that a soil disturbance will increase the density of *T. tephroleuca* was tested to assist landowners and conservationists in making informed decisions about management of existing populations.

MATERIALS AND METHODS

Study Site

Fieldwork was conducted on three populations in Webb and Zapata Counties, Texas, from September 1999 to June 2001. The three populations were digitally mapped using a Magellan Global Positioning System (GPS) unit with multipath resistant antenna and ± 0.5 m precision. The population perimeters were outlined with the unit then transposed onto an aerial photo of the site using Digital Orthophoto Quarter-Quadrangle (DOQQ) imagery and Arcview Global Information Systems (GIS) computer capabilities. From these data, population area in hectares was determined.

Climate and Species Associated with the Habitat

Climatic data were obtained from the National Climatic Data Center in order to elucidate the relationship between rainfall and phenology of *T. tephroleuca*. Precipitation data were obtained from stations in Laredo and Zapata, Texas for May 1999 to July 2000. The Laredo station is within 20 km of the population in the northern extent of the ashy dogweed range. The Zapata station is within 15 km of the population in the southern extent of its range. Precipitation data were also obtained from the Laredo station for August 2000 to July 2001 to evaluate its effects on germination in the disturbance experiment.

Plant species growing in *T. tephroleuca* habitat at the three monitored population sites were collected and identified following Correll and Johnston (1979). Herbarium specimens were prepared and deposited in the Southwest Texas State University (SWT) Herbarium.

Pollen Viability and Floral Visitors

Plants cultivated from achenes at SWT in 1999 and field plants in 2000 and 2001 were tested for pollen viability. Pollen taken haphazardly from multiple inflorescences in the populations was deposited onto a slide and immersed in a drop of 1% lactophenol-aniline blue stain (Kearns and Inouye, 1993). Pollen grains were allowed to stain for 2.5 hours and examined using a compound light microscope under 100x magnification. Pollen grains that stained dark blue were considered viable, while those that were faintly stained or not stained at all were considered nonviable. All pollen on each slide was observed and scored as either viable or nonviable.

Field observations were made to determine floral visitors of *T. tephroleuca.* Insects were captured then identified by the Texas Melittological Institute in Austin, Texas.

Breeding System Experiments

Cultivated individuals were used for analysis of the breeding system in *T. tephroleuca*. All breeding system experiments were conducted following Berry and Calvo (1989).

1) Autogamy. This is a test to determine within-flower fertilization. Stigmas were clipped on all florets except for one disk floret prior to anthesis. Exclosure bags

were then used to eliminate crosses other than autogamous ones from occurring. A total of 50 disk florets from 50 inflorescences were used for the experiment.

2) Geitonogamy. This is a test to determine fertilization between pollen and ovules of different flowers on the same genet. Buds were initially bagged to exclude floral visitation. At anthesis, exclosure bags were removed and pollen was transferred by hand from other inflorescences on the same plant to the stigmas of the experimental inflorescences. After hand pollination, bags were put back on the inflorescences. A total of 2188 florets from 46 inflorescences were used for this experiment.

3) Xenogamy. This is a test to determine fertilization between pollen and ovules of different genets. At anthesis, florets were cross-pollinated by transferring the pollen from another plant to the stigmas of the experimental inflorescences. A total of 348 florets from 8 inflorescences were used for this experiment.

In all experimental crosses, development of an embryo within an achene signified that fertilization had occurred. If fertilization did not occur, no embryo was found within the achene. A total of 200 florets from seven inflorescences were not manipulated and served as controls.

Achene Viability

Achenes collected in May 1999 and June 2000 were tested for viability using a 1% tetrazolium stain (Weber and Wiesner, 1980). Achenes were agitated in a 1:4 bleach:water solution for ten minutes. Achenes were then placed in an open-faced petri dish, covered with nylon and placed under running tap water overnight. Achenes were then rinsed with deionized (DI) water and allowed to remain in the DI water an additional night. The pericarp was then cut longitudinally, exposing the embryo for stain preparation. The stain was prepared by adding 1 gm of tetrazolium to one hundred ml of tap water at pH 7.0. Achenes were placed in the stain immediately after cutting the pericarp to prevent desiccation. Embryos that stained red after four hours were considered viable.

An achene repository was also initiated. Achenes were collected from each population following Center for Plant Conservation guidelines (Falk and Holsinger, 1991) and stored under refrigeration in dry paper bags at SWT.

Phenology, Size Structure and Density

To monitor life history traits of *T. tephroleuca*, permanent belt transects 50 m in length were established in two populations following Lesica (1987). A 1 m^2 quadrat was positioned along one side of each transect and individuals in this quadrat were monitored. A total of 50 contiguous quadrats were established for each transect. Canopy diameter, height and number of inflorescences were determined for each plant along the transect every month from September 1999 to August 2000, with the exception of March. Seedling recruitment and population density were also determined for each population as represented by the transects.

Disturbance Experiment

To test the effects of anthropogenic disturbance on *T. tephroleuca*, a series of controlled experiments was conducted at population 3. The experimental design was pseudoreplicated due to geographic constraints of the population, as well as limitations on disturbing an endangered species in which population numbers are unknown. In addition, the only location accessible to the heavy machinery with *T. tephroleuca* individuals was the strip of land the experiment was conducted on. Three treatments plus controls were randomly selected along this strip of land and replicates within each treatment were contiguous. The treatments were as follows: root-plow, root-plow seeded with buffelgrass, and blade. Treatments were pseudoreplicated 20 times totaling 80 plots, each 2.5 m X 2.5 m in size (Appendix 1). Microhabitat measurements were made throughout the plots to document the environmental homogeneity of the site. Measurements taken included elevation, light intensity, soil moisture, and wind speed. Elevation was recorded in meters above sea level with the GPS unit. Light intensity at ground level was measured in lumens/m^2 with an Extech 401025 Digital Light Meter. Relative soil moisture was determined 15 cm into the soil using an Aquaterr 200 Moisture Meter. Wind at10 cm above ground level was measured using a Kestrel 3000 Pocket Weather Meter. Three random measurements per treatment were taken for each environmental parameter at midday in June 2001.

The soil and vegetation of the site was disturbed once on June 17, 2000. A 75 hp Caterpillar tractor with a 4-cylinder engine was used to perform all disturbances. For the root-plow treatment, a root-plow attachment capable of trenching 0.5 m into the soil was utilized. This treatment simulates what ranchers do to remove woody vegetation in pastures to improve grazing conditions. For the blading treatment, a bulldozing attachment was used to scrape off all vegetation near ground level. This disturbance is performed by landowners to create roads or sites for oil and gas operations. After the treatments were conducted, buffelgrass seed was broadcasted over 20 of the root-plow replicates to test the effects of disturbance and competition. As a measure to control cattle grazing, a cattle panel fence 1.5 m in height was constructed around the perimeter of the experiment *Thymophylla tephroleuca* density was recorded monthly between July 2000 and June 2001 to determine recruitment into each treatment. In addition, a random sample of seven individuals within each treatment was tagged in February 2001 when initial germination was observed. These individuals were harvested in June 2001 and dried for 24 h at 50°C. Dry weight was recorded on above and belowground biomass for each individual.

To document the effects of disturbance on nutrient levels, soil samples (n=1) from each treatment were collected 15 cm below the surface in March 2001 and sent to the Texas A & M University Soil Testing Laboratory in College Station, Texas. Total nitrogen, phosphorus, potassium, calcium, magnesium, and pH were analyzed.

RESULTS

Population Area

The three monitored population sites are shown in Figure 1. Population 1 is located in Webb County and represents the northern extent of the known range of *T. tephroleuca*. This population has an area of 1.4 hectares (Figure 2). Population 2 is located in Zapata County and represents the southern extent of the known range. The delineated part of the population has an area of 66.2 hectares (Figure 3). Plants were observed on the adjacent property, however, access has not been granted to complete mapping. Population 3 is also located in Zapata County and is part of the highway population previously mentioned (Figure 4). This population has an area of 172.0 hectares.

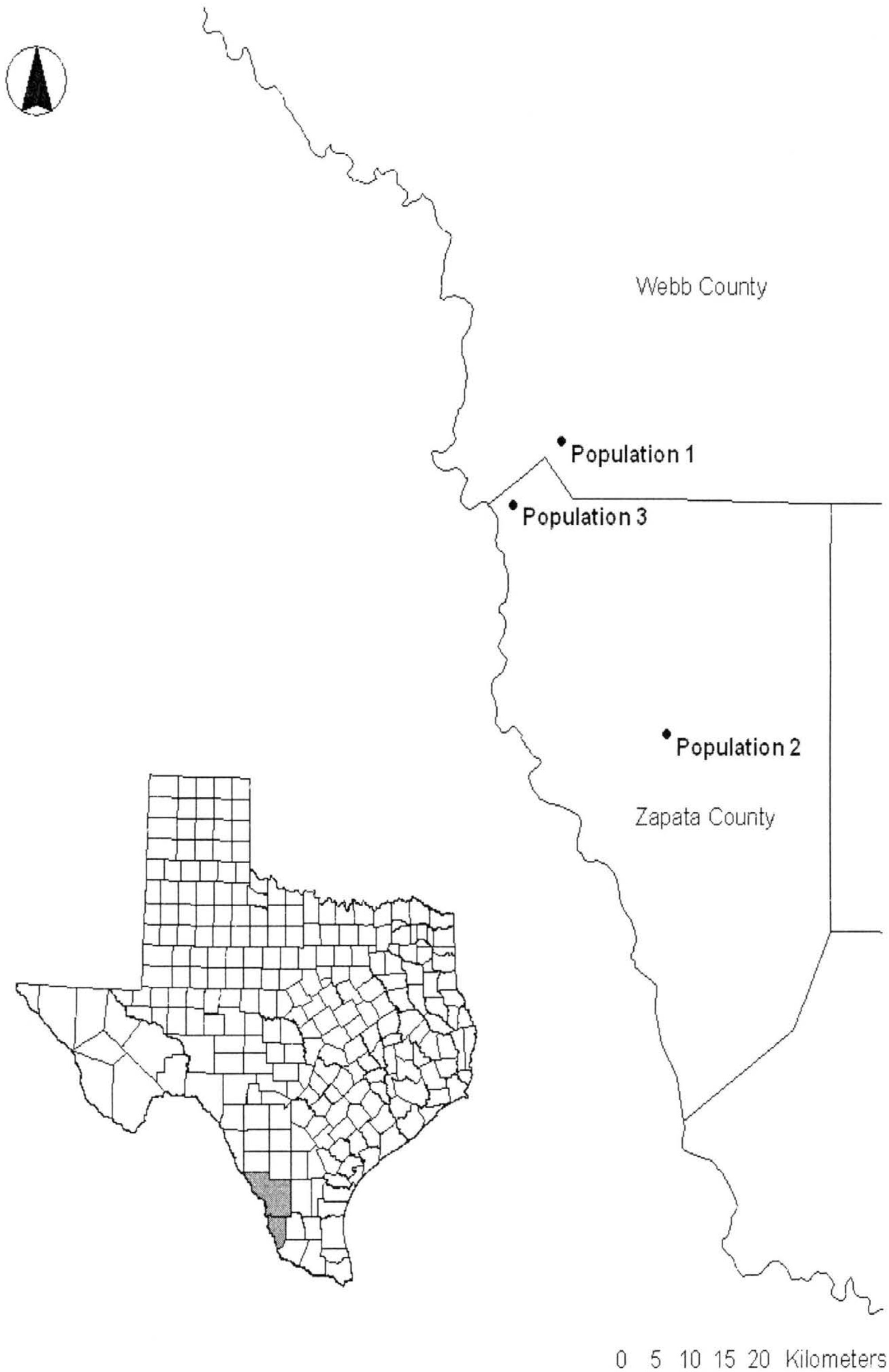


Figure 1. Map of Texas showing distribution of *T. tephroleuca*.

Population 1

Population 1
- 1.41 hect.

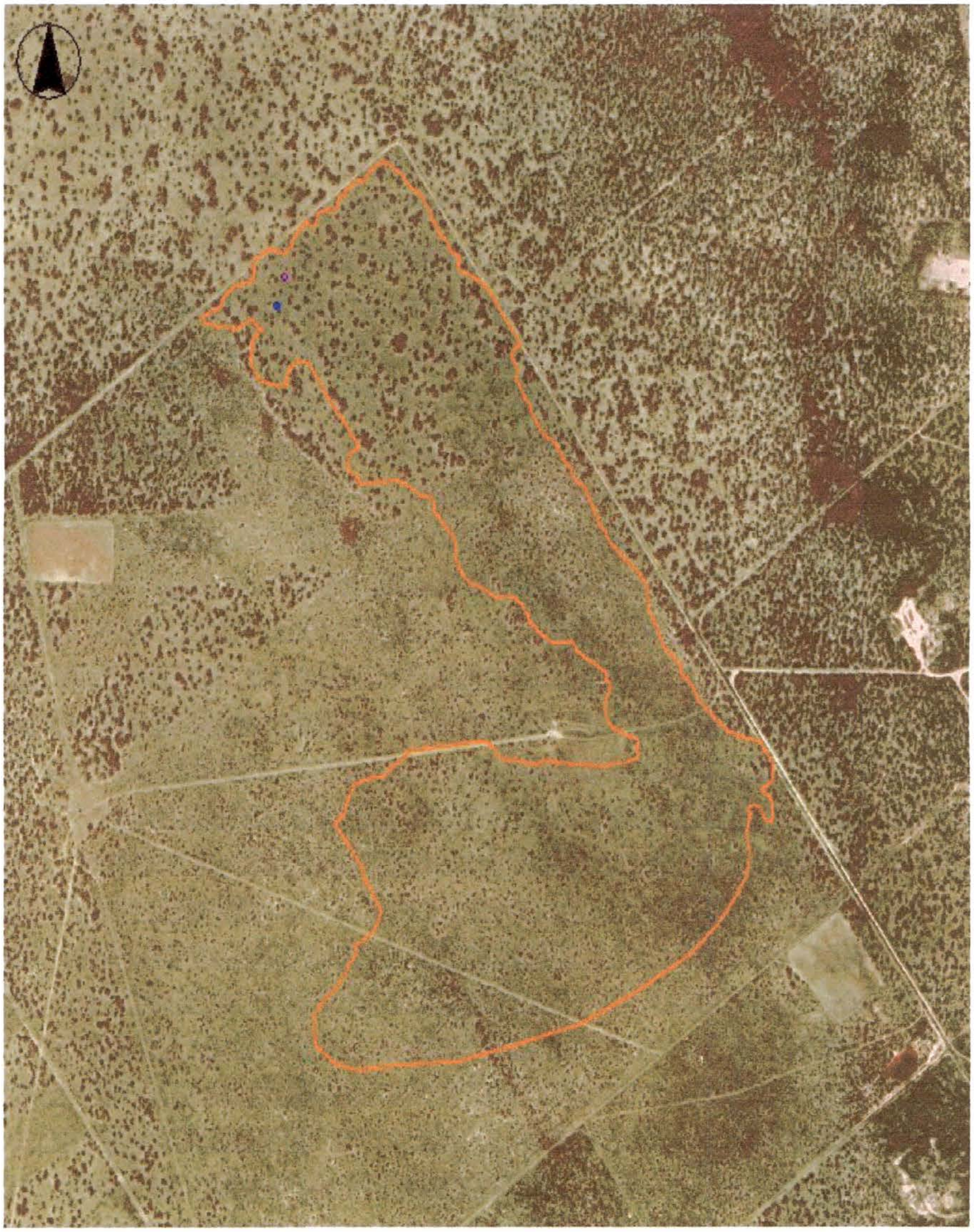
Transect
- 01
- 50

Figure 2. Delineation of Population 1 in Webb County.

0 50 100 150 200 250 Meters

Created by: SWTSU Biology Dept.
TP&WD
October 2001
Source: 1m Texas DOQQ's
for Blancas Creek S
Scale: 1:5,000

Population 2



Population 2
66.21 hect.
Transect
01
50

Figure 3. Delineation of Population 2 in Zapata County.

0 100 200 300 400 500 Meters

Created by: SWTSU Biology Dept.
TP&WD
October 2001
Source: 1m Texas DOQQ's
for Megotes Hill
Scale: 1:10,000

Population 3

Population 3
- 172.04 hect.
- Hwy 83
- Disturbance Site

Figure 4. Delineation of Population 3 in Zapata County.

0 250 500 750 Meters

Created by: SWTSU Biology Dept.
TP&WD
October 2001
Source: 1m Texas DOQQ's
for O'Keefe Lake
Scale: 1:12,000

Climate and Species Associated with the Habitat

The climate record for the region indicates an average precipitation of 51 cm per year (Bomar, 1983). Total precipitation recorded for the 1999–2000 study period was 58.3 cm from the Laredo station and 56.0 cm from the Zapata station. These 14-month totals indicate an average year of precipitation for the region. The majority of precipitation in Laredo fell between February and October with peaks in March and May (Figure 5). Precipitation primarily fell in Zapata between April and October, with peaks in May and October (Figure 6). Although precipitation in the region does not appear to be seasonal, November and December consistently had lower rainfall totals. The annual mean maximum temperature throughout the 1999–2000 study period was 30.7 °C for Laredo and 31.0 °C for Zapata. The annual mean minimum temperature was 17.5 °C for Laredo and 17.4 °C for Zapata.

Plants growing in association with *T. tephroleuca* at the three monitored population sites combined are listed in Table 1. This list is partial and represents plants collected within 1 m of a *T. tephroleuca* individual in the spring and summer of 1999 and 2000.

Table 1. Partial list of associated species collected at populations 1, 2 and 3.

Scientific Name	Common Name	Family Name
Froelichia floridana	Snake-cotton	Amaranthaceae
Cynanchum barbigerum var. *breviflorum*		Asclepiadaceae
Gaillardia pulchella	Firewheel	Asteraceae
Tetraneuris scaposa	Bitterweed	Asteraceae
Thymophylla pentachaeta var. *pentachaeta*	Parralena	Asteraceae
Tiquilia canescens	Oreja de Perro	Boraginaceae
Evolvulus sericeus		Convolvulaceae
Cassia pumilio	Dwarf Senna	Fabaceae
Caesalpinia caudata		Fabaceae
Sida helleri	Copper Sida	Malvaceae
Sida filicaulis		Malvaceae
Acalypha radians	Three-seeded Mercury	Euphorbiaceae
Schrankia latidens	Sensitive Brier	Fabaceae
Desmanthus velutinus		Fabaceae
Indigofera miniata var. *miniata*	Scarlet Pea	Fabaceae
Parkinsonia texana	Paloverde	Fabaceae
Prosopis glandulosa	Honey Mesquite	Fabaceae
Nama hispidum		Hydrophyllaceae
Krameria ramosissima	Calderona	Krameriaceae
Linum imbricatum	Tufted Flax	Linaceae
Allionia incarnata	Umbrella-wort	Nyctaginaceae
Portulaca mundula	Chisme	Portulacaceae
Castela texana	Allthorn Goatbush	Simaroubaceae
Hermannia texana		Sterculiaceae
Lantana horrida	Texas Lantana	Verbenaceae

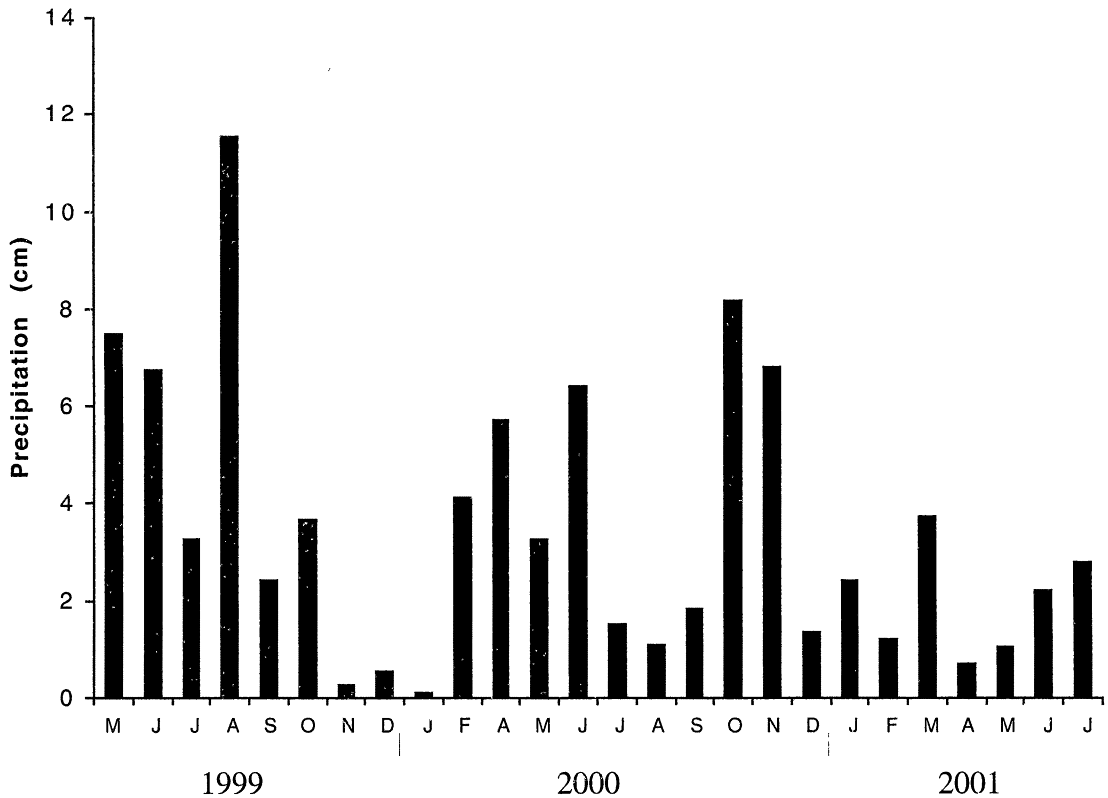


Figure 5. Monthly precipitation recorded in Laredo, Texas, from May 1999 to July 2001.

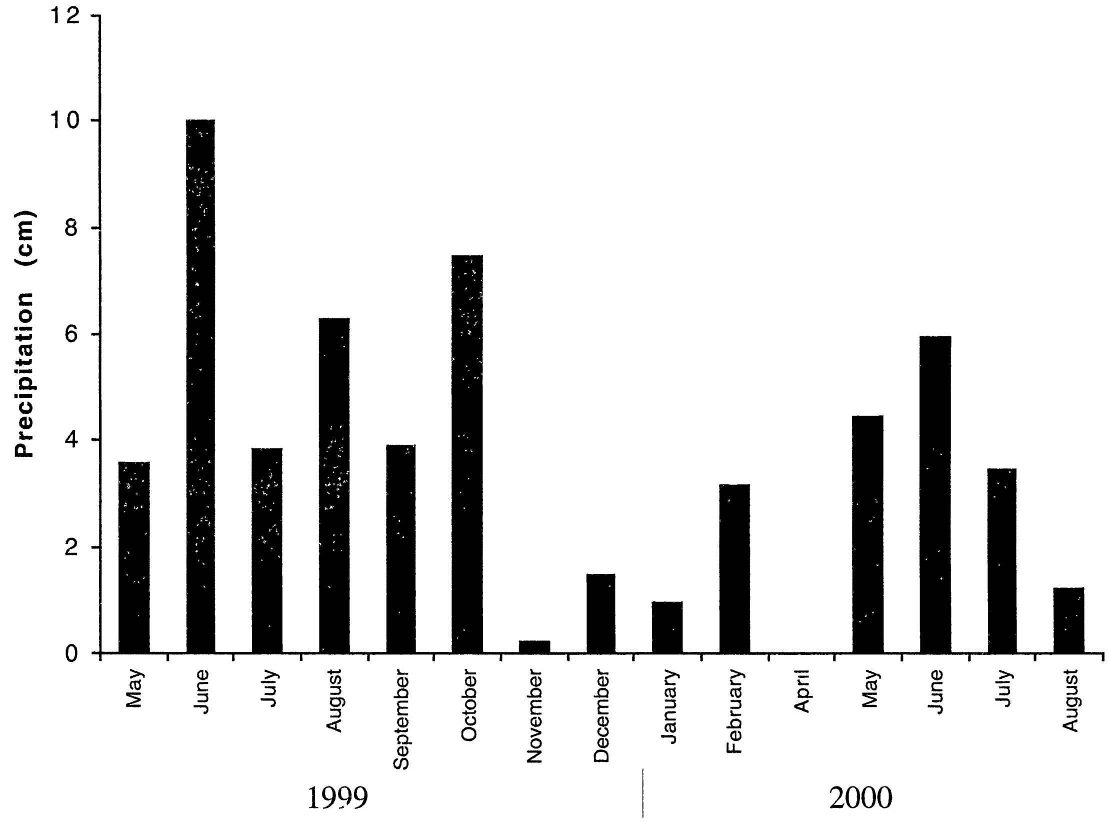


Figure 6. Monthly precipitation recorded in Zapata, Texas, between May 1999 and August 2000. No precipitation was recorded for April 2000.

Pollen Viability and Floral Visitors

Results of the pollen analysis are shown in Table 2. Pollen viability of cultivated plants (n=3 plants/389 pollen grains) averaged 73%. Viability of pollen taken from population 2 plants (n=3 plants/752 pollen grains) in 2000 averaged 82.5%. Viability of pollen taken from population 3 plants (n=3 plants/1422 pollen grains) in 2001 averaged 86%. Diurnal floral visitors observed and captured on *T. tephroleuca* inflorescences are listed in Table 3.

Breeding System Experiments

Results of the crossing experiments are shown in Table 4. No fruit set occurred in the autogamous crossing. The geitonogamous cross produced an achene set of 0.3%. The xenogamous crosses yielded an achene set of 88.8%

Achene Viability

Results of the tetrazolium staining are illustrated in Figure 7. Achenes collected in 1999 (n=200) had an average viability of 36.5%, while achenes collected in 2000 (n=200) had an average viability of 8.3%.

Table 2. Pollen viability in *T. tephroleuca*. Pollen analyzed in 1999 was collected from cultivated plants. Pollen analyzed in 2000 and 2001 was collected from plants in the field. All pollen was collected in June of the indicated year. Three plants were used for analysis from each population.

Year	Population	Percent viable +/- S.D.
1999	SWT	73.0 +/- 9.17
2000	2	82.5 +/- 2.12
2001	3	86.0 +/- 2.24

Table 3. List of insect visitors to *T. tephroleuca* flowers.

- Coleoptera
  - Buprestidae
    - *Acmaeodera mixta* (n=2)
- Diptera
  - Bombyliidae
    - 4 unidentified genera
- Hymenoptera
  - Apidae
    - *Anthophorula compactula* (n=2)
    - *Tetraloniella* sp. B (n=1)
  - Halictidae
    - *Augochlorella bracteata* (n=3)
  - Megachilidae
    - *Megachile (Argyropile)* aff. *parallela* (n=1)
    - *Ashmeadiella maxima* (n=3)
    - *Ashmeadiella meliloti* (n=1)
    - *Stelis* sp. (n=1)
  - Andrenidae
    - *Perdita (Pentaperdita) albovittata* (n=2)
  - Vespidae
    - *Parancistrocerus* sp. (n=1)
  - Sphecidae
    - *Glenostictia* sp. (n=2)
- Lepidoptera
  - Pyralidae
    - *Diastictis fracturalis* (n=1)

Table 4. Percent achene set in experimental crosses conducted to determine breeding system in *T. tephroleuca*. Crosses were conducted on plants cultivated at SWT. Unmanipulated flowers served as controls.

Cross	No. Flowers	No. Embryos	% Achene Set
Autogamous	50	0	0
Geitonogamous	2188	7	0.3
Xenogamous	348	309	88.8
Controls	200	0	0

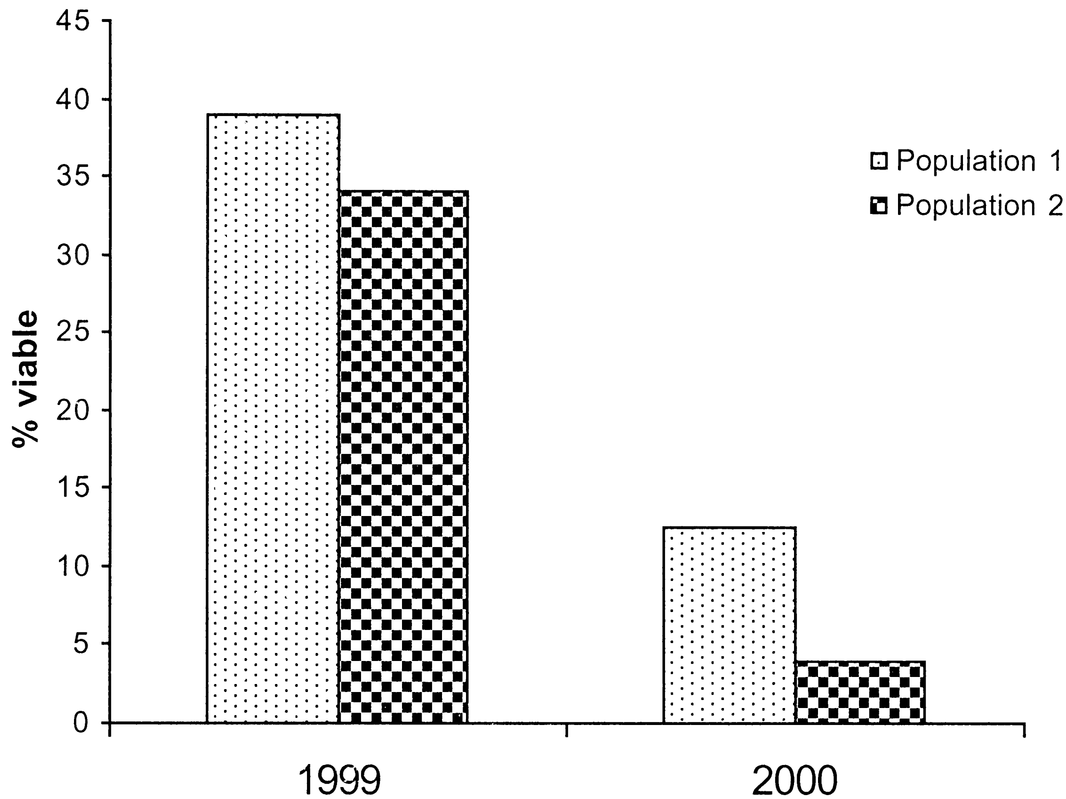


Figure 7. Percent achene viability of *T. tephroleuca* from populations 1 and 2.

Phenology, Population Density and Size Structure

In cultivated plants, canopy diameter increased over the year (Figure 8). Height increased for several months, then eventually decreased as plants became more prostrate (Figure 8). Initial flowering in plants occurred three months after germination. Plants steadily increased floral production as they aged, with a decline in January and February (Figure 9). Given a constant watering regime, such as in cultivated plants, *T. tephroleuca* exhibited steady growth and constant flowering. In the field, however, water appeared to be a limiting factor in reproduction. Results of phenological data indicated a peak in floral production between September to December with a decline in January-May (Figure 10). Flowering was observed in all months, however, with the exception of one. Differences in size structure of individuals, population density, recruitment and site characteristics were observed between the two populations. In population 2, recruitment within the transect was nonexistent, with no new seedlings or plant mortality over the year. Plant density in the population transect remained unchanged throughout the year at 0.6 plants/m^2 (Figure 11). Population 2 is dominated by large, mature individuals in an undisturbed site Plants at the end of monitoring had an average canopy diameter of 54.2 cm and an average height of 22.7 cm. (Figures 12, 13). In population 1, germination within the transect was prevalent, and was highest following months that experienced a high amount of precipitation (Figures 5, 14). Mortality, on the other hand, was temporally sporadic and was observed primarily for seedlings. Death of individuals appeared to be highest in the summer of 2000 (Figure 14), coinciding with low rainfall totals for those months (Figure 5). In addition, hoof prints were often visible in spots that were once occupied by plants, suggesting trampling or herbivory may also have

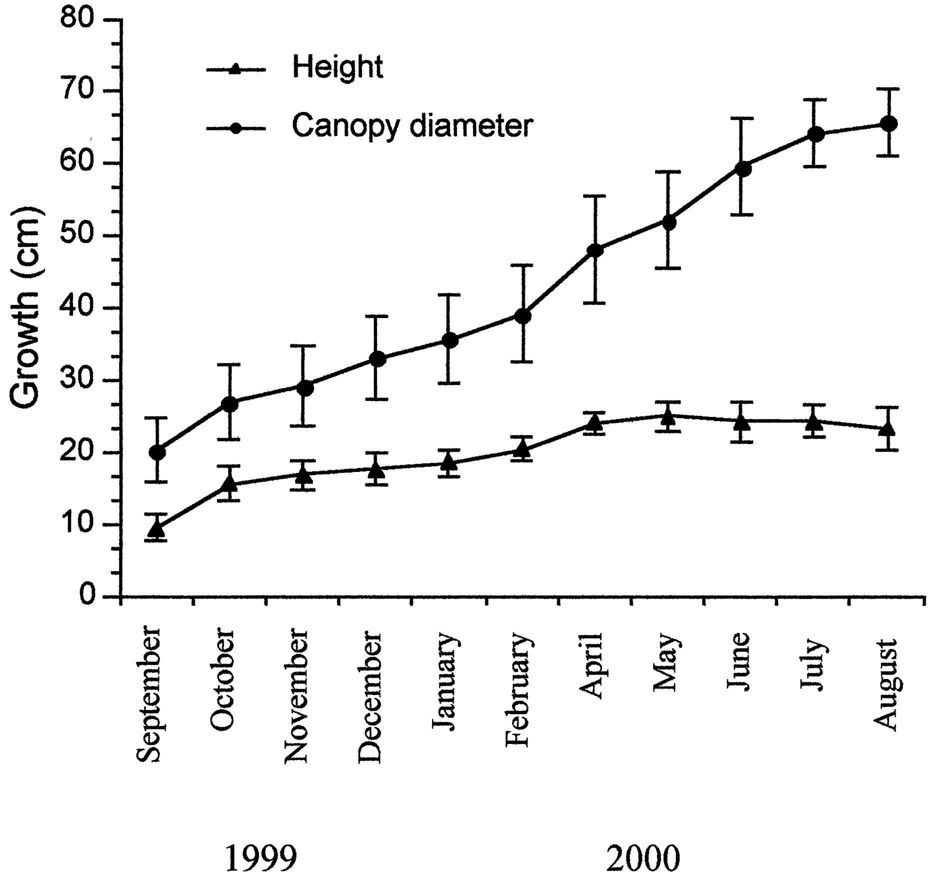


Figure 8. Average growth of plants (± S.E.) cultivated at SWT during 1999–2000 study period.

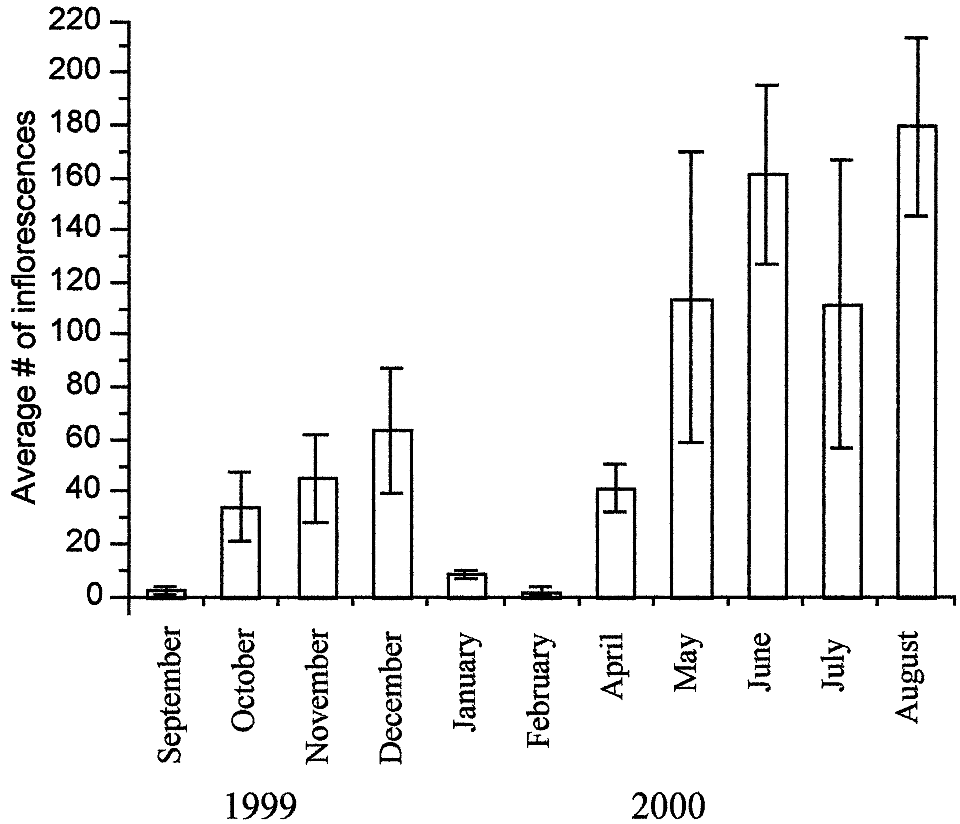


Figure 9. Average number of inflorescences (± S.E.) produced by plants cultivated at SWT during 1999–2000 study period.

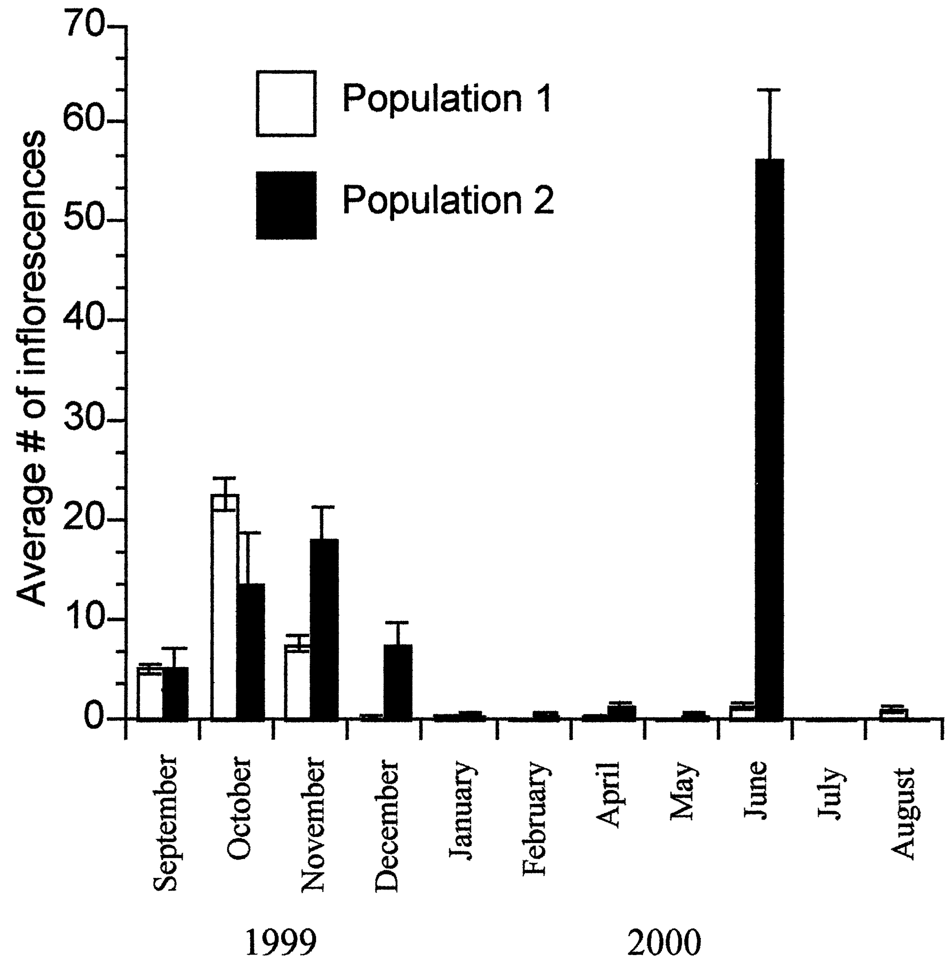


Figure 10. Average number of inflorescences (± S.E.) produced by plants along population transects during 1999–2000 study period.

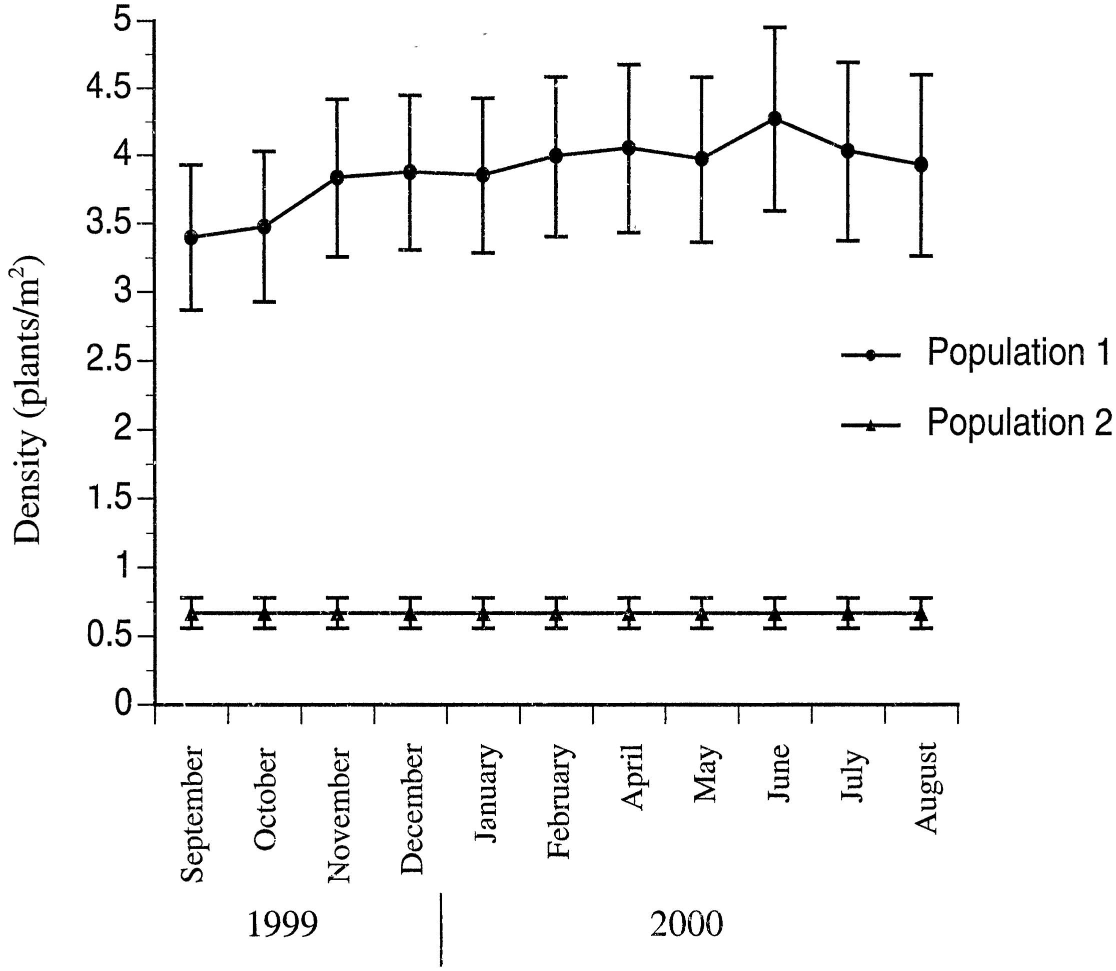


Figure 11. Density of *T. tephroleuca* individuals (± S.E.) monitored along transects. Population differences are significant through time ($P < .0001$, Repeated Measures ANOVA).

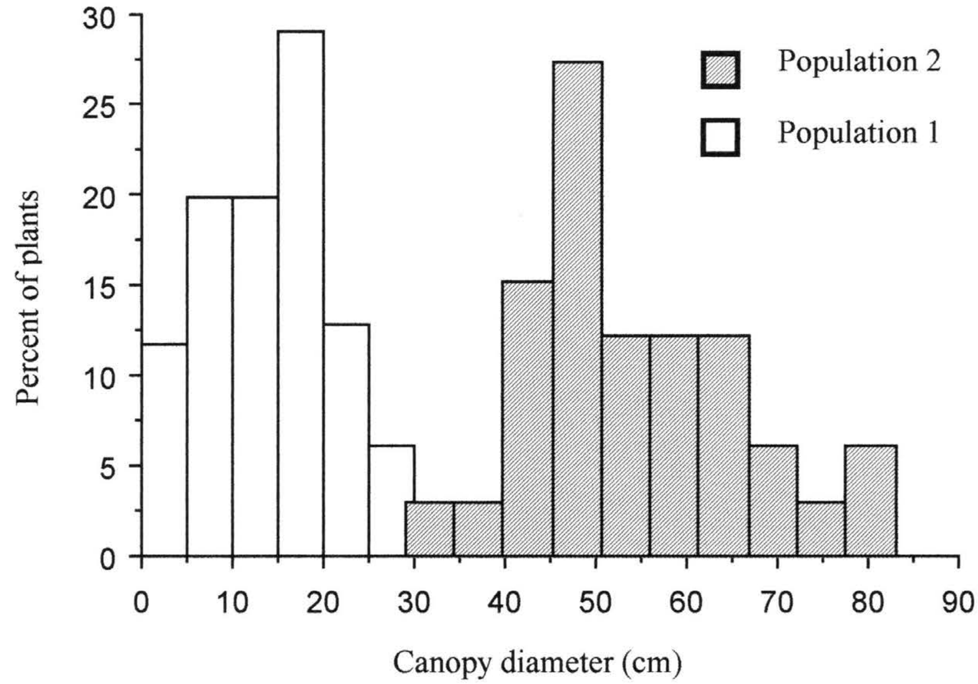


Figure 12. Histogram illustrating the canopy diameter size structure of individuals along the population transects in August 2000. Differences observed between the population means are significant (P < .0001, t-test).

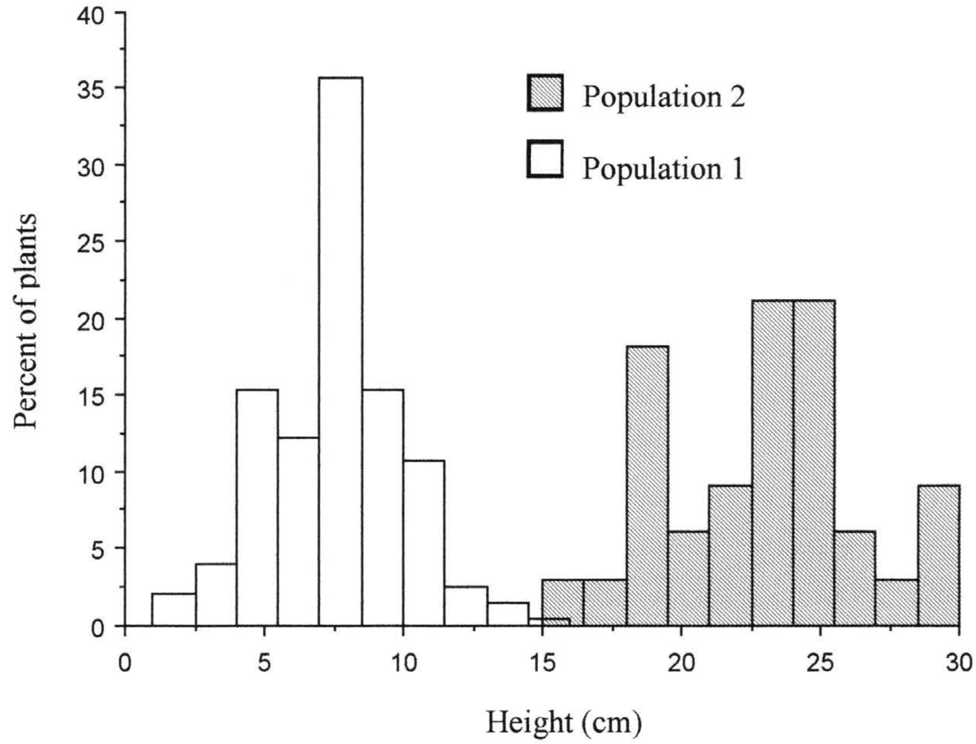


Figure 13. Histogram illustrating the height structure of individuals along the population transects in August 2000. Differences observed between the two population means are significant ($P < .0001$, t-test).

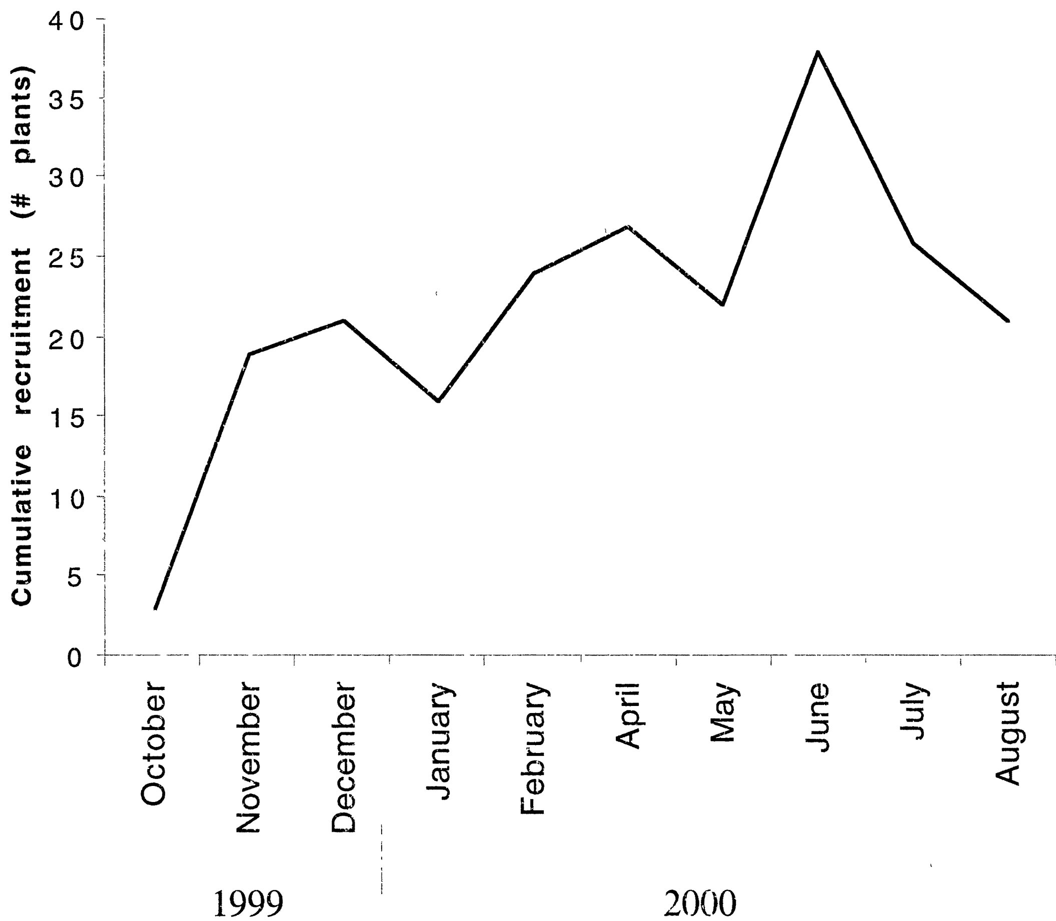


Figure 14. Cumulative recruitment of *T. tephroleuca* individuals into population 1 transect. Recruitment figured monthly as # germinated - # dead or missing. Population 2 had no recruitment over the course of the study period. Final results are significant ($P < .0001$, t-test).

contributed to the decline of individuals. Recruitment into the transect by the end of year was 21 plants and was significantly higher than that of population 2 (P <.0001, t-test). Plant density in population 1 increased from 3.4 plants per m^2 in September 1999 to 4.1 plants per m^2 in August 2000 (Figure 11), significantly higher than in population 2 (P < .0001, Repeated Measures ANOVA). The population is dominated by seedlings and small adults in a previously disturbed site. Plants at the end of monitoring had an average canopy diameter of 13.7 cm and an average height of 7.3 cm (Figures 12, 13). This was significantly lower than the final average canopy diameter and height for population 2 (P < .0001, t-test). The differences observed between the two populations were the basis for the disturbance experiment conducted at population 3.

Disturbance Experiment

Statistical analysis indicated that environmental parameters (elevation, light intensity, soil moisture, wind speed) were not significantly different across treatments (P > .05, ANOVA; Table 5). Because of the environmental homogeneity within the experimental site, analysis was therefore derived from a completely randomized design. All plants growing in the experimental plots prior to the disturbance were either killed immediately or eventually died as a result of the disturbance treatments. The number of reproductive individuals in the plots pre-disturbance was assumed to be correlated with the number of seedlings that emerged post-disturbance and were therefore used as a covariate in the final analysis.

Table 5. Average measurements ± S.D. of environmental parameters in control and treatment plots of the experimental site. No difference was observed for parameters between treatments (P > .05, ANOVA, Bonferonni Post Hoc).

	Elevation (m)	Light Intensity (lumens/m^2)	Soil Moisture (%)	Wind Speed (km/hr)
Control	8.7 +/- 0.9	2215 +/- 77.4	24.8 +/- 5.9	3.4 +/- 0.5
Blade	128.5 +/- 1.4	2204 +/- 76.7	30.8 +/- 4.9	3.5 +/- 0.3
Root-plow w/ buffel	127.9 +/- 1.5	2451 +/- 15.1	26.8 +/- 2.0	3.1 +/- 0.5
Root-plow	127.0 +/- 0.6	2419 +/- 91.4	28.3 +/- 10.2	2.7 +/- 0.2

T. tephroleuca density within treatment plots was monitored monthly from June 2000 to June 2001. Seedling emergence in all plots occurred between December 2000 and January 2001. However, no data were recorded until February. In the root-plow treatment, mean density declined 49.1% from 10.7 plants/m^2 in February to 5.4 plants/m^2 in June (Figure 15). In the same time period the number of plants/m^2 in the root-plow with buffelgrass treatment declined 58.1% from 6.2 to 2.6, while the number of plants/m^2 in the blade treatment declined 45.7% from 4.6 to 2.6. Buffelgrass was found growing within the seeded plots in moderate densities equivalent to the spring annuals. The control plots also declined in density by 78.4% from 3.7 plants/m^2 in February to 0.8 plants/m^2 in June. Treatment comparisons of seedling emergence in June indicated that mean density was significantly greater in root-plow plots than in control and root-plow with buffelgrass plots ($P < .05$, ANCOVA, Bonferroni Post Hoc; Figure 16). No significant effect of treatment on mortality was observed over time ($P > .05$, Repeated Measures ANOVA).

Root and shoot biomass weights of the sampled plants were significantly different between the root-plow and root-plow with buffelgrass treatments and the control and blade treatments ($P < .05$, ANOVA, Bonferroni Post Hoc; Figure 17). Results of the soil analysis are shown in Appendix 2. Significance of disturbance treatment effects on nutrient levels were not statistically determined due to lack of replication. Correlations between nutrient levels and disturbance type were therefore not determined.

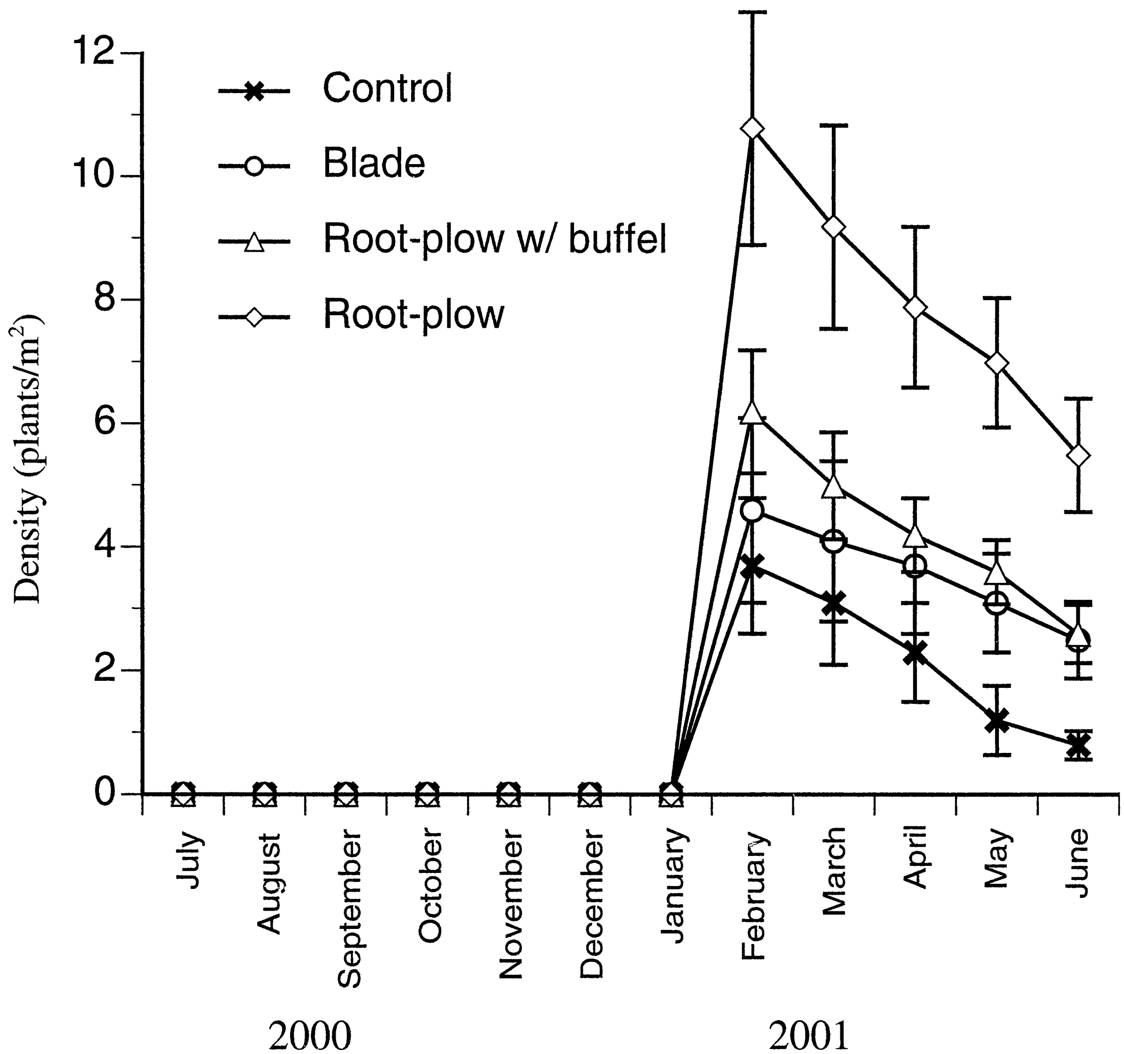


Figure 15. Comparison of disturbance treatment effects on *T. tephroleuca* density (± S.E.) over time. Plots disturbed once in June 2000 and monitored monthly from July 2000 to June 2001. All seedlings emerged between December 2000 and January 2001. No data were recorded until February 2001. No significant treatment effect on density decline was observed over time ($P > .05$, Repeated Measures ANOVA).

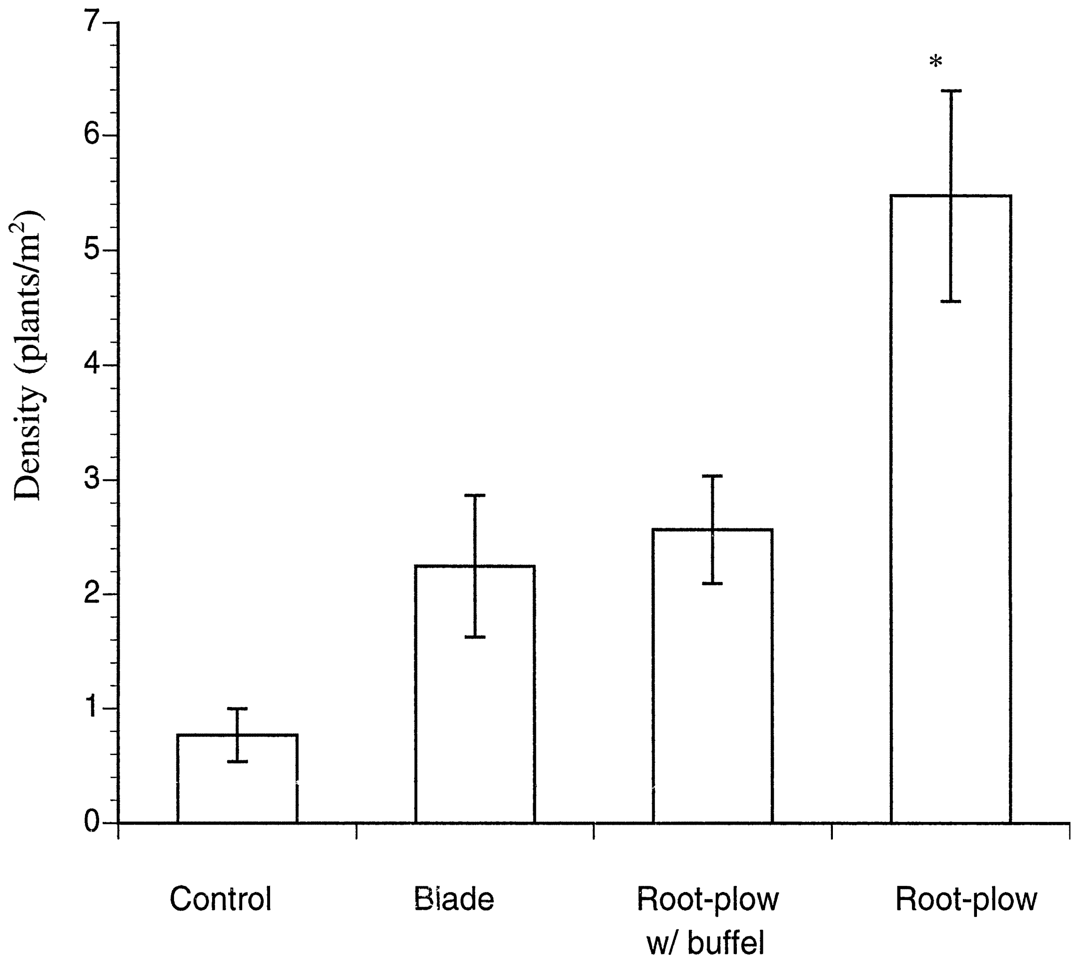


Figure 16. Comparison of disturbance treatment effects on *T. tephroleuca* final density (± S.E.). Asterisk indicates significance to controls and root-plow with buffelgrass plots ($P < .05$, ANCOVA, Bonferonni Post Hoc).

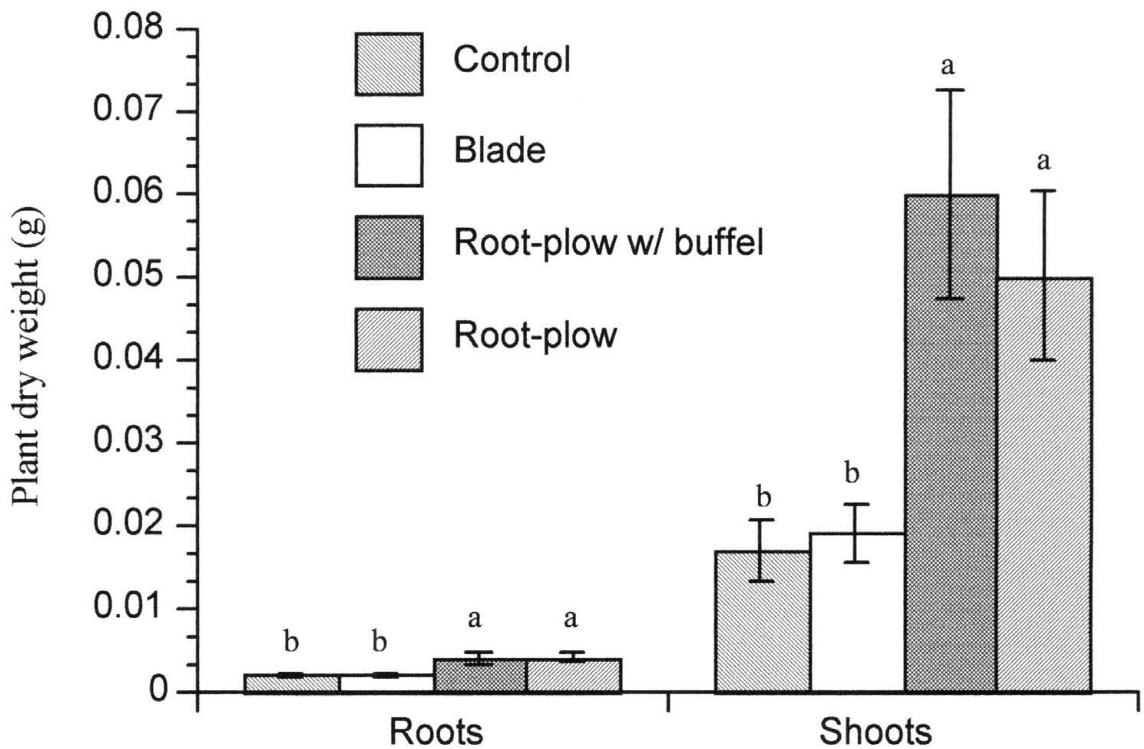


Figure 17. Comparison of disturbance treatment effects on root and shoot biomass accumulation (± S.E.) in *T. tephroleuca*. Different letters indicate significance between treatments for roots and shoots (P < .05, ANOVA, Bonferroni Post Hoc).

DISCUSSION

Comparisons of population level attributes, as well as the disturbance experiment indicated that *T. tephroleuca* responds positively to soil disturbance. In addition, life history data suggest a correlation between phenology and water availability. *Thymophylla tephroleuca* produces low numbers of viable achenes in the summer months. Achenes of *T. tephroleuca* can be shed at anytime throughout the year due to the correlation of precipitation and phenology. Seasonal achene viability differences are not known and should be investigated further.

It was determined that visitation to *T. tephroleuca* flowers was not exclusive to any one insect species, a feature common in the Asteraceae (Richards, 1986). Insect visitors included bees, wasps, beeflies, one moth and one beetle species. Bees in the order Megachilidae were the most numerous insects captured. Floral features in *T. tephroleuca* consistent with melittophily include a yellow inflorescence and a sweet odor (Faegri and van der Pijl, 1979).

Flowers of *T. tephroleuca* are protandrous. The stamens mature 2–4 days before the stigmas become receptive. This is a mechanism known to promote outcrossing in plants (Richards, 1986). Results of experimental crosses in *T. tephroleuca* indicate that plants experimentally crossed autogamously did not set fruit and plants crossed geitonogamously set few achenes. It has been shown that some geitonogamy will occur in plants with a large number of flowering ramets, as in *T. tephroleuca,* and that this method of self-incompatibility is often based on a multi-allelic sporophytic system common in the Asteraceae (Richards, 1986). Plants crossed xenogamously had 88.8% achene set, indicating that *T. tephroleuca* is primarily an outcrossing species.

Plant size, density and recruitment varied significantly between population 1 and 2. Population 2 was dominated by large, mature individuals in an undisturbed site. Seedling emergence and mortality were nonexistent and density remained unchanged. The large size structure of individuals within the population may have kept cattle trampling from killing whole plants. Likewise, the large taproot of these individuals may have prohibited desiccation during droughts. The population 1 site, however, had been disturbed within the past five years by a pipeline that had been installed by a gas company (pers. comm.). This population was dominated by a high density of seedlings and small adults. Seedling emergence exceeded mortality over the year, yielding a positive recruitment of individuals into the transect. Comparisons of density, recruitment, size structure and physical characteristics of the population 1 and 2 sites suggest that the soil disturbance had a positive effect on *T. tephroleuca* germination and establishment.

The effect of soil disturbance on increased seedling emergence has been demonstrated in various species and ecosystems (Armesto and Pickett, 1985; Chambers et al., 1990; Miao and Bazzaz, 1990; Parker et al., 1993). Physical disturbances create "safe sites" for germination by reducing competition for nutrients, light and moisture (Sousa, 1984). If the soil profile is plowed into a uniform layer (as in root-plowing), organic and mineral horizons may mix, resulting in increased soil aeration, microbial activity, mineralization rates and nutrient release (Carson and Pickett, 1990; Bazzaz, 1996), particularly nitrogen (Drew and Saker, 1975; Robertson, 1984; Vitousek and

Matson, 1985; Carson and Pickett, 1990). A further increase in nutrients may result when resident vegetation is incorporated into and decomposes in the soil as a result of the disturbance. The loss of vegetative cover from a disturbance will also decrease competition for soil moisture, as well as increase the amount of light incident on the soil surface.

Species responses to disturbance are typically associated with their life history and physiological traits, as well as the type and magnitude of the disturbance (Chambers 1995; McIntyre et al., 1995). Physiologically, species vary in dormancy and stratification cues based on adaptive responses to an ecosystem (Peterson and Bazzaz, 1978; Baskin and Baskin, 1992). *Thymophylla tephroleuca* has shown to increase germination from 23.8% without heat-stratification to 48.9% with heat-stratification (Poole, 1992). These data suggest that achenes heat-stratify during the summer months and emerge from the seed bank throughout the rest of the year depending on precipitation events, a phenomenon common for species adapted to semi-arid environments (Jordan and Nobel, 1979; Marone et al., 2000). This is consistent with population 1 transect data in which mortality greatly exceeded seedling emergence for the summer months. Germination was highest in November 1999 and between February and June 2000, following months in which precipitation was high. This also occurred in the disturbance plots in which no seedlings emerged until late fall following the disturbances in June. Precipitation data from Laredo (station closest to disturbance site) indicated a high amount of precipitation in the fall of 2000. The availability of soil moisture following the fall was likely responsible for the germination of plants in the winter.

Sousa (1984) stated that a disturbance may create a gap in the vegetation, but the specific characteristics of the gap will control what grows there. Subtle changes in the characteristics of the gap may produce radically different recruitment rates of target species. This is illustrated when comparing recruitment differences in the disturbance treatments. In the control plots where no plant biomass was removed and the soil was left intact, density decline was most pronounced at 78.4%. The final density of these plots was 0.8 plants/m^2. This is consistent with density values obtained from the population 2 transects in which no previous disturbance had occurred to the population site. In the root-plow with buffelgrass plots, density decline was 58.1% and final plant density was significantly lower than root-plow plots. It has been demonstrated that invasive, exotic plant species in other ecosystems have deleterious effects on native plant populations due to competition (Sher et al., 2000; Durand and Goldstein, 2001). Although this was not tested for in this study, its possible that buffelgrass had the same competitive effects on *T. tephroleuca* recruitment. Blading was determined to have no effect on increased recruitment of *T. tephroleuca.* Initial germination in the bladed plots was lower than both root-plow and root-plow with buffelgrass treatments. When blading, the bulldozer attachment had the effect of removing the top 3-5 cm of soil in addition to the resident vegetation. This possibly resulted in the removal of much of the seed bank necessary for germination following a disturbance. In addition, soils in the bladed plots were more compacted than those in the root-plow plots. Tilled soils have shown to increase soil moisture relative to compacted soils (Potvin, 1993; Voorhees, 1977). Tillage loosens the soil and increases pore space, making water infiltration to dormant seeds more efficient. Thus, the compacted soil in addition to the reduced seed bank may have interacted to produce fewer seedlings in the bladed plots. The decline of individuals in these plots, however, was the lowest at 45.7 %. In all treatments, a gap was created in the vegetation. Only in the root-plow plots, however, were the characteristics of the gap such that initial germination and subsequent recruitment were high. Density decline was 49.1% to 5.4 plants/m^2 at the end of monitoring. This density is consistent with results obtained from the population 1 transect in which a previous disturbance had occurred to the population site.

Results of this study can be used to formulate land management programs so that landowners that utilize root-plowing, blading or buffelgrass planting can be informed of its effects on ashy dogweed populations that reside on their ranches.

Appendix 1. Design of disturbance experiment illustrating pseudoreplication.

Control	Blade	Root-plow w/ buffelgrass	Root-plow
(n=20)	(n=20)	(n=20)	(n=20)

Appendix 2. Soil nutrient concentrations and pH values in disturbance treatment plots.

	Control	Blade	Root-plow w/ buffelgrass	Root-plow
pH	7.8	6.7	6.8	8.1
		Nutrient concentrations (ppm)		
N	5	13	15	7
P	3	2	1	1
K	153	169	235	179
Ca	1375	1082	873	1069
Mg	78	88	111	115

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VITA

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