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Herbivory and the Population Biology of a Rare Annual Plant, the Bracted Twistflower (*Streptanthus bracteatus*)

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Herbivory and the Population Biology of a Rare Annual Plant, the Bracted Twistflower (*Streptanthus bracteatus*)

by

David Benjamin Zippin, B.A.

Dissertation

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Dedication

To my parents, Calvin and Patricia Zippin, with the deepest love and gratitude.

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Herbivory and the Population Biology of a Rare Annual Plant, the Bracted Twistflower (*Streptanthus bracteatus*)

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I investigate herbivory and habitat specificity as potential causes of the rarity of an annual plant, the bracted twistflower (*Streptanthus bracteatus*; Brassicaceae). First, I conducted a two-year observational and experimental study of five natural populations. I found that at some sites plants eaten by insects have significantly lower rates of stem elongation, survival, and seed production than uneaten plants. Plants eaten by white-tailed deer experience even larger reductions in these parameters at some sites.

To investigate the combined effects of insects and deer, I planted a population of *S. bracteatus* in habitat similar to that of natural populations. Over a two-year period, deer and insects ate few of these plants because they were much smaller than plants at natural populations. However, caged plants had significantly

greater survival than uncaged plants. This suggests that deer, but not insects, can have a negative effect on *S. bracteatus* populations at low rates of herbivory.

Streptanthus bracteatus may have specific woodland habitat requirements that account for its rarity. Observational data suggest that this species also favors a grassland habitat but is excluded from it by herbivory or competition. However, in a two-year experimental study, plants in a grassland in which herbivory and competition were reduced had significantly lower survival than plants in a woodland. Thus grassland is not a favorable habitat for *S. bracteatus*, at least at this site.

Finally, I predict the effect of deer on the population growth rate of *Streptanthus bracteatus*. I constructed matrix models from observational and experimental data collected during three years at natural populations and a planted seed bank. Populations at two of three sites may be increasing in size even in the presence of deer. Excluding deer may improve the population persistence time of one of the three populations studied. Most populations of *S. bracteatus* have lower rates of deer herbivory than at the three sites for which predictive models were developed. Therefore, deer exclusion will probably improve the population size of this species only at some sites. Habitat destruction poses the greatest threat to the persistence of this species.

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Chapter 1: The Effects of White-Tailed Deer (*Odocoileus virginianus*) on Plant Performance, Populations, and Communities in North America[1]

ABSTRACT

I review the literature on the effects of white-tailed deer on plant communities in North America. The high density of this selective herbivore suggests that it has large effects on plant populations and changes plant community composition and structure. Deer often reduce the growth or change the morphology of heavily browsed plants. Such effects are not always correlated with reductions in survival or fecundity. Moreover, exclosure experiments describe many species that experience no change or an increase in abundance following deer exclusion. Deer affect plant community composition, sometimes causing a shift in dominance patterns. A gap in the smallest size class of palatable trees is often attributed to deer. However, few studies show a clear causal link between deer herbivory and this size class gap. Experimental data indicate that large negative effects of deer are restricted to particular sites and to particular taxa. However, because of the methodological constraints and biases of many studies, the hypothesis that deer effects are substantial cannot be rejected.

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[1] This chapter was co-written with F. Leland Russell

INTRODUCTION

White-tailed deer in North America may have major effects on individual plants, populations, communities, and ecosystem properties, for several reasons. First, white-tailed deer occur throughout most of the United States and southern Canada east of the Rocky Mountains. They are also the most abundant wild ungulate on the continent (Gill 1988). Moreover, white-tailed deer now occur in some regions at densities considered to be two to four times higher than before European settlement (Behrend et al. 1970; Alverson et al. 1988; Anderson 1994; Van Deelen et al. 1996).

Second, white-tailed deer populations have been this high only recently. By the late 19th and early 20th century, due primarily to widespread and unrestricted hunting, populations in North America dropped to approximately 2% of pre-European settlement levels (McCabe and McCabe 1984). Moreover, their range contracted dramatically, causing extirpation from many states. Beginning in the 1930's and 40's, programs were established to improve deer populations that included predator elimination and strict hunting restrictions. As a result, and because of concurrent changes in land use, white-tailed deer began to increase in abundance and expand their range (Leopold 1943; Doman and Rasmussen 1944; Cook 1945; Leopold et al. 1947; Taylor and Hahn 1947; Banfield 1949; Mohler et al. 1951; Schorger 1953; Habeck and Curtis 1959; Hough 1965; Behrend et al. 1970; Gill 1988). Today, white-tailed deer have recolonized or have been translocated into their entire former range. They are even slowly expanding westward into formerly unoccupied areas (Gill 1988).

Finally, white-tailed deer may have large effects on plants because they are selective feeders (e.g., Petrides 1941; Smith 1949; Webb 1959; McMahan 1964; Allen 1968; Healy 1971; Telfer 1972; Cross 1984; Medcraft and Clark 1986). Thus they are expected to impact only certain species, potentially leading to dramatic changes to plant communities and ecosystem properties.

There have been many observational studies that claim dramatic effects of deer on plants and plant communities (Beals et al. 1960; Hough 1965; Behrend et al. 1970; Anderson and Louks 1979; Whitney 1984; Frelich and Lorimer 1985; Anderson and Katz 1993). The results of these studies require confirmation with experimental work from a variety of habitats throughout the range of white-tailed deer. I provide a review of such studies here.

There have been many regional reviews of the effect of white-tailed deer on plants (Neils et al. 1956; Marquis and Brenneman 1981; Alverson et al. 1988; Witmer and deCalesta 1992), some of which have generated controversy (Alverson et al. 1988; Mladenoff and Stearns 1993). A wider, continental perspective may resolve some of the issues and clarify what research is needed. For example, recent regional reviews suggest that white-tailed deer have widespread negative effects on plant growth (Marquis 1981; Marquis and Brenneman 1981; Alverson et al. 1988; Van Auken 1993). In this review, I did not find substantial evidence to support this conclusion. Instead, negative effects of deer appear to be localized and restricted only to certain plant taxa. Moreover, in several exclosure studies, many plants either did not respond or responded positively to the exclusion of deer.

METHODS

I limit this review geographically to the effects of white-tailed deer within the United States and Canada. However, because of inflated populations of other deer species in Europe (Gill 1988; Clutton-Brock and Albon 1992), these results may have application elsewhere. Hereafter I use the term "deer" to refer only to *Odocoileus virginianus*. I consider data on the effects of other North American ungulates such as mule deer (*O. hemionus*), pronghorn (*Antilocapra americana*), moose (*Alces alces*), and elk (*Cervus elaphus*) only in cases when data on white-tailed deer effects are absent, scarce, or inadequate. In such cases priority is given to data regarding species in the order listed above. Effects of mule deer and pronghorn are often considered jointly because they could not be separated in field experiments. Furthermore, data on the effects of white-tailed deer in regions outside of North America are considered only generally.

I concentrated my search on six primary types of published evidence, each of which I classified into direct (i.e., stronger) and indirect (i.e., weaker) forms of evidence. Direct evidence of deer effects include exclosure studies and observational studies, both at the single-species and community levels. Indirect evidence consists primarily of clipping studies (i.e., simulated deer herbivory) but also includes studies of diet and habitat preference. I consider clipping studies to be indirect evidence because they often fail to mimic the effects of herbivores in nature (Strauss 1988; Baldwin 1990; Krause and Raffa 1992). With a few exceptions, I have excluded from this review data that are published in the non-peer reviewed gray literature, primarily in the form of reports.

Much of the literature on the effects of white-tailed deer is widely dispersed in the forestry and wildlife management journals and addresses questions not immediately of interest to plant ecologists. By re-interpreting much of these data in light of the effects of white-tailed deer on plants, plant communities, and ecosystems, I hope to bring these important sources to the forefront. I gathered references by searching electronic databases. In cases where a journal had a high frequency of relevant papers (e.g., *Journal of Wildlife Management, Journal of Forestry, Journal of Mammalogy*), I searched the entire journal from 1930 to the present.

There is one danger in a review such as this that does not employ a quantitative meta–analysis. By simply tallying, or "vote-counting", conclusions are biased towards finding no effect by treating studies with higher statistical power (i.e., those more likely to detect significance) equal to those of lower power (Gurevitch and Hedges 1993). In order to account for these factors, I considered both the potential magnitude of the effects and the level of statistical power in the experimental design in my subjective weighting of results.

I organize the discussion of this review hierarchically by the level at which the effects may occur: on individuals, populations, communities, and ecosystems. For each level, I address the following questions: Does an effect exist? if so, what is the direction and magnitude of the effect? what is the variation in time and space of the effect? are there consistent patterns of the effect across taxa or functional groups? and finally, what is the strength of the evidence for these patterns? When necessary, I separate the discussion into effects on different functional groups, primarily herbs, shrubs, and trees.

RESULTS

Effects on Individuals and Populations

Effects on plant growth, morphology, and development

In the short term, growth rates of most species appear to be either unaffected by deer herbivory or show positive responses. For example, despite heavy browsing, two *Acer* species showed little to no change in overall twig or stem length relative to controls (Krefting et al. 1966; Jacobs 1969). At one well-studied site in New York, plant height was unaffected by herbivory for as many taxa as it was negatively effected (Webb et al. 1956; Tierson et al. 1966). Repeated browsing can sometimes increase stem elongation, producing an above-ground growth response that is can be fully compensatory or even greater than controls. For example, simulated heavy winter browsing (75% of new growth removed) for two seasons stimulated growth in *Acer rubrum*, producing greater biomass and shoot lengths in clipped plants than in controls (Canham et al. 1994).

Experimental evidence of the positive effects of deer herbivory on the growth of trees, shrubs, and herbs is presented in Table 1.1. In woody plants, stem diameter may also increase as a result of deer browsing (Webb et al. 1956; Jacobs 1969). This added radial growth may eventually hide morphological changes such as crooks that are associated with the regrowth of terminal stems following herbivory. In addition, root/shoot ratios are expected to increase in many species as below-ground resources are mobilized to replace lost tissue (Crouch 1966).

By contrast, for many tree seedlings, field studies consistently demonstrate that repeated deer browsing can retard or stop growth above-ground for several years. Successive removal of terminal buds can cause individuals to remain in the understory (Krefting and Stoeckeler 1953; Marshall et al. 1955; Switzenberg et al. 1955; Tierson et al. 1966; Harlow and Downing 1970; Ross et al. 1970; Marquis and Grisez 1978; Tilghman 1989; Trumble et al. 1989; Inouye et al. 1994; McLaren 1996). However, even in the heavy browse conditions of deer yards, where deer congregate in very high densities (> 100 deer km^{-2}) in winter, stems are capable of growing out of reach of deer in less than 10 years (Switzenberg et al. 1955). There may even be a threshold height for some species below which deer do not browse plants (Trumble et al. 1989).

Often one of the hallmarks of mammalian herbivory on woody plants is a dramatic change in plant morphology (Crawley 1983). The most common of these changes is removal of apical dominance and the production of abundant lateral stems. Plants browsed by deer often have greater stem density than unbrowsed controls (Marshall et al. 1955; Switzenberg et al. 1955; Tierson et al. 1966; Jacobs 1969; Paige and Whitham 1987; Paige 1992). The frequency of browsing is probably more important than its intensity in determining such changes (Marshall et al. 1955), because the number of sites at which meristematic tissue can form along the stem increases as stem number increases.

A common observation in areas of high deer density is a distinctive "browse line" below which deer are able to crop stems and twigs of tree saplings and shrubs (e.g., Adams 1949; Aldous 1952; Marshall et al. 1955; Neils et al. 1956; Webb et al. 1956; Halls and Crawford 1960; Trumble et al. 1989). Where herbivore pressure is high, all woody tissue may be removed below this line. This creates a barren understory with an overstory that is neatly trimmed up to the level at which deer can reach. A browse line is typically 2.5m high but may be lower in drier habitats where deer are smaller in stature. For example, deer on the Edwards Plateau of Texas have a mean body weight that is typically < 50% of deer in more northern latitudes (Teer et al. 1965). Deer effects on other aspects of plant morphology such as internode length, branching pattern, leaf size and shape, and allocation to leaf vs. woody tissue have not been documented. Studies from other animal-plant systems indicate that many of these responses are correlated with effects on plant performance and competitive ability (Crawley 1983; Huntly 1991).

Deer browsing can also cause phenological changes in plants. Deer herbivory can alter normal plant development by delaying events such as anthesis, fruit maturation, or seed set (Gedge and Maun 1994). The timing of herbivory may be the most important determinant of the magnitude of these effects. If herbivory occurs later in the season a plant may not be able to reproduce at all. On the other hand, early-season herbivory may have no measurable effect on phenology (Gedge and Maun 1992, 1994). Delays in flower production, if they are of sufficient duration, may even preclude or reduce pollinator visits and thus limit pollination success (Allison 1990a).

Effects on mortality and fecundity

The ultimate test of the effects of deer on individuals is in terms of their impact on fitness. Because plant fitness will vary so widely in response to herbivory, it is useful to decompose fitness into two general categories, survival and fecundity. It is also useful to consider separately the effects of deer on different plant life stages and life forms. I begin the examination of the effects of deer herbivory on fitness with granivory, or herbivory at the seed stage. Later, I consider fitness effects on tree seedlings, other woody plants, and herbs. I conclude this section by discussing some of the common pitfalls in addressing deer effects of this type.

Despite the importance of seeds to deer nutrition, the limited data available suggest that deer impact survival and germination at this stage only minimally (McCarthy 1994). For example, acorns of *Quercus* sp. constitute a significant portion of deer diets during the autumn (McCaffery et al. 1974; Harlow et al. 1975; McCullough 1985; Weckerly and Nelson 1990). Despite this, studies in the Shenandoah Valley of Virginia (McShea and Schwede 1993) and of mule deer in California oak woodlands (Griffin 1976; Borchert et al. 1989) suggest that *Odocoileus* affects the mortality rate of acorns very little relative to other predators, especially gophers and cucurlionid beetles. In coastal California, mule deer even facilitate the germination of the South African succulent, *Carpobrotus edulis*, more than any other seed-eating mammal. Mule deer disperse seeds into favorable recent burn habitats because seed viability is only minimally effected by gut passage (D'Antonio 1990; D'Antonio et al. 1993).

Most research on the effects of deer on woody plant mortality focuses on the seedling (or sapling for trees) stage, and for good reason. For most woody plants, this is the stage at which all above-ground biomass is within the reach of deer. Moreover, a larger proportion of plant biomass is palatable to deer at this stage. The effects of deer on seedling mortality appear to vary in a complex way according to the timing, frequency, and intensity of the herbivory. This is consistent with what is known about the effects of other herbivores on plant mortality and fecundity (Crawley 1983; Huntly 1991). For example, in an experiment with three species of hardwoods in New York, *Acer rubrum*, *Prunus serotina*, and *Fraxinus americana*, the frequency of simulated browsing (once or twice per year) did not affect mortality (Canham et al. 1994). Instead, the timing of herbivory was the critical factor. Light and heavy winter clipping (25 and 75% of new growth removed, respectively) had little to no effect on the mortality of these species. On the other hand, simulated heavy summer browsing resulted in a two-fold increase in mortality of *Acer* and *Prunus* and a five-fold mortality increase in *Fraxinus* when compared to winter browsing or unclipped controls. Because heavy summer deer browsing on these species is uncommon (Canham et al. 1994), these data suggest that the effect of deer herbivory is disproportionately larger than its frequency might suggest.

Other studies show simple linear negative effects on survivorship with increasing levels of clipping intensity (Krefting and Stoeckeler 1953). Low to moderate levels of simulated deer herbivory often have no effect on either seedling or adult mortality (Krefting and Stoeckeler 1953; Crouch 1966; Tilghman 1989;

Strauss 1991; Inouye et al. 1994; Singer and Renkin 1995; McLaren 1996). Observational studies suggest a link between deer herbivory and seedling survivorship. These studies document fewer tree seedlings of certain species in areas of high deer density than in similar habitats with a low deer density (Hough 1965; Anderson and Louks 1979; Frelich and Lorimer 1985; Balgooyen and Waller 1995). Such data are useful for generating hypotheses about the causes of these patterns. But these data do not provide strong evidence for widespread negative effects of deer because other explanations such as differences in light or nutrient availability are also consistent with these observations.

Effects on shrub mortality vary widely and appear to be species– and site–specific. For example, cover and biomass of *Artemisia tridentata* was dramatically reduced by elk, pronghorn, and mule deer in Yellowstone National Park (Singer and Renkin 1995). This appeared to be due more to increased seedling mortality rather than adult mortality. Several workers have documented declines in *Rubus* sp. abundance where deer densities are high (Harlow and Downing 1970; Marquis and Grisez 1978; Trumble et al. 1989). Further experiments are needed to determine the magnitude of deer effects on shrub mortality.

Many workers have suggested that deer can have large effects on the survival of herbaceous plants. All of the above-ground tissue of herbs is accessible and potentially palatable. Moreover, they are less able to recover from herbivory than shrubs or trees (e.g., Miller et al. 1992; Anderson 1994; Balgooyen and Waller 1995). During the spring and summer deer often rely on forbs for a significant portion of their diets (Dunkenson 1955; Halls and Crawford 1960; Kohn and Mooty 1971; Korschgen et al. 1980; Crawford 1982; Irwin 1985; McCullough 1985; Case and McCullough 1987; Weckerly and Nelson 1990). At one extreme, in South Texas during the summer, herbs may constitute 90% of deer diets (Chamrad and Box 1968).

The limited data available suggest that large impacts on herbs from deer occur in only a minority of cases. For example, in a study of old field herbs only one species experienced negative effects on cover (assumed to be closely related to mortality) while twenty species were unchanged and four species were affected positively (Bowers 1993). In a New York deciduous forest, the density and cover of six herbaceous species were negatively affected by deer but six were positively affected (Webb et al. 1956). Moreover, palatable and unpalatable species showed each type of response. In both instances, deer were probably causing a combination of direct effects on survival and fecundity and indirect interspecific interactions such as competition. For other species, deer herbivory affects mortality only at high simulated browsing intensities, similar in intensity to that experienced by some wild plants (Gedge and Maun 1992, 1994).

Deer effects on plant fecundity are similarly complex and species-specific, and depend on plant vigor, the timing of herbivory, and the type of herbivory. Such effects are most readily studied in annual herbs, although examples are few. In the annual *Corispermum hyssopifolium*, simulated deer browsing resulted in reductions in fecundity only after clipping late in the season (Gedge and Maun 1992, 1994). In contrast, another dune species, *Cakile edentula*, showed interactive effects of intensity and timing on fecundity. Reductions in fruit number were proportional to the clipping intensity when performed early in the season but effects were greatly magnified when clipping was performed late in the season just before anthesis. Natural and simulated browsing by mule deer in northern California on the perennial herb *Sanicula arctopoides* had negative effects on seed production only at severe clipping intensities or after clipping treatments applied much later than natural herbivory typically occurred (Lowenberg 1994). At low to moderate levels of herbivory, plants may be able to recover completely because of reductions in competition from neighbors that are also browsed. In the fewer studies in which it was measured, seed mass was unaffected by clipping (Gedge and Maun 1992, 1994; Lowenberg 1994). It is unknown what effects deer herbivory has on seed viability, an important determinant of plant fitness.

The effect of deer herbivory on the lifetime fecundity of woody plants has been difficult to quantify because of the long lifespan of many woody species. Effects manifest in a single year may be insignificant when compared with reproductive success during other years (e.g., in a wet year with low browsing pressure). This may be especially true for masting species such as oaks. Indeed, it took up to five years for significant negative effects of deer to be evident on fruit production in the shrub *Taxus canadensis* in Wisconsin (Allison 1990b). In the Great Basin, simulated winter mule deer and elk herbivory resulted in negative effects on flowering stem production only in one of two dominant shrubs, *Artemisia tridentata*, and only then at the greatest of two clipping intensities (Bilbrough and Richards 1993). But effects on this species appear site-specific. There was no effect on flower number in *A. tridentata* from herbivory by mule deer, pronghorn, and elk in Yellowstone, despite dramatic reductions in plant biomass (Singer and Renkin 1995). There is evidence that, in unique cases, ungulate herbivory may enhance plant fitness (Paige and Whitham 1987; Bergelson and Crawley 1992; Paige 1992).

Because it is difficult to measure the effects of deer on the fecundity of perennial plants, one might be tempted to infer such patterns using data on aboveground growth responses. Indeed, this is often done. However, because herbivory can strongly affect plant resource allocation (Crawley 1983), changes in growth patterns may not be correlated with changes in fecundity. The importance of directly measuring mortality and reproductive output is illustrated by several studies. One worker found significant negative effects on fruit production, pollination success, and seed set in a shrub (Allison 1990a, b). However, no significant effect on plant size was observed. In contrast, other studies have found a lack of effect on plant biomass but a significant effect on fitness measures such as fruit number, seed number, seed size, or population size (Bergelson and Crawley 1992; Gedge and Maun 1992).

Effects on population structure

If it is severe enough, herbivory can cause tree seedling or sapling mortality that leads to a pronounced gap in size structure. In less extreme cases, such a gap can simply result from the retardation or cessation of growth within a particular age class. Gaps in tree size structure have been seen in many habitats and have often been attributed to deer overbrowsing (Griffin 1976; Marquis and Grisez 1978;

Anderson and Louks 1979; Frelich and Lorimer 1985; Alverson et al. 1988; Trumble et al. 1989; Anderson and Katz 1993; Van Auken 1993). However, this pattern does not appear consistently among regions for any one taxa, weakening the inference that deer cause this pattern. Some have suggested that this pattern is a result of a complex suite of factors, of which deer overbrowsing is just one component (Jacobs 1969; Trumble et al. 1989; Mladenoff and Stearns 1993; Romme et al. 1995). Data from exclosures has clearly shown that deer cause gaps in tree size structure in few cases (Webb et al. 1956; Tierson et al. 1966; Whitney 1984). For example, elk caused marked reductions in overall shrub cover outside exclosures in Washington (Woodward et al. 1994). In contrast, the size class distribution of the palatable shrub *Acer circinatum* outside these exclosures changed little over half a century.

Exclosure studies provide the most reliable evidence on the effects of herbivores on individual plants and on community dynamics. However, the short time scale of most exclosure studies limits their conclusions to the effects of deer on the smallest size classes. If effects on the entire size structure are inferred from these data, one must assume that future conditions will be unchanged. Alternatively, one could determine the lifetime effects of herbivory by obtaining a complete static size class distribution and inferring causation from it (e.g., Brandner et al. 1990).

Effects on populations dynamics

In spite of the widespread belief that deer do alter plant population structure, their effects on underlying population dynamics remain poorly understood. There has been limited study of the effects of deer on particular life-stage transitions or growth and survival within a life-stage. No study has examined their effects on the complete set of transitions in the life-cycle of a plant. Among woody species, germination and seed production are the only life-stage transitions for which deer effects have been investigated under field conditions (Griffin 1976; Borchert et al. 1989; Allison 1990b). Studies of the effects of deer herbivory on the survival and growth of juveniles of woody species have not been of sufficient duration to encompass growth above the browse line, let alone the entire sequence of transitions to reproductive size (Krefting et al. 1966; Jacobs 1969; Inouye et al. 1994). Among herbaceous species, only the effects of deer on seed production have been investigated under field conditions using actual herbivore damage (Lowenberg 1994). These studies of deer effects on survival and growth during particular life-stages have been discussed in previous sections of this review.

Hypotheses about the relative magnitudes of deer effects on different life-stage transitions can be generated from studies involving similar ungulates. Studies of the effect of ungulates on perennials suggest that seed production is the life-stage most likely to be affected by herbivory. In separate studies, browsing by European roe deer and free-ranging sheep were shown to cause a larger reduction in fecundity than in survival or growth in two species (Bastrenta 1991; Ehrlén 1995a). Heavy browsing (removal of >50% of aboveground biomass) of one species did increase the probability of reproductive shoots decreasing in size and dying, but it eliminated seed production in all three years of the study (Ehrlén 1995a). In contrast, sheep grazing reduced fecundity only in years with favorable environmental conditions (Bastrenta 1991).

An excellent way to quantify the effect of herbivory on population dynamics is to incorporate herbivory into demographic models and to predict its effect on λ, the finite population growth rate. Ehrlén (1995b) and Bastrenta et al. (1995) combined empirically determined grazing effects on transition probabilities with stage-based matrix models. They found that the magnitude of grazing effects on λ in these perennial herbs was highly temporally heterogeneous. For example, in 2 of 3 years, the growth rate of severely grazed populations of *Lathyrus vernus* was nearly identical that of ungrazed or mildly grazed populations. But in one year, heavily grazed populations had a significantly lower growth rate than ungrazed populations. This change was sufficient to drive the growth rate below the replacement level (Ehrlén 1995b). The effects of grazing on λ were usually smaller than those of meristem-feeding mollusks, but they were greater than the effects of weevil seed predators. In populations of *A. vulneraria*, sheep grazing had a much larger effect on population dynamics in wetter years (Bastrenta et al. 1995). Simulations showed that in more favorable years, λ in grazed populations was 27 to 69% of that of ungrazed populations. In contrast, in years when plants experienced a moisture deficit, their models predicted that grazed populations would grow at a rate 63 to 124% of that of ungrazed populations.

Effects on Plant Communities

Changes in the population structures of forest trees as a result of large deer populations beg the question of how these and other changes are manifest at the community level. Community properties such as species richness, evenness and successional dynamics may be affected by deer herbivory, especially if dominant species are browsed. Data on the effects of deer on the population structure of trees exist only for economically valuable canopy and sub-canopy trees. From these data, preliminary conclusions can be drawn concerning the effects of deer on overstory species composition and succession in conifer-hardwood forests. Deer effects on woodlands, shrublands, herbaceous communities, and the herbaceous components of forest communities remain largely unknown. In this section I summarize the effects of deer on the species composition and successional dynamics of plant communities.

Effects on species composition in mature communities

Changes in species composition can be described at two different scales, that of individual taxa and that of life-forms or functional groups. Deer exclosure studies have largely measured changes in the abundance of taxa within a single plant life-form. They also typically measure changes in the density or coverage of a particular life-form, such as shrubs or herbs. These studies provide information about deer effects on the species diversity of sub-sets of taxa in plant communities and on the physical structure of plant communities.

Exclosure studies in conifer-hardwood forests suggest that deer do not affect the species composition of canopy trees on a large-scale across habitats. Instead, impacts are restricted to preferred habitats where deer densities are high. For example, in an uncut Adirondack forest, ambient deer densities did not cause a change in the species composition of tree regeneration between protected and exposed plots even after 15 years (Webb et al. 1956). On the Allegheny Plateau deer at approximately the mean regional density did not affect the species composition of tree regeneration (Tilghman 1989). However, deer at an experimentally elevated density (approximately twice the mean regional density) did reduce the species richness of stems taller than 0.9 m. Deer at densities greater than the most dense treatment used in Tilghman's study have been documented in deer yards and in preserves on which deer hunting is not permitted (Larson et al. 1978; Storm et al. 1989). Therefore, deer may affect the diversity and richness of tree regeneration in heavily-used habitats.

The effects of deer on the shrub and herbaceous layers of forest communities are poorly understood. In Adirondack conifer-hardwood forests, Webb et al. (1956) found that deer increased the evenness of shrub and herbaceous species composition. Where deer were excluded, coverage by wood fern increased from 25 to 45%. In contrast, coverage by violet (*Viola* spp.) and wood sorrel (*Oxalis montana*) decreased by 17 and 12%, respectively. However, in Allegheny hardwood forests deer did not affect the percent coverage of *Rubus* spp. and ferns, two understory dominants (Tilghman 1989). Too few studies currently exist from which to generalize about patterns of the effects of deer on herbaceous communities.

Ungulates, including mule deer, can have pronounced effects on the dominance patterns of shrubs in xeric shrub/grasslands of western North America. In Rocky Mountain National Park mule deer and elk altered the dominance patterns of shrubs over a 24 year period (Gysel 1960). Canopy coverage of *Artemisia tridentata* increased 13 to 15 times inside exclosures. In unprotected sites *A. tridentata* cover declined or remained constant. In contrast, canopy coverage of *Chrysothamnus viscidiflorus* remained constant inside exclosures, but increased 2 to 10 times in unprotected areas. Unfortunately, the effects of mule deer and elk were confounded so the contribution of mule deer to these changes can not be determined.

If deer affect species composition, they may, in turn, affect the physical structure of plant communities. This would occur if the species which are increasing (either in abundance, biomass or both) have pronounced morphological differences from those which are decreasing. For example, moose reduce tree biomass and increase shrub and herbaceous biomass in conifer-hardwood forest on Isle Royale (McInnes et al. 1992). No studies which compare the effects of deer on the abundance of different plant life-forms currently exist. However, we can infer information about the future physical structure of plant communities with high deer populations from studies of deer effects on particular life-forms.

As I have previously discussed, deer can reduce the average height of regenerating trees. They can also alter the size distributions of regenerating stems by preventing the growth of seedlings into larger size classes (Webb et al. 1956; Stoeckeler et al. 1957). A reduction in saplings of canopy species is currently affecting the physical structure of forest communities by reducing the density of tall stems in the understory. Eventually, canopy coverage in these forests and woodlands may be reduced if canopy individuals die and are not replaced. The regeneration of canopy species has received greater attention than that of trees which remain in the understory as tall adults. But there is evidence that regeneration of sub-canopy species is also restricted by deer in certain sites. For example, Stoeckeler et al. (1957) found that deer eliminated regeneration of *Acer rubrum* greater than 1.4 m tall.

It remains unclear whether deer affect the physical structure of forests and woodlands on a regional scale or whether these effects are confined to sites characterized by high deer usage. Tilghman (1989) found that deer caused a reduction in the number of canopy species' saplings only when deer density was approximately twice the regional mean. The effects of deer on the abundance of canopy regeneration also appear to be more pronounced in high light environments than in low light. In Allegheny hardwood forests, deer exclusion led to enhanced seedling and sprout growth only when 60 to 70% of the canopy basal areas was removed (Butterworth and Tzilkowski 1990). The trend was not statistically significant, but was visually apparent. As in the case of tree species diversity and richness, deer effects on the total quantity of regeneration may be confined to particular sites within a vegetation type.

Ungulates also change the physical structure of the shrub canopy of xeric shrub/grassland in the West. In Yellowstone National Park, mule deer, pronghorn, and elk reduced the average height of dominant canopy shrubs. The most pronounced effects were a 25 and 42% reduction in the height of *Artemisia tridentata* and *Chrysothamnus nauseous*, respectively (Singer and Renkin 1995).

Deer might affect the physical structure of understory vegetation both directly, via biomass removal, and indirectly, via their effect on canopy coverage and height. However, little is known about deer effects on the physical structure of understory vegetation. Webb (1956) found that deer improved the cover, but reduced the stem density of shrubs and herbs in Adirondack conifer-hardwood forest. Further studies are needed to determine if deer can alter the abundance of shrubs and herbs in forest understories.

Effects on succession

In forest communities, white-tailed deer and mule deer prefer to feed in disturbed or early successional habitats (Kohn and Mooty 1971; Wallmo et al. 1972; Kearny and Gilbert 1976). Studies of deer and succession find that deer affect the rate of canopy recovery and the direction of succession. Data are insufficient to determine whether the observed patterns of habitat use is related to changes in the rate of succession. Deer effects have been examined largely in post-logging forest communities and old fields, so the current literature concerning deer effects on succession represents a limited set of disturbance types in a limited number of plant communities.

In forest communities deer appear to have site-specific effects upon the rate of woody species invasion immediately following a disturbance. For example, after four to six years of deer exclusion in an old-field and in a clear-cut, seedling density was the same inside and outside the exclosures (Harlow and Downing 1970; Inouye et al. 1994). In contrast, following clear-cutting of a hardwood forest deer caused a 75% reduction in the number of stems above the browse line (Harlow and Downing 1970). Thus deer may slow the rate of canopy closure in some sites because of their negative effects on seedling growth (Harlow and Downing 1970; Marquis and Grisez 1978; Trumble et al. 1989).

The magnitude of deer effects on the rate of canopy closure following a disturbance appears to be temporally as well as spatially heterogeneous. Studies have shown that deer infrequently influence canopy closure rates or do so only at high densities (Tilghman 1989; Inouye et al. 1994). But detection of changes in the rate of overstory regeneration may be hindered by year-to-year variation in the magnitude of deer effects on seedling growth. Inouye et al. (1994) examined the effect of deer on seedling growth rate of three tree species in a Minnesota old-field over a ten year period. They found that deer had a significant negative effect on the relative growth rate of these seedlings in only one, two, or four years out of ten, depending on the species.

Deer alter the direction of the successional sequence of canopy species in seral forest communities in which woody stems have succeeded in growing above the browse line. For example, deer reduced the species richness and evenness of canopy tree species which grew above the browse line in early- and mid-successional forests (Harlow and Downing 1970; Ross et al. 1970). In one case, deer caused a shift in the dominant canopy species from a conifer, *Pinus strobus*, to a hardwood, *Betula papyrifera* (Ross et al. 1970). Deer may only affect the direction of succession in sites with high deer densities. In one forest, only a high deer density reduced the evenness of regenerating stems, resulting in a near monoculture of *Prunus serotina* (Tilghman 1989).

Effects on Ecosystem Properties

To begin to understand the effects of deer on ecosystem dynamics, it would be useful to measure nutrient flow through deer. We could compare these values to other energy and nutrient pathways to determine the relative impact of deer. To my knowledge, the only estimates of these values have been made in a northern hardwood forest. The average annual energy flow through deer was 3.8 kcal m^{-2} or 0.8% of net primary productivity (Pletscher et al. 1989). By comparison, the deer mouse *Peromyscus maniculatus* consumed an average of 4.0 kcal m^{-2} yr^{-1}. Unfortunately, this site had lower deer densities (0.5 to 3.9 deer km^{-2}) than in other sites of similar habitat. Therefore, deer probably affect nutrient flow on a regional level more than that seen at this site.

Hypotheses about the effects of deer at the ecosystem level can be generated from studies of other mammalian herbivores. One hypothesis is that deer indirectly affect the energy and nutrient flow in ecosystems by changing the species composition of plant communities. In a conifer-hardwood forest moose affect the relative productivity and biomass among the tree, shrub and herbaceous layers

(McInnes et al. 1992). Moose caused a reduction in litter quantity that resulted in smaller amounts of surface carbon and nitrogen.

Changes in litter quantity and chemistry also may result from changes in the species composition within a particular plant functional group. Mixed forests may be particularly susceptible to such changes because, in general, conifers and hardwoods produce a different quantity and quality of litter. For example, conifer leaf litter loses dry weight and releases nitrogen more slowly than hardwood litter (MacLean and Wein 1978; Moore 1984; McClaugherty et al. 1985). Moose browsing causes an increase in conifer litter and a decrease in hardwood litter (Pastor et al. 1993). As a result, the concentration of soil nitrogen decreases and the ratio of lignin to nitrogen increases. Thus moose indirectly affect soil chemistry and the rate of decomposition. Clearly, further study is needed on the effects of deer on ecosystem functions.

Productivity and deer herbivory

Productivity can be critical in determining plant response to herbivory (Crouch 1966; Bryant et al. 1983; Cox and McEvoy 1983; Coley et al. 1985; Maschinski and Whitham 1989; Canham et al. 1994). Current research suggests that the ability of an individual plant to tolerate herbivory is enhanced under higher resource conditions. For example, in an old field from which competition was removed, seedlings of three common trees were subjected to full sun or 8% of full sun in combination with a variety of simulated herbivory treatments (Canham et al. 1994). The growth and mortality of all three species was determined more by the availability of light than by the clipping treatments. Plants in full sun had better survival and growth than in the low-light environment in almost all cases. These findings support theoretical and empirical evidence from other plant-herbivore systems that plant tolerance to herbivory is positively correlated with resource levels (e.g., Bryant et al. 1983; Coley et al. 1985).

However, some data do not support this hypothesis. For example, in a 31-year study in a steppe community, the effects of ungulates on the dominant shrubs were much greater at the drier, lower elevation sites than at higher elevation sites (Bilbrough and Richards 1993). This results was not explained by differences in ungulate density between the two sites.

Resource levels may also influence plant density, which may, in turn, affect deer feeding behavior. In some cases, there may be a negative correlation between plant density and browsing pressure. In a study on reforestation plots of *Pinus ponderosa* and *Pseudotsuga menziesii*, white-tailed deer browsed proportionally fewer seedlings as plant density increased (Adams 1949). The proportion of *Abies balsamea* saplings with recent moose damage is negatively correlated with stem density (Brandner et al. 1990). These studies suggest that palatable, sparsely distributed taxa may be more susceptible to deer effects than more common taxa. However, this pattern is not universal. Moose browse proportionally more plants of the herb *Aralia nudicaulis* when plant density is high (Edwards 1985).

Plant density may also indirectly affect the regeneration of canopy trees. The effect of moose herbivory on *Abies balsamea* is determined more by plant density than by herbivore density (Brandner et al. 1990). Moose effects are strongest at lowest fir densities irrespective of moose density. This pattern may be due to lower browsing intensities at higher plant densities (i.e., predator satiation). Alternatively, high plant density may be an indicator of high resource levels, which may enable plants to recover from herbivory more effectively. Data from other herbivore-plant systems suggest that the relationship of plant density to browsing pressure and subsequent plant response is one of general importance (e.g., Van de Koppel et al. 1996).

DISCUSSION

Generalizations and Future Directions

This review reveals less evidence of the negative effects of deer on vegetation than I expected it would. This paucity of strong deer effects may have a temporal explanation: the major effects of deer may have already taken place in the past. The most dramatic shifts in deer density occurred in the late 19th and early part of the 20th century (Doman and Rasmussen 1944; Cook 1945; Leopold et al. 1947; Taylor and Hahn 1947; Banfield 1949; Mohler et al. 1951; Schorger 1953; Gill 1988). As a result, the greatest potential for community and ecosystem changes would have also been during that period. Strong effects in the past may have eliminated species that are most sensitive to herbivory. Alternatively, deer herbivory may have reduced plant density to a level from which recovery is very slow and, thus, difficult to detect. Effects seen today may be a result of range shifts and density fluctuations that are on a much smaller scale than the changes seen in the past. I would expect these effects to be of a relatively small magnitude.

Can effects of low magnitude that are sustained over a long period of time (even ones that may be non-significant on a short time scale (e.g., Inouye et al. 1994)), produce large effects on plants, communities, or ecosystems? Answering this question will require a greater level of detail than that measured in traditional deer exclosure studies (Table 1.2).

Not surprisingly, many studies demonstrated that deer browsing led to a temporary reduction in plant growth. This change was often accompanied by marked morphological changes such as increased stem production, reduced height, increased stem diameter, and pruning of lower tree boles. However, because there was often a concomitant above-ground response that was either partially or fully compensatory, these effects usually did not manifest themselves as reductions in fitness. When such effects did occur, however, they were most often due to reductions in growth and fecundity, rather than increased mortality. This may be a result of the higher frequency of studies on woody species. Although data are sorely lacking, negative effects on herb survival were also present and tended to be quite strong.

The timing of herbivory had a profound impact on the magnitude of the effect of deer on individual growth and fecundity. For example, browsing in winter had little to no effect on woody species (Switzenberg et al. 1955; Jacobs 1969; Canham et al. 1994) while browsing of both woody and herbaceous species late in the growing season (although an uncommon natural phenomenon for some species) had very strong effects on plant performance (Gedge and Maun 1992, 1994; Canham et al. 1994; Lowenberg 1994). More studies that manipulate the timing of herbivory are needed to confirm these important results. An alternative method to traditional clipping studies is to add or remove cages at different times in a season. Linking such results with information on the temporal pattern of deer movements would provide a powerful predictive tool.

Differences in deer effects among taxa may reflect the differences in species-specific patterns of the timing of deer herbivory. For example, this may explain why negative effects have been found on *Fraxinus* (Canham et al. 1994) and not in other commonly-browsed taxa such as *Prunus* and *Acer*. The former is often browsed in the summer (Bramble and Goddard 1953) while browsing of the latter taxa often occurs in the winter (Krefting et al. 1966; Jacobs 1969; Canham et al. 1994). I expect that others will find strong negative effects of deer browsing on other commonly used shrubs such as *Cornus* sp. that are heavily browsed in the spring and summer (Petrides 1941; Webb 1959; Irwin 1985; Strole and Anderson 1992).

One of the most important conclusions of this review is that the effects of deer on both individual plants and plant communities tended to be highly restricted in spatial extent. This may be due simply to spatial variation in deer density. On the largest scale, deer population densities within North America range over at least three orders of magnitude, from less than 0.1 to over 100 deer km^{-2}; typical values are within the range of 2 to 8 deer km^{-2}. More importantly, however, is the range of density within broad vegetation types. Regional mean deer densities are often used to predict effects on vegetation at the local level (e.g., within and adjacent to exclosures). However, this metric may be a poor predictor of deer impacts at a smaller spatial scale.

Effects of large magnitude may be seen only in areas with very high deer concentrations. For many species, negative effects were seen only at high clipping or browsing intensities. Such herbivory levels would be seen only in uncommon situations such as deer yards, near urban areas (Witham and Jones 1990), or in small, isolated woodland fragments (Nixon et al. 1991; Strole and Anderson 1992). For example, forest successional stage was an important correlate of the magnitude of deer effects. Effects immediately after clear-cuts and in mid-successional forests appeared to be stronger than those in mature forests (Harlow and Downing 1970; Ross et al. 1970), although not in every case (Tilghman 1989; Inouye et al. 1994). This may be because deer use these seral habitats more than other habitats (Kohn and Mooty 1971; Wallmo et al. 1972; Kearny and Gilbert 1976). Effects in these habitats may be short-lived, however. Higher productivity in early-successional habitats may permit the rapid recovery of browsed plants and the competitive release of unbrowsed plants.

The existence of size class gaps of many dominant trees in forests of the Northeast and West is often cited as evidence for extreme deer overbrowsing. However, there are few well-designed experiments that provide a clear causal link between deer herbivory and this size class gap (but see Webb et al. 1956; Tierson et al. 1966). Deer may be one factor among many that are producing such patterns (Jacobs 1969; Trumble et al. 1989; Mladenoff and Stearns 1993; Romme et al. 1995). Because strong negative effects of deer tend to be evident only at high browsing intensities, are gaps in tree size structure only evident in deer yards? And how important are deer yards in determining plant population dynamics on a regional scale?

Restricted areas of high deer population impact have been recognized as early as the 1940s (Leopold 1943; Leopold et al. 1947). In a review of deer populations throughout the United States, Leopold et al. identified dozens of regional "problem areas". Most of these areas were very localized and occurred in only five states: Pennsylvania, New York, Michigan, Wisconsin, and Texas. It may be no coincidence that the vast majority of long-term exclosure studies have been established in those five states. Not until studies from other regions specifically address the occurrence and magnitude of deer effects will we know the actual geographical extent of the effects of deer on plants and plant communities.

Methodological Issues

There were a number of common biases and sources of uncertainty in the literature on the effects of deer on plants. Many of these problems, especially those related to experimental design and statistical analysis, are not unique to this body of literature (Hurlbert 1984; Fowler 1990). However, designs involving exclosures or enclosures pose several unique challenges to the field ecologist (Table 1.3). Because exclosures are one of the most powerful techniques available to predict the effects of deer on plants and plant communities, it is worth examining them in more detail.

One of the most serious potential biases in deer herbivory studies was the subjective placement of plots. This was also the most difficult to evaluate. In many cases, I could only infer that plots were subjectively located based on a vague description of the study sites. In some cases there may have been a bias towards establishing plots in areas of unusually high deer density (e.g., deer yards) or where there was evidence of recent intense deer browsing (e.g., low herb or shrub density, high stem number per plant). Such a bias would surely overestimate the effects of deer in a region. In some cases, however, non-random plot placement was part of the experimental design (e.g., Brown and Doucet 1991; Van Deelen et al. 1996). As long as this was clearly stated in the objectives of the study, results could be interpreted appropriately.

One issue that needs further study is the possibility of "fence effects". Control plots are often positioned adjacent to exclosures to minimize differences in initial vegetation condition. This is an important consideration, but is deer behavior in control plots affected by the presence of fences nearby? Deer may be attracted to fences and thus browse control plots more intensively than they would if the control was cited in equivalent habitat away from the fence (Heady 1968; Woodward et al. 1994). If this bias is present, it jeopardizes the critical assumption that treatments are independent.

Studies with small sample sizes are less likely to detect treatment effects because of their low statistical power. Many of the exclosure studies I reviewed had relatively small sample sizes (mean N = 5.4, s.d. = 4.8, range = 1 to 20, N = 16 studies). Therefore, taken together, they may have underestimated the presence of deer effects. Larger samples become especially important when the variance in the effects is high. This is often the case with deer effects on plants.

Some studies also had very small plots (minimum plot size was 10.5 m^2). Many of the community-level processes of interest to researchers occurred at spatial scales much larger than the exclosure sizes in the studies reviewed here. Thus it was often difficult to interpret results in light of this mismatch in scale. There is often a trade-off to be made between sample size and plot size. However, this did not appear to be the case with these studies. Unexpectedly, sample size and plot size were uncorrelated (Spearman rank correlation coefficient = –0.10, $p > 0.7$; N = 13). If community-level properties are of interest, then experimenters should consider using large plots at the expense of a large sample.

An important question that remains unresolved is how different deer densities affect plant population dynamics. Clipping studies have begun to address this by investigating the components of deer herbivory (e.g., browsing intensity, frequency, or timing). But we do not know how deer density itself is related to these components of deer browsing. Field exclosure experiments will not be of much use in such studies; they are necessarily designed with two density treatments, either a deer density of zero or a deer density of the background, and often fluctuating, level.

Incorporating a variety of natural deer densities as fixed treatments without confounding site-to-site environmental differences can be very difficult. When observational studies do not take this into consideration their conclusions are severely weakened (e.g., Frelich and Lorimer 1985). Several workers have addressed this issue by utilizing natural systems of archipelagos with islands of differing deer densities. These conditions exist on the Apostle Islands of Lake Superior (Beals et al. 1960; Allison 1990a, b; Balgooyen and Waller 1995). However, this method is still not ideal. Deer densities still may be confounded with other environmental factors that affect plant fitness. Another method is to use relatively small enclosures into which varying numbers of deer are placed to simulate large-scale variation in density (e.g., Tilghman 1989). Yet another method is to perform clipping experiments at a range of simulated browsing intensities. Of the methods currently available, a combination of clipping experiments and exclosures in natural populations will yield the most useful data on the effects of white-tailed deer on plants.

Table 1.1. Species on which positive responses in above-ground growth in response to natural or simulated deer herbivory have been demonstrated, categorized by life-form. All experiments were performed in the field.

Species	Type of herbivory	Location	Reference
Trees			
Acer rubrum	natural	NY	(Canham et al. 1994)
Acer saccharum	natural	N.E. WI	(Jacobs 1969)
Fraxinus americana	natural	NY, N.E. WI	(Stoeckeler et al. 1957; Webb et al. 1956)
Tsuga canadensis	natural	N.E. WI	(Stoeckeler et al. 1957)
Shrubs			
Acer spicatum	natural	N. MN	(Krefting et al. 1966)
Purshia tridentata	simulated*	N. UT	(Bilbrough and Richards 1993)
Rhus glabra	natural	MN old field	(Strauss 1988; Strauss 1991)
Viburnum alnifolium	natural	NY	(Tierson et al. 1966; Webb et al. 1956)
Herbs			
Cakile edentula	simulated	S. Ontario	(Gedge and Maun 1992; Gedge and Maun 1994)
Corispermum hyssopifolium	simulated	S. Ontario	(Gedge and Maun 1992; Gedge and Maun 1994)

*mule deer and elk herbivory

Table 1.2. Selected questions on the effects of deer herbivory on plant communities of North America that remain largely unanswered or have been not been addressed. References are included that provide examples of studies that address the question or provide related data.

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1. Effects on individual plants (i.e., growth, morphology, fitness)

   - How widespread are positive indirect effects of deer herbivory?
   - Is deer preference correlated with effect severity in other habitats besides the NE deciduous forest (where no correlation appears to exist)?
   - Are there effects on plant performance at low deer density? (Tilghman 1989)
   - Does the effect of herbivory depend upon the interaction between plant density and deer density? Or are these effects simply additive? (Brandner et al. 1990)
   - Are deer effects on fecundity proportional to reductions in plant size or does herbivory limit recovery even further?

2. Effects on plant populations dynamics (i.e., mortality, fecundity, population growth)

   - "Deer yards" are common but are they important for plant population dynamics at the landscape level?
   - Effects of herbivory on herbaceous species (especially annuals) are understudied; what further generalizations can be made? (Gedge and Maun 1992; Gedge and Maun 1994; Lowenberg 1994)
   - Can we identify life–history traits associated with species that are particularly vulnerable to deer? (Miller et al. 1992)
   - How does the proportion of plants attacked and the amount of biomass removed change as plant density increases? (Brandner et al. 1990)
   - How do the effects of deer herbivory on plant growth, survival and fecundity change with increasing plant density?
   - What is the direction, magnitude and frequency of deer effects on the growth rate (i.e., λ) of plant populations? (Bastrenta et al. 1995; Ehrlén 1995b)
   - Do deer have a more pronounced effect on λ in high productivity years or sites than in low productivity years or sites?
   - Are refuges from deer herbivory important to plant population dynamics?

Table 1.2. Continued

3. Effects on plant communities

   - Does the time deer spend in various habitat types help explain the magnitude of the effect on those habitats? Or at least the rankings of those effects?
   - Are early or mid–successional forest stages most susceptible to deer herbivory? Or are these communities just experiencing greater amounts of herbivory? (Kearny and Gilbert 1976; Kohn and Mooty 1971; Wallmo et al. 1972)
   - What are the effects of deer on a community relative to other herbivores? (Inouye et al. 1994)
   - What is the nature of the relationship between deer density and the effect on plant communities? Is the relationship linear?
   - How does deer herbivory affect the species composition and physical structure of herbaceous communities?
   - How do deer affect the rate and direction of succession in naturally occurring disturbances (as opposed to clear-cuts or old-fields) ?
   - Deer yards function as protection from winter elements. Are their locations independent of community composition but not of community structure (e.g., tree density, canopy cover) and physiography ? (Frelich and Lorimer 1985)

4. Effects on ecosystem processes

   - What is the magnitude of energy and nutrient flow through deer in ecosystems where effects on community composition are observed? (Pletscher et al. 1989)
   - Do shifts in dominant species as a result of deer herbivory result in altered nutrient cycling? Do feedback mechanisms help maintain this new dominance state? (McInnes et al. 1992)
   - Do deer affect the distribution of biomass and productivity patterns among different plant life–forms (i.e., herbs vs. shrubs vs. trees) in plant communities?
   - How does deer herbivory affect the relative abundance of conifers and hardwoods in mixed forests and how does this affect nutrient cycling?

Table 1.3. Common biases and sources of uncertainty in the design and analysis of exclosure or enclosure experiments that investigate the effects of deer on plants and plant communities.

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1. Biases

- subjective plot placement in areas with greater deer effects
- small plot size relative to ecological processes that drive community dynamics
- locating control plots too close to fenced plots: potential "fence-effects"
- lack of control plots
- lack of baseline data collected before fence installation. This would ensure that experimental plots have initial conditions similar to controls
- for long-term exclosures, later sampling methods differed from early sampling methods, compounding the inherent problem of observer bias
- little or no replication of exclosures
- strong geographical bias of studies towards the NE US

2. Sources of uncertainty

- confounding of effects with environmental differences among sites; e.g. time since clear-cutting, type of disturbance, abiotic factors, grazing history, time since fire
- large effects of deer may have already occurred in the past
- deer density is often unmeasured (or measured with dubious surrogates such as hunting records) among study sites or across years and may be confounding results
- the high variance of effects (partly due to low N and small sample plots) makes detection of effects difficult
- deer effects may occur infrequently in time and thus will be difficult to detect with short-term studies
- or, alternatively, effects are of low magnitude evenly across years, making detection possible only with high statistical power

3. Analysis and Publication

- pseudoreplication
- no significance tests presented or measures of data variation that would be required to perform these tests after publication
- there may be a publishing bias towards studies where effects of deer are detected; i.e. "no effect" experiments are not submitted or not accepted for publication

Chapter 2: The Patterns and Effects of Insect and Deer Herbivory on a Rare Annual Plant, *Streptanthus bracteatus*

ABSTRACT

I investigate the effects of herbivory on the individual performance of a rare annual plant, the bracted twistflower (*Streptanthus bracteatus*; Brassicaceae). My principal hypotheses are: (1) insect herbivory causes lower plant growth, survival, and seed set, and (2) herbivory by white-tailed deer (*Odocoileus virginianus*) also causes reductions in these parameters. To test these hypotheses, I conducted an observational study at four natural populations over two years.

I found that plants eaten by insects, primarily the butterfly *Anthocharis midea*, have significantly lower stem elongation, survival, and seed production than uneaten plants at some sites. Plants eaten by deer also have significantly lower values of these parameters. However, deer have a greater negative effect on *S. bracteatus* than insects do because deer remove proportionally more tissue, feed on larger plants, and cause more physical damage to plants than insects do.

Next, I further tested the hypothesis that deer cause reductions in the survival, biomass, and seed set of *Streptanthus bracteatus*. I conducted a two-year experiment at a fifth natural population, in which I compared caged and uncaged plants. I found that caged plants had significantly higher survival, biomass, and seed set than uncaged plants in at least one of the two years.

INTRODUCTION

Herbivory is known to influence the development and performance of many plant species. For example, herbivory reduces plant recruitment, survival, growth, and fecundity (Hendrix 1979; Inouye et al. 1980; Rausher and Feeny 1980; Kinsman and Platt 1984; Brown et al. 1987; Reichman and Smith 1991; Swank and Oechel 1991; Bergelson and Crawley 1992; Rees and Brown 1992; Ehrlén 1995a). The effects of herbivory on these factors often have a spatial component (Maschinski and Whitham 1989; Huntly 1991). As a result, herbivores also affect the local distribution of plants (Parker and Root 1981; Boyd 1988; Louda and Rodman 1996).

The effects of herbivory have been studied almost exclusively on common species. Their effects on rare plants are almost unknown because management efforts often do not consider interspecific interactions (Louda 1994). Because it is well-documented that herbivory can limit the distribution and abundance of common species, we should expect herbivory to have similar effects on less common species. Indeed, there is evidence that herbivory limits the abundance of rare plants (Willoughby 1986; DeMauro 1994; McEachern et al. 1994). Anecdotal evidence suggests that one common herbivore, white-tailed deer (*Odocoileus virginianus*), may have large negative effects on populations of rare plants (Miller et al. 1992). The magnitude and spatial extent of the effects of white-tailed deer on common species is poorly known (Chapter 1), so it is difficult to predict what effect deer may have on rare species.

Streptanthus bracteatus A. Gray (Brassicaceae) is endemic to the Edwards Plateau of central Texas. It is eaten by several herbivores, including white-tailed deer (McNeal 1989; Dieringer 1991). On the Edwards Plateau, white-tailed deer (hereafter referred to simply as 'deer') are found at approximately 20 km^{-2} (Young and Richards 1994). This is one of the greatest regional densities in North America (Gill 1988). Deer density near urban areas, where most populations of *S. bracteatus* occur, may be even higher due to hunting restrictions and the increased availability of food in winter. The high density of deer in Texas is a relatively recent phenomenon (Leopold et al. 1947; Doughty 1983; Young and Richards 1994) that may have caused the rarity of this species.

Annual plants may be particularly susceptible to deer herbivory where deer densities are high. In the spring and early summer, annual herbs constitute a significant proportion of deer diets (Dunkenson 1955; Halls and Crawford 1960; Kohn and Mooty 1971; Korschgen et al. 1980; Crawford 1982; Irwin 1985; McCullough 1985; Case and McCullough 1987), including in central Texas (McMahan 1964; Bryant et al. 1981; McPherson and Rasmussen 1989). Furthermore, annual plants often lack underground storage reserves that allow many plants to recover from herbivory (Crawley 1983). Annuals also have a relatively short life-cycle within which recovery from herbivore damage is possible.

My field observations suggest that insects are also common herbivores of *S. bracteatus*. Insects have significant negative effects on plant performance in many common taxa (Crawley 1983, 1989a), but their effect on rare plants has not been investigated. Recent studies suggest that different herbivores can have dramatically different effects on the same plant (Inouye et al. 1980; Strauss 1991; Meyer 1993; Hulme 1994, 1996). In species like *S. bracteatus*, on which multiple herbivores feed, separating the effects of these herbivores is thus critical to understanding the overall effect of herbivory.

In this chapter, I address the following hypotheses: (1) insect herbivory causes lower plant growth, survival, and seed set of *S. bracteatus*, and (2) deer herbivory also causes reductions in these parameters. To test these hypotheses, I conducted an observational study at four natural populations in two years. I found that plants eaten by insects have lower growth, survival, and seed production than uneaten plants. Plants eaten by deer also have lower values of these parameters. However, deer have a greater negative effect on *S. bracteatus* than insects do.

Next, I further tested the hypothesis that deer cause reductions in the growth, survival, and seed set of *Streptanthus bracteatus*. I conducted an experiment in two years at a fifth natural population, in which I compared caged and uncaged plants. I found that caged plants have significantly higher biomass, survival, and seed set than uncaged plants in at least one of the two years. I also describe the natural pattern of herbivory at eight populations throughout the range of *S. bracteatus*.

METHODS

Study Species and Sites

I conducted this study along the eastern and southern margin of the Edwards Plateau in central Texas. This region is characterized by highly dissected

Cretaceous limestone hills (Riskind and Diamond 1986, 1988) with shallow (< 50 cm) soils that frequently have a calcareous hardpan (caliche). Mean annual precipitation on the eastern Plateau is 85 cm yr^{-1}. Rainfall is extremely variable, with little seasonal pattern. Twelve-month rainfall totals during this study (September to August of 1993–1994 and 1994–1995) were much lower and much higher than average, respectively (76 and 143% of the 30–year seasonal mean, respectively). The average yearly temperature is 19°C with mean August maximum and mean December minimum temperatures of 36°C and 16°C, respectively. The mean January minimum temperature is 3°C. Potential evaporation exceeds precipitation by an average of 58 cm yr^{-1}.

The vegetation of the study sites was mixed woodland, composed primarily of *Juniperus ashei* and several species of oaks, primarily *Quercus fusiformis*. Common understory shrubs included *Berberis trifoliolata, Diospyros texana, Sophora secundiflora,* and *Q. fusiformis*. These woodlands were interspersed with savannas containing a diverse assemblage of graminoids: abundant species included *Schizachyrium scoparium, Aristida* spp., *Bouteloua rigidiseta,* and *Stipa leucotricha*.

Streptanthus bracteatus is a winter annual that produces a basal rosette of leaves before bolting in early spring, when it typically produces a single flowering stalk. *S. bracteatus* is found in moderately-to-deeply shaded understories of juniper-oak woodlands on the southern and eastern margins of the Edwards Plateau. It also grows in this region in areas where the overstory has been cleared but the shrub-dominated understory remains relatively intact. During this study *S.*

bracteatus was known from about 12 populations in four Texas counties: Uvalde, Medina, Bexar, and Travis; most populations occurred in Travis County. This study was conducted at nine of these sites, all of the sites to which access was possible and in which the population was large enough to allow meaningful monitoring. More details of the basic biology of *S. bracteatus* can be found elsewhere (Appendix 1).

I assessed the effects of herbivory on *Streptanthus bracteatus* using two approaches, (1) a detailed observational study and (2) a manipulative field experiment. I focused most of my effort on the observational study because the collection of basic demographic data was my first priority. Moreover, the small spatial extent of populations (often < 100 m^2) prevented the establishment of truly independent manipulative treatments (e.g., cages would have affected uncaged plots) and human activity at most sites prevented the use of cages or insecticides.

Observational data collection

I followed individuals of *S. bracteatus* throughout their lifetime at four sites in Travis County (the 'intensive censuses'). I performed a census at the other five sites at least once in the spring and once in the early summer. Repeated censuses throughout the study were not possible at two sites; the population at Lakewood was destroyed by a housing development in 1994 and the Eisenhower Park population was not discovered until 1995. Two other populations, Mesa and Valburn, were extirpated at the end of this study by development. At the end of the final year of the Lakewood, Mesa, and Valburn populations, I collected all plants and seeds. I then dried and weighed these plants and counted the number of seeds per fruit. A summary of all nine sites and the dates on which I performed each census or harvest is presented in Table 2.1. The methods used in the intensive censuses are described below. The methods used in the other five sites were the same except that at these sites the entire site was treated as a single plot.

I established permanent plots of either 0.5, 1.0, or 2.0 m^2 in April 1993. When plants occurred in relatively small areas, I arranged plots in a grid; otherwise I centered individual plots on plant clusters. I began censuses on 5 November 1993 and 10 October 1994 and continued them monthly through March (Table 2.1). From April on (after bolting), I performed censuses bi-monthly until all plants set seed (in July or August). Beginning with the first census in April, I took the following measurements on every adult, using dial calipers and a retractable ruler: stem basal diameter, length of growing stems, number of new growing stems, number of open and closed flowers, number of fruits, and the length of each fruit. I measured eleven morphological characters in a preliminary study of this species to determine which one(s) would provide the best surrogate for biomass. After exploring these characters with stepwise multiple regression models, I found that stem basal diameter was the best predictor ($R^2 = 0.95$, $N = 27$) of dried plant biomass.

I also used linear regression techniques to generate models of estimated seed number from the sum of fruit lengths per plant. I pooled the data from the sites from which plants were harvested and seeds counted (Lakewood and Mesa in 1994; Valburn and Mesa in 1995). I used these data to estimate seed set of plants at sites at which seeds could not be counted directly. When linear models differed between eaten and uneaten plants, as determined by a t-test comparing slopes (Zar 1986), I used separate equations to estimate seed number in each group.

I quantified herbivory on immature plants (i.e., rosettes) in winter by noting any completely defoliated or uprooted plants. I further classified defoliated plants as either having died or having survived to bolt in the spring. I made a single survey in early February 1994 to quantify the fraction of immature plants moderately to severely damaged by insect herbivory. I also made qualitative notes of herbivore damage to immature plants throughout the study.

Data on stem herbivory formed the basis for quantifying herbivory on adults because this was its major form. I defined stem herbivory as the removal of, or damage to, an apical or lateral meristem. I took the following measurements at each census: number of stems newly eaten, length of newly eaten stems, and herbivore type. I classified herbivores as either pathogen, insect, deer, or 'unknown'. Identification of herbivores was based primarily on stem morphology: the tip of a stem damaged by deer tended to be rough with a flat cross-section and often showed epidermal tearing; some of these plants were also uprooted, either partially or wholly. In contrast, the tip of a stem damaged by insects tended to be smooth and diagonal in cross-section with little or no evidence of epidermal tearing. Plants attacked by pathogens (either viral or fungal) often had severely damaged meristematic tissue, resulting in deformed stems, upper cauline leaves, flower buds, or fruits. Because the effects of pathogens appeared to be similar to that of other herbivores, I classified them as another herbivore. I classified damaged stems that could not be categorized unambiguously as 'unknown'.

Observational data analysis

In order to determine the effects of herbivory on *S. bracteatus*, I compared plant responses among different categories of naturally-damaged plants. This approach may have introduced biases due to non-random selection of plants by the herbivore. Wherever possible, in my analyses I statistically "adjusted" for preference based on plant size. In order to identify the stage or stages of plant development at which herbivory had the greatest effect, I separated the effects of herbivory on adults into effects on growth, morphology, mortality, and fecundity. Herbivory effects on fecundity were further divided into pre-dispersal seed predation (i.e., herbivores eating or damaging fruits) and effects that occurred before fruit set (i.e., due to changes in growth or morphology). In most cases it was also possible to further separate these effects by herbivore type and site. Separating the effects of herbivory into these levels often required a detailed description of herbivore activity in the spring that was obtained only by the more frequent, intensive censuses. Thus, I performed most of the analysis described below using data from only the four sites at which more frequent censuses were performed.

For analyses in which the effects of deer and insects were compared, it was desirable to maximize sample size. To do this I randomly assigned plants in which the herbivory type was unknown to either insect or deer in a ratio of 3:1. This value was determined subjectively based upon a suite of evidence. For example, the pattern of herbivore damage (e.g., amount and proportion of tissue removed) in most of these plants was similar to the pattern of damage of plants eaten by insects. In other cases, plants disappeared between intervals while their tags remained behind, strongly suggesting they were completely eaten or carried off by deer. However, a small percentage these 'missing' plants were within cages (see below), suggesting that insects were at least partially responsible. Missing plants were randomly assigned to insect or deer in a 1:3 ratio. I performed analyses using both the full data set (including the unknown and missing cases) and the subset of cases for which herbivory type was known. If results differed between analyses, I present both.

I analyzed the effects of herbivory on above-ground growth using stem elongation rates from the first three adult censuses (April and early May). After this point, stem elongation rates of all plants (eaten or not) quickly fell, causing variances to increase dramatically and making testing unreliable. To test for differences in the effects of deer and insects on stem elongation I created a measure, α, of the growth rate of eaten plants relative to uneaten plants using the following equation:

$$\alpha = \frac{\phi_{obs} - \phi_{\exp}}{\phi_{\exp}}$$

where ϕ_{obs} is the difference in total stem length of eaten plants between censuses. The value $\phi_{\exp}$ is the expected growth of a plant if it goes uneaten, based on its stem basal diameter (which is not affected by herbivory). Values of $\phi_{\exp}$ were calculated for each site and for each interval using regressions of log-transformed data from uneaten plants. Values were back-transformed for use in the equation above.

I quantified the effect of herbivory on morphology by comparing (1) the number of stems produced in a plant's lifetime and (2) the number of intact stems at the final census, both by herbivory type. I considered only plants that experienced a single herbivory type in their lifetime. I used X^2 tests of contingency tables to test for significant differences among categories of stem number. To ensure adequate numbers of observations in each cell, I categorized lifetime stem number as either 1, 2, or ≥ 3 and final stem number as 0, 1, or ≥ 2. If a significant difference was found, I performed X^2 tests on the three possible pairs of categories to determine which were significantly different, with alpha values adjusted accordingly. Because of the nature of these tests, I could not adjust values by plant size.

Analyses of the effects of herbivory on survival probability were limited by small sample sizes. The numbers of plants eaten by deer were very low at all sites in 1994 and at all sites but Valburn and Bee Creek in 1995. In addition, there were few uneaten plants at Bee Creek in 1995. I could not pool sites to increase sample size because of the fixed empty cell for Mt. Bonnell and herbivory type; deer were absent from this site *a priori*, a "structural zero" (Bishop et al. 1975). I could only compare the effects of herbivore type at Valburn in 1995. Sample sizes of insect-eaten plants were sufficiently large at Barton Creek in both years to permit modeling of the effects of insects alone.

I analyzed the effects of herbivory on the probability of surviving using logistic regression models. Logistic regression utilizes a logit link function and a binomial probability distribution. It is very similar in structure to traditional regression techniques. I fitted the following model to the Valburn 1995 data, using maximum likelihood estimation, for observation *i*,

$$\ln\left(\frac{\hat{p}_i}{1-\hat{p}_i}\right) = \beta_0 + \beta_1 SIZE_i + \beta_2 HERB_i(j) + \beta_3 SIZE_i \times HERB_i(j)$$

where p is the probability of survival to the final census. The main effects in these models were stem basal diameter (*SIZE*) and herbivory type (*HERB(j)* = none, deer, or insect). I omitted pathogen-eaten plants from the analysis due to small samples sizes. I included the interaction term, *SIZE* x*HERB*, in the model because (1) I expected deer to exhibit size-based browsing preference and (2) in general, survival is highly correlated with plant size so its inclusion would have likely improved model fit. I investigated effects in a hierarchical fashion by building the model with single terms and evaluating the difference in log-likelihood values (equivalent to the *G* test statistic) between the model with the new term and the model without it (Hosmer and Lemeshow 1989). I evaluated the overall fit and stability of the models using traditional residual diagnostics as well as values such as leverage, Cook's D, and DfBeta that allow the identification and quantification of the effect of outliers (Norusis 1994).

I analyzed the effects of herbivory on reproduction in three steps. First, I quantified the probability of a plant setting seed and being present at the last census, including plants that had all of their fruits eaten just before the final census. Second, I examined the effects on seed set of fruit damage or removal. Third, I analyzed the effects of herbivory on seed set that occurred before fruit set. Analyses of the effects of herbivory on the probability of reproduction were again limited by small sample sizes. However, sample sizes were still adequate to evaluate the effects of insect herbivory alone at Barton Creek in both years. As with survival, the effects of insects and deer could both be analyzed only at Valburn in 1995. I analyzed these data using logistic regression equations identical to those described for the survival analysis. I coded the dependent variable as 1 for 'did reproduce' and 0 for 'did not reproduce'.

To quantify the effects pre-dispersal seed predation, I estimated the fraction of tissue removed from damaged fruits to the nearest 10%. Estimation of seed predation by fruit removal was also possible because the length of fruits changed < 10% between censuses. I estimated the number of seeds removed from the difference in fruit length before and after the herbivory took place (both values were based on the regression equations described above). This method assumed that there was no compensation for the lost fruit tissue by increased seed production in remaining fruits. This was a reasonable assumption because in only four cases (out of 109) were new fruits produced following removal. Moreover, the length of damaged fruits did not change after herbivory. Second, I estimated the effects of herbivory before fruit set on fecundity using analysis of covariance (ANCOVA) models with stem basal diameter as a covariate and all sites pooled.

I explored the effect of herbivory on the timing of flowering using logistic regression models similar to those used in the survival analysis. I pooled the time at first flower emergence into a single binary variable which took a value of either ‘early’ or ‘late’ (corresponding to the first three or last three of the six adult censuses, respectively). I could not separate herbivory by type so I categorized it as occurring or not. In order to remove the effect of plant size and site, I fitted logistic regression models to these data. To take potential size preferences into account I included the size x herbivory interaction term if its inclusion significantly improved model fit.

Caging experiments

In May 1994, a new population of *S. bracteatus* was discovered. Because I knew this population would be destroyed within 2-3 years (it was on a planned development site, Mesa), I decided to use it for experimentation rather than for the observational studies described above. The population’s relatively large size, large spatial extent, and lack of human presence made it particularly suitable for this purpose. My goal was to separate the effects of deer from that of the joint effects of insect and deer. I did this by caging a subset of plants and comparing them to those in uncaged plots. Because plants were highly clumped, I assigned treatments randomly to plant groups. I defined groups as being at least 3 m apart to minimize cage effects on uncaged plots. I classified plant groups into three density categories and made treatment assignments randomly within each category. I replicated treatments six times in 1994 and nine times in 1995.

Cages were 1 to 2 m in diameter and 1.5 m tall, and constructed of 14-gauge galvanized welded wire fabric (i.e. hardware cloth) with a mesh size of 2 x 4 in. All adult measurements were identical to those described above. In 1994, I installed cages immediately after the population was discovered and permission to work on the site was secured. By this time, 26% of the plants were already eaten. To account for this, it would have been best to analyze these data with an additional "pre-treatment" factor. But the occurrence of plants that were already eaten was, by chance, unevenly distributed between the caged and uncaged plots, which would have resulted in unacceptably small numbers of observations in some cells. Instead, I performed separate analyses using all plants and the subset of initially uneaten plants. Where results differed, I present data from each analysis. In 1995, I installed cages in March, before bolting. As a result, I could also compare spring rosette survival between treatments.

To test for differences in treatment effects on the probability of survival and the probability of reproduction, I used non-parametric Mann-Whitney U tests. To test for differences in the effects on final biomass and seed production, I analyzed data using ANCOVA. In these analyses, I considered treatment to be a fixed effect. I considered plot, nested within treatment, to be a random effect because only a portion (albeit a majority) of the population was sampled. Data were log-transformed to meet assumptions of normality and homoscedasticity. All analyses were performed using SPSS version 6.1.

RESULTS

Patterns of herbivory damage

Defoliation of *S. bracteatus* seedlings and rosettes in winter was common. In February 1994, immature plants at Barton Creek, Bee Creek, Mt. Bonnell, and

Valburn had moderate to heavy leaf damage on 25, 52, 60, and 45% of plants, respectively. Complete defoliation, however, was relatively rare: less than 8% of recruits were completely defoliated at any one site in either year. The net effect of this herbivory on winter survival was negligible at three of the four sites (Figure 2.1). Mortality was relatively low even among completely defoliated seedlings and rosettes: 25 to 50% of these survived to bolt in the spring.

Deer and their sign (scat and prints) were observed throughout the winter at every site except Mt. Bonnell. Despite this, uprooting was extremely rare, suggesting that winter mammal herbivory was not common. No uprooted plants were found in 1993–1994 at any site; only three uprooted plants were found at all sites in 1994–1995. Many seedlings experienced wilting without any signs of above-ground damage.

Beginning in early April, herbivore feeding patterns changed substantially. As expected, animals that fed on adult *S. bracteatus* were white-tailed deer and several insects, primarily larvae of the pierid butterfly *Anthocharis midea* (Table 2.2). These herbivores typically ate apical meristems but also ate flowers, fruits, and leaves, often in conjunction with stem herbivory. In contrast, flea beetles, common in one year at one site, fed mostly on cuticular stem tissue late in the season after leaf fall.

The frequency of plants whose stems were eaten varied among sites and years from 12 to 91% (Figure 2.2). The rate of insect herbivory was similar among sites and years (15 to 30% of herbivory was due to insects). However, the proportion of herbivory attributable to deer varied from 0 to 69%. Herbivory of an unknown type accounted for up to 37% of all eaten stems. Pathogen damage to apical meristems was absent at many sites and was relatively common only at Scenic Loop in 1995. Herbivores occasionally uprooted plants, either partially or totally (5 and 9% of all adults at the three intensively-sampled sites in which deer were present, in 1994 and 1995, respectively). Bee Creek consistently experienced the highest proportion of uprooted plants (up to 24%). Missing plants accounted for 5 and 7% of adults in 1993 and 1994, respectively.

The timing of herbivory varied among year and types of herbivore. In the first year, most forms of herbivory (as well as total herbivory) were relatively constant throughout the growing season, with peaks of deer herbivory in early May and at the end of the growing period (Figure 2.3A). In the next year, total herbivory and deer herbivory peaked in late April (Figure 2.3B). In both years, deer had a strong preference for larger plants, while insects showed no size preference (Figure 2.4).

Effects on growth and morphology

Deer and insect effects on stem elongation were always negative (Figure 2.5). Total stem length was significantly and positively correlated with final above-ground biomass (Pearson correlation coefficient = 0.79, N = 199, Valburn 1995 data), strongly suggesting that herbivory also negatively affected above-ground growth. Deer had greater negative effects on stem length than did insects in two of the spring censuses in 1994 and in all three of the censuses in 1995. However, these differences were statistically significant only in the early May interval of each year. Effects of both herbivore types and of deer increased with time in 1994 and 1995, respectively, while insect effects in 1995 remained relatively constant. The difference in magnitude of the effects of deer and insects may be due, in part, to differences in the amount of stem tissue removed by each herbivore. Deer removed about twice as much tissue per herbivory event than did insects, in both seasons (Table 2.3). Furthermore, deer removed a greater proportion of stem tissue.

On average, plants eaten by insects or deer produced twice as many stems during their lifetime as uneaten plants. In 1994, plants eaten by insects or deer produced approximately the same number of stems (X^2 test, $p = 0.45$ for estimated herbivory), while in 1995, insect-eaten plants produced more stems than plants eaten by deer ($X^2 = 33.3$, $p < 0.0001$). In contrast, the number of intact stems at the last census was relatively similar among uneaten plants and plants eaten by insects or deer (1994: $X^2 = 3.4$, $p = 0.18$; 1995: $X^2 = 77.5$, $p < 0.0001$). All combinations of pairs were significantly different in 1995: deer-eaten plants produced 70% more stems than uneaten plants. The mean number of stems at the final census did not differ between uneaten plants and insect-eaten plants; the significant X^2 value was due to differences in their distributions. The same stem was almost never eaten twice, and once eaten its stem length remained unchanged. In the majority of instances (70 and 85% in 1993 and 1994, respectively), herbivores attacked all of a plant's active meristems. Moreover, the proportion of stems attacked did not differ among herbivore types (Mann-Whitney U test, $p > 0.05$).

Effects on survival

Overall survival rates of adults in 1994 were about 79% at three of the four sites (Figure 2.6A). In 1995, however, survival rates at these three sites varied from 66 to 98% (Figure 2.6B). At Bee Creek, the probability of survival was about 40% in both years. At two sites in each year, plants that experienced herbivory always had a lower survival rate than those that did not. When herbivory of an unknown type was taken into account, only at Bee Creek did eaten plants have a higher survival rate than uneaten plants (in both years). The relative effects of different herbivore types on survival appeared to vary substantially both across sites within years and across years within sites. The effects of deer on survival were more severe in 1995 than in 1994 at all sites, while magnitude of the effects of insects across years was more site-specific.

At Barton Creek, plant size had little to no effect on the chances of survival in either year (Table 2.4). In the first year, the effect of insect herbivory was significant, strong, and negative. At Valburn in 1995, few of the model terms were significant. Despite this, the model was able to predict 87% of the cases correctly. The size x herbivory interaction term was significant only at Valburn for deer; the negative value suggests that, of plants that were eaten by deer, larger plants had less chance of survival than smaller plants.

Effects on reproduction

The magnitude and pattern of reproduction probabilities were similar within each site in both years and most values were at least 10 to 20% higher in 1994 than in 1995 (Figures 2.1 and 2.7). Reproductive probabilities were consistently lowest at Bee Creek (18 and 13% in 1994 and 1995, respectively). The probability of an eaten plant reproducing was almost always lower than that of uneaten plants; cases in which they were not occurred in sites with very few eaten plants. Insect herbivory significantly and strongly reduced the probability of reproducing (Table 2.5). Effects were greater in the first year than in the second. At Valburn in 1995, all model terms were significant except those involving deer herbivory. This may be due to the relatively small number (N = 16) of plants eaten by deer. The size of uneaten plants was strongly and positively correlated with the chance of reproducing (Figure 2.8).

The timing of flowering differed significantly between eaten and uneaten plants in both seasons ($X^2 = 42.4, 77.4$, d.f. = 1, in 1994 and 1995, respectively). The median flowering time of uneaten plants was early May while that of eaten plants was late May. When site and size were taken into account there were different results in each year (Table 2.6). The herbivory term in the 1994 model was very sensitive to the removal of outliers, indicating a generally poor model fit (note the large standard errors). However, the term remained positive, so the effect of herbivory was to delay flowering but the magnitude of the effect is unclear. The second year model was quite robust to adjustment of the model terms and the overall result was the same as that of the first year model. The effect of size was always strong and negative. That is, larger plants flowered earlier in the season.

Linear regression of total fruit length per plant on seed number at the two sites from which plants were harvested showed that total fruit length was a good surrogate for seed number in both years (adjusted $R^2 = 0.70$ to 0.93). In the second year, regression lines of uneaten plants had a significantly steeper slope but lower y-intercept than the eaten plant lines. Fruit damage and removal reduced overall seed production in the two seasons by 13 and 24%, respectively (Table 2.7). Fruit damage accounted for less seed loss than did fruit removal (24 and 10% of these effects in 1993 and 1994, respectively). Within a site, the proportion of plants attacked closely corresponded to the proportion of fruits attacked, suggesting that impacts were distributed relatively evenly among attacked plants. These fecundity effects could not be separated by herbivory type. However, I suspect that most of the fruit predation was due to insects because of the pattern of damage and the infrequent coincidence of stem herbivory (which would be expected if fruit predation by deer was more common).

The effects of herbivory before fruit set on fecundity differed markedly by year. In 1994, the assumption of slope parallelism was met (TREATMENT x SIZE term within the saturated ANCOVA model non-significant, $p = 0.11$, $F_{2,78} = 2.27$). The reduced ANCOVA model indicated that mean seed number differed significantly among treatments ($p < 0.001$, $F_{2,80} = 15.97$). Mean seed production, adjusted by size, was significantly lower in plants eaten by deer than it was in either uneaten plants or plants eaten by insects (Figure 2.9). In 1995, the assumption of parallel slopes was not met (TREATMENT x SIZE term, $p = 0.005$, $F_{2,155} = 5.52$). However, the slopes of the two eaten treatments were parallel (interaction term $p = 0.16$, $F_{1,53} = 2.06$). An ANCOVA showed that the effects of deer and insects were not significantly different ($p = 0.94$, $F_{1,54} < 0.01$). The net effect of herbivory on fecundity at one site, Bee Creek, was large: the estimated seed production in the population was 16 and 30 seeds in 1994 and 1995, respectively.

Caging experiments

The exclusion of deer at Mesa significantly increased plant performance of *S. bracteatus* in both years. The probability of survival, the probability of reproduction, final above-ground plant biomass, and seed set were greater in caged plots than in uncaged plots. These differences were significant in at least one year (Figure 2.10, Table 2.8). Plants outside cages produced much less seed per plant than caged plants in 1995, but this difference was not significant (Figure 2.10D, Table 2.8). The significant PLOT(TREAT) term suggests that high variance in seed production among plots obscured the treatment effect in this year. When plots were pooled the negative effect of deer became significant ($p = 0.002$).

The proportion of missing plants also differed by treatment: 21 and 31% of plants were missing outside cages versus 5 and 6% inside cages in each year, respectively. Differences in responses between years were not consistent among the variables. In most cases, deer reduced the performance of *S. bracteatus* more during the wet year (1995) than during the dry year. The proportion of plants eaten by insects was the same in both years whether deer were present or not (Figure 2.11).

DISCUSSION

Several major conclusions can be drawn from my results. Herbivory had strong negative effects on all aspects of plant development and performance of *Streptanthus bracteatus*, including growth, survival, and fecundity. There was substantial spatial variation in these effects (among sites) but less temporal variation. The magnitude of these effects appeared to be correlated with the intensity of deer herbivory, not insect herbivory. Finally, as I argue below, herbivory has the potential to cause local extinctions of *Streptanthus bracteatus* and of rare plants in general, especially of annuals.

The most common insect herbivore observed feeding on *S. bracteatus*, *Anthocharis midea*, is a specialist on the Brassicaceae (Scott 1986). This was a new feeding record for this species (C. Durden, Texas Memorial Museum, *personal communication*), but it was not unexpected. *A. lanceolata* has been recorded feeding on a rare *Streptanthus* in Oregon (Shapiro 1984). Moreover, herbivory by other pierid butterfly larvae has been recorded on other *Streptanthus* species (Karban and Courtney 1987). Indeed, pierids are common pests of the Brassicaeae (Bonnemaison 1965; Root 1973; Zhang 1994; Gomez 1996). Adults of *A. midea* are found in central Texas in late February through early April (Durden 1990) and I observed their larvae feeding on *S. bracteatus* from late April through May. Therefore, this common predator can only affect *S. bracteatus* during its adult stage.

Flea beetles may be a more important herbivore of *S. bracteatus* than my results suggest. *Psylliodes* is a specialist on the Brassicaceae (E. Riley, Texas A &

M University, *personal communication*) and other chrysomelid beetles commonly attack mustards (Louda 1984; Lamb 1988; Louda and Rodman 1996). Pathogen damage was absent at most sites and rare at all other sites. Because pathogen damage was low in both the wet and the dry year, it is unlikely that it had major effects on *S. bracteatus* performance. In contrast, in another system pathogens have been found to have effects at least as great in magnitude as those of insect herbivores (Hatcher 1996).

Herbivory is much less important in the winter than in the spring. Survival of *S. bracteatus* rosettes in winter was unexpectedly high at three of the four intensively-monitored sites in both years, despite the prevalence of damaged leaves or defoliation. This suggests that winter herbivory has little or no effect on seedling or rosette survival. Because of the pattern of leaf damage, most of this herbivory was probably due to insects or possibly to snails or slugs, although some of the damage was consistent with small mammal herbivory (e.g., complete defoliation of seedlings). At Mt. Bonnell, where winter survival was much lower than at the other sites, above-ground herbivory was only partially responsible since many seedlings were visibly water-stressed but showed no signs of herbivory before they disappeared (D. Zippin, *personal observation*). Frost is a common cause of winter mortality of annuals in other regions (Regehr and Bazzaz 1979). The infrequent occurrence of frosts in central Texas may partly explain the high winter survival of *S. bracteatus*.

This species appears to have a remarkable ability to recover from severe seedling herbivory. Many seedlings that were completely defoliated survived to bolt in the spring. This pattern is also seen in other species (Dirzo and Harper 1980; Pyke 1987). Furthermore, these results are consistent with other studies that show that insects have little to no effect on seedling survival or the number of flowering plants (Louda 1982; Brown et al. 1987; Hulme 1994). However, seedling herbivory may have indirectly affected adult growth through a reduction in below-ground storage reserves (Hatcher 1996).

Although the effect of herbivory on the growth of adults was always negative, the low to moderate magnitude of these effects in the early spring suggests that *S. bracteatus* may be able to compensate, at least partially, for tissue removed then. Herbivory later in the season caused greater reductions in growth. Growth of uneaten plants ceased in late May, so any herbivory at or after that time resulted in a severe net loss of tissue. Because many plants eaten at the beginning of the season were also eaten later, it was not possible to separate the effects of early from late season herbivory.

In experimental studies of other forbs, herbivory later in the growing season is known to have larger effects on plant performance than it does earlier in the season (Benner 1988; Canham et al. 1994; Gedge and Maun 1994; Lowenberg 1994). For example, in the annual *Corispermum hyssopifolium*, simulated deer browsing resulted in reductions in fecundity only after clipping late in the season (Gedge and Maun 1992, 1994). Interestingly, simulated deer herbivory caused reductions in fruit number in another species that were proportional to the clipping intensity when performed early in the season. But when clipping was performed late in the season just before anthesis, the negative effects were greatly magnified.

In populations of *S. bracteatus*, most of the adult herbivory occurs in the beginning of the spring. However, herbivory later in the season appears to have a much larger effect on plant fitness because there is little time for plant recovery.

Deer reduce the growth of *S. bracteatus* more than insects did for at least two reasons. First, deer remove more plant tissue and a greater proportion of plant tissue. Second, deer may affect plant vigor because of the physical disturbance that browsing causes. Partial uprooting by deer, while relatively uncommon (< 5% of adults in both seasons), always caused heavy damage to fine roots and resulted in the taproot being partially exposed. Similar but hidden damage to fine root systems may occur in other deer-eaten plants. In a study of biennial composite, simulated below-ground herbivory had a much greater effect than above-ground herbivory on biomass, survival, and flower production (Reichman and Smith 1991). Deer may damage the roots of *S. bracteatus* as much or more than they damage above-ground tissue.

Stem number is a critical aspect of plant architecture and determines the number of meristematic sites available for future seed production. Herbivore effects on stem production have been hypothesized to be the mechanism through which herbivores affect plant fitness (Paige and Whitham 1987; Paige 1992). Although herbivory did increase lifetime stem production in *S. bracteatus*, the number of stems capable of producing fruits at the end of the season was not affected. This suggests that, if *S. bracteatus* can survive herbivory to reproduce, it is able to compensate for herbivory on a per-meristem basis. This result contradicts other studies of herbs in which herbivory increased stem number (Islam and

Crawley 1983; Paige and Whitham 1987; Benner 1988; Paige 1992; Bergelson et al. 1996; Escarre et al. 1996).

Deer herbivory greatly reduced survival in 1995. Effects in 1994 appeared to depend on location. The deleterious effects of insects on survival varied from apparently absent to moderate and were never greater than those of deer at a given site. At Mesa, deer reduced plant survival by up to 40%. This strong effect is surprising given that deer-eaten plants were so much larger than other plants and would be expected to have a greater chance of survival than smaller plants. A positive correlation between plant size and mortality was also found in another study (Watkinson et al. 1979).

The greater proportion of missing plants outside cages at Mesa strongly suggests that deer ate or carried away many entire plants. Moreover, below-ground disturbance of non-uprooted plants as described above could also be causing the greater reductions in survival by deer than by insects. These results are consistent with some studies in which moderate to large effects of mammal herbivory on adult survival of herbaceous species are found (Bishop and Davy 1984; Reichman and Smith 1991; Bergelson and Crawley 1992; Gedge and Maun 1994; Ehrlén 1995a). Except in cases of pest outbreaks or in their use as biocontrol agents, insect herbivores typically have little to no effect on the survival of adult perennial plants (Crawley 1989a). However, their effect on adult annual plant survival has received comparatively little attention.

Herbivory has pronounced effects on all aspects of the reproduction of *S. bracteatus*. Herbivory reduces the chance of producing flowers, delays flowering by at least two weeks, and reduces seed set. Deer appear to have a greater effect on seed set via reductions in growth than insects do. Although differences in pre-dispersal seed predation by deer and insects could not be separated by these analyses, insects are probably more important in this respect than deer (Louda, 1983; Crawley, 1989; D. Zippin, *personal observation*). In contrast to other annual species (Gedge and Maun 1992, 1994), *S. bracteatus* did not compensate for fruit damage or removal.

The delay in reproduction may have caused some of the reduction in seed set. Plants that reproduce later almost certainly experience more drought stress at the end of the season, which may reduce the time available for fruit and seed maturation. Secondarily, the timing of flowering and the synchrony of its occurrence are known to be important determinants of pollination success and seed set in some obligate outcrossing plants (Schemske 1977; Auspurger 1981; Crawley 1983; Gross and Werner 1983). However, the effect of herbivory on the phenological pattern of most host plants is essentially unknown (Crawley 1989a). One bee species, *Megachile comata*, has been observed visiting *S. bracteatus* (Dieringer 1991). If the activity of this pollinator decreases in the late spring, seed set in *S. bracteatus* might be reduced. Fewer plants flower at the end of the season (Appendix 1), so even if the activity level of the pollinator does not change, the attractiveness of the population to pollinators might be reduced. Furthermore, plants flowering later in the season might receive fewer effective visits. A study conducted in 1989 at Valburn showed that seed set in *S. bracteatus* can be partially limited by effective delivery of outcross pollen (Dieringer 1991). One would expect a higher proportion of self pollen being delivered when fewer plants are in flower. This might also reduce seed set or result in the production of smaller seeds (Kalisz 1989).

Conservation implications

Given the strong effects on the performance of *S. bracteatus* that were observed in this study, herbivory may be limiting its population growth. Indeed, if these negative effects continue, local population sizes may decline. However, herbivory is unlikely to drive the species to extinction because of the high variation in deer herbivory rates throughout this species' range. Consistently strong negative effects of deer herbivory were evident only at Bee Creek. If seed set at that site remains as low as it did in the two years of this study, intensive management will almost certainly be required to prevent extinction. At other sites, the management of deer may only be required during wetter years, when their effects appear to be greatest. Because populations of *S. bracteatus* appear to respond mostly to winter rainfall (Appendix 1), appropriate management action can be taken well in advance of the spring and early summer when deer affect adult plants.

The differences among sites in the rates of deer herbivory on *S. bracteatus* may be related to differences in deer density. Alternatively, they may be due to differences in feeding behavior in response to different vegetation. For example, the population in Medina County that experienced a very low rate of deer herbivory in 1995 grew along a rural road right-of-way, which may have served as a refuge from deer herbivory. Many of the plants at this site were also within dense shrub cover (Appendix 1), possibly affording further protection. The substantial spatial variation in deer herbivory among sites may also influence the spatial distribution of *S. bracteatus* populations. Herbivory is strong enough to influence the spatial distribution of plants in other systems (Inouye et al. 1980; Parker and Root 1981; Louda 1983; Swank and Oechel 1991; D'Antonio et al. 1993; Louda and Rodman 1996). The relationship between the density of herbivores and the magnitude of their effect is a phenomena of general interest that requires further study (Chapter 1).

Site conditions could also alter herbivore behavior through differences in plant community structure. For example, higher forb cover or diversity at a site may reduce the herbivory rates on a single species, assuming there are other equally or more desirable substitutes nearby. This may explain the relatively low rates of herbivory at Barton Creek, where herb cover and diversity is very high. However, it has been suggested that some especially desirable plants, or "ice cream plants", may be so attractive to an herbivore that it will seek the species out wherever it is found (Crawley 1989b). The very high rates of herbivory on *S. bracteatus* observed at some site suggests that it may be an "ice cream plant", at least to deer. Although vertebrate herbivores tend to have a greater frequency of highly preferred species than insects (Crawley 1989b), there are cases of insects preferentially feeding on plants and causing high mortality (Parker and Root 1981; Thomas 1986). A study of the digestibility and nutrient quality of *S. bracteatus* would provide useful data relevant to this question.

Insects and mammals may not feed independent of one another (Danell and Huss-Danell 1985; Doak 1991; Strauss 1991). However, in *S. bracteatus*, there is a lack of correlation between the herbivory rates of insects and deer among sites and seasons. This suggests that deer and insects do feed independently of one another. The results of the caging experiment provide stronger support for this hypothesis: when deer were excluded, insect attack rates did not change in either year.

This bodes well for managers interested in improving the performance of *S. bracteatus* by excluding or removing deer. Resource managers planning the reduction or removal of one herbivore from a system in which multiple herbivores are present must consider the indirect effects on the remaining herbivores. Such a manipulation might result in the increase of the population of other herbivores and a subsequent increase in their effects on the target species. If the shift is large enough, the same net negative effect on the rare host may occur. Although this does not appear to be true of *S. bracteatus*, caging experiments in other natural populations should be done to confirm that insects and deer feed independently of one another.

Herbivory may be responsible for the rarity and continued decline of other rare plants. For example, white-tailed deer have been cited as having detrimental effects on at least 98 rare taxa in the eastern United States (Miller et al. 1992). Furthermore, rare plants that are eaten by generalist herbivores like deer may be subject to herbivory rates that are much higher than those experienced by more common taxa. The feeding pattern of some herbivores has been shown to be inversely density-dependent (Adams 1949; Brandner et al. 1990; Van de Koppel et al. 1996) (but see Edwards 1985; Thomas 1986). As a species becomes less common, an herbivore may be able to find and feed on a larger proportion of the population. There is also evidence that sparser species are more palatable to insects than are common species (Landa and Rabinowitz 1983), although it is unclear whether this is a cause or an effect of rarity. Rare plants, including *S. bracteatus*, almost certainly constitute a very small portion of the diet of white-tailed deer. The population size of generalist herbivores like deer and only one of their food plants is not linked. Thus a rare plant could, theoretically, be eaten into extinction without any consequence to the herbivore.

CONCLUSIONS

In this study I show that plants of *Streptanthus bracteatus* that are eaten by deer have significantly lower survival, stem elongation, and fecundity than uneaten plants. These effects appear to be stronger in wet years than in dry years. Plants eaten by insects have significantly lower stem elongation and fecundity than uneaten plants, but these effects are similar between years. Deer have a greater negative effect on *S. bracteatus* than insects because deer have a strong preference for large plants, eat proportionally more tissue than insects, and uproot more plants than insects. Deer may also indirectly damage the below-ground tissue of plants by the physical action of browsing. Extreme examples of this include partial or complete uprooting, which almost always results in death.

Because deer and insects appear to feed independently of one another, a reduction in deer herbivory will not result in an increase in insect herbivory. Thus a simple method of improving the performance of *S. bracteatus* is to exclude deer. This is particularly important at sites in which deer herbivory rates are highest, and in the wet years when deer herbivory effects are greatest.

Table 2.1. Census dates of wild populations of *Streptanthus bracteatus* in central Texas. Some censuses occurred over 2–3 days; in these cases, only the final census date is given. Two dates within the same month are separated by a comma. Underlined dates denote a census in which plants were harvested.

Site	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
1993–1994											
TRAVIS CO.											
Barton Creek		23	29		8	11	4, 18	4, 24	7	22	
Bee Creek		5	5	5	11	11	6, 18	1, 20	6	19	9
Mt. Bonnell		10	13	14	12	9	2, 17	3, 20	6	19	
Valburn		15	13	15	12	12	2, 17	4, 20	6	19	
Lakewood								18		4, 20	
Mesa							20			14	
MEDINA CO.											
Scenic Loop								7	8		
Lakeview								7	8		
1994–1995											
TRAVIS CO.											
Barton Creek	12	14	10	6	2	10	11, 27	8, 24	6	13	
Bee Creek	13	10	7	4	2	7	8, 24	8, 23	5	13	
Mt. Bonnell	13	9	9	4	1	7	6, 25	7, 23	5	13	
Valburn	10	17	8	4	1	7	6, 26	7, 22	4	10	2
Mesa						11	14	12	19	3, 21	8
MEDINA CO.											
Scenic Loop								4		11	
Lakeview								4		11	
BEXAR CO.											
Eisenhower Park								17		11	

Table 2.2. Observations of herbivores that feed on adult *S. bracteatus* at each study site in central Texas. "++" represents a species that was seen on multiple occasions and "+" indicates that a species that was seen only once.

				Lepidopterans			
Sites	Deer	Pathogen†	*A. midea*[1]	*Hyles lineata*[2]	*R. ou*[3]	*Udea rubigalis*[4]	flea beetles[5]
TRAVIS CO.							
Barton Creek	+	++	++	+			+
Bee Creek	++	+	++		+		++
Mt. Bonnell			*				
Valburn	++	+	++			+	
Lakewood	++		*				
Mesa	++	+	*				+
MEDINA CO.							
Lakeview	+	+	++				
Scenic Loop	+	++	++		+		
BEXAR CO.							
Eisenhower Park	+	++	*				

† Includes powdery mildew and viral-like infections

* Species not observed but damage consistent with this common species was present

[1] *Anthocharis midea annickae* dos P.&K., falcate orange-tip (Pieridae: Pierinae); det. by C. Durden, Texas Memorial Museum, U. of Texas, Austin, TX

[2] *H. lineata* Fabricius, white-lined sphinx (Sphingindae: Macroglossinae); det. by C. Durden

[3] *Rachiplusia ou* (Gn.), gray looper moth (Noctuidae: Plusiinae)

[4] *U. rubigalis* Guenee, greenhouse leaf-tier (Crambidae: Spilomelinae); det. by M. A. Solis, Systematic Entomology Lab, USDA, Beltsville, MD.

[5] *Psylliodes convexior* LeConte, flea beetles (Chrysomelidae: Alticinae); det. by E. Riley, Dept. of Entomology, Texas A&M University, College Station, TX.

Table 2.3. The estimated amount and proportion of tissue of *S. bracteatus* removed by herbivores at four sites (pooled) in Travis County, Texas, in two seasons. Letters indicate statistically similar groups based on one-way ANOVAs performed on the mean stem length in each season. 's.e.' = standard error.

	Herbivore Type		
	Deer	Insect	Unknown
1994			
N	53	45	26
mean est. stem length removed (cm)* ± s.e.	5.9 ± 0.8^{a}	2.9 ± 0.5^{b}	3.7 ± 0.8^{ab}
mean est. % stem removed ± s.e.	59.4 ± 5.2	42.0 ± 5.0	51.0 ± 5.8
No. (%) cases where post– ≥ pre–herbivory length**	6 (10)	51 (53)	11 (30)
1995			
N	95	101	61
mean est. stem length removed (cm) ± s.e.	10.1 ± 0.8^{a}	3.4 ± 0.5^{b}	5.0 ± 0.6^{c}
mean est. % stem removed ± s.e.	55.0 ± 3.3	38.0 ± 3.3	63.7 ± 3.7
No. (%) cases where post– ≥ pre–herbivory length	123 (56)	131 (56)	52 (46)

* calculated by the difference in stem length before and after herbivory

** because of the high proportion of cases in which stem regrowth after herbivory exceeded the amount of tissue removed, the values in this table are underestimates of the true values

Table 2.4. Results of logistic regressions testing the effect of size and herbivory on the probability of survival of ***Streptanthus bracteatus*** at two sites in Travis County, TX. At Barton Creek, only insects and uneaten plants are compared. At Valburn, insects, deer, and uneaten plants are compared. The reference category for herbivory is NONE.

Model	d.f.	β	s.e.	$e^{\beta *}$	$p^{\dagger}$
1994					
Barton Creek					
Constant	1	2.50	0.72		***
SIZE	1	0.12	0.50	1.13	N.S.
HERBIVORY	1	–2.21	0.60	0.11	***
1995					
Barton Creek					
Constant	1	3.06	0.89		**
SIZE	1	–0.27	0.55	0.76	N.S.
HERBIVORY	1	0.91	0.84	2.50	N.S.
Valburn					
Constant	1	1.18	1.26		N.S.
SIZE	1	2.73	1.81	15.35	N.S.
HERBIVORY	2				N.S.
DEER	1	–0.66	1.55	0.51	N.S.
INSECT	1	–3.10	2.17	0.04	N.S.
HERBIVORY x SIZE	2				*
DEER x SIZE	1	–3.24	1.86	0.04	+
INSECT x SIZE	1	3.04	3.26	20.80	N.S.

* The exponent of the coefficient indicates the proportional change in the odds ratio with a change of one unit of the variable. No effect = 1; very small or very large values indicated large effects.

[†] N.S. = not significant, + = $p < 0.1$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$; significance levels are based on the Wald statistic; when d.f. = 1, this statistic equals the square of the ratio of the coefficient to its standard error (s.e.).

Table 2.5. Results of logistic regressions testing the effect of size and herbivory on the probability of *Streptanthus bracteatus* reproducing at two sites in Travis County, TX. The reference category for herbivory is NONE. Footnotes are the same as in Table 2.4.

Model	d.f.	β	s.e.	$e^{\beta *}$	$p^{\dagger}$
1994					
Barton Creek					
Constant	1	−1.44	0.97		N.S.
SIZE	1	3.04	0.96	20.84	**
HERBIVORY	1	−2.38	0.72	0.09	***
1995					
Barton Creek					
Constant	1	−1.70	0.80		*
SIZE	1	2.22	0.70	9.24	**
HERBIVORY	1	−1.56	0.56	0.21	**
Valburn					
Constant	1	−3.82	1.14		***
SIZE	1	6.34	1.53	568.78	***
HERBIVORY	2				*
DEER	1	−7.97	6.67	0.0003	N.S.
INSECT	1	3.41	1.34	30.28	*
HERBIVORY x SIZE	2				**
DEER x SIZE	1	0.72	4.19	2.06	N.S.
INSECT x SIZE	1	−6.01	1.66	0.002	***

Table 2.6. Results of logistic regressions testing the effect of size, herbivory, and site on flowering time in four Travis County, Texas, populations of *Streptanthus bracteatus*. Model coefficients indicate effects on flowering later. The reference category for herbivory and site is NONE and BARTON CREEK, respectively. Footnotes are the same as in Table 2.4.

Model	d.f.	β	s.e.	$e^{\beta *}$	$p^{\dagger}$
1994					
Constant	1	1.87	0.68		**
BDIAM	1	−2.99	0.63	0.05	***
HERBIVORY	1	6.57	3.40	711.01	+
HERBIVORY x BDIAM	1	−0.91	1.79	0.40	N.S.
SITE	3				***
BEE CREEK	1	0.08	1.12	1.08	N.S.
MT BONNELL	1	1.56	0.90	4.77	+
VALBURN	1	2.37	0.59	10.70	***
1995					
Constant	1	4.20	0.78		***
BDIAM	1	−4.39	0.67	0.01	***
HERBIVORY	1	−1.51	0.84	0.22	+
HERBIVORY x BDIAM	1	4.18	0.71	65.18	***
SITE	3				***
BEE CREEK	1	−2.48	0.76	0.08	**
MT BONNELL	1	0.65	0.59	1.91	N.S.
VALBURN	1	−0.65	0.40	0.52	N.S.

Table 2.7. The amount of silique damage to and removal from *S. bracteatus* by herbivory, separated by site. The number of seeds removed was estimated assuming no compensation after herbivory. At many sites, censuses were not frequent enough to estimate whole fruit loss (–).

Site	No. plants with fruits removed (%)[†]	No. fruits removed (%)[†]	No. plants with damaged frts (%)	No. fruits damaged (%)	Estimated no. seeds removed (%)
1994					
TRAVIS CO.					
Barton Creek	12 (16.0)	13 (12.7)	8 (10.6)	8 (8.9)	112 (7.9)
Bee Creek	0 (0.0)	0 (0.0)	1 (33.0)	1 (25.0)	2 (11.1)
Mt. Bonnell	2 (22.2)	2 (10.0)	1 (11.1)	1 (5.6)	16 (4.4)
Valburn	10 (32.3)	13 (22.4)	5 (16.1)	5 (11.1)	145 (38.4)
Lakewood	–	–	2 (5.0)	2 (2.3)	–
Mesa*	–	–	6 (20.7)	6 (17.6)	–
MEDINA CO.					
Lakeview	–	–	3 (100.0)	8 (10.8)	–
Scenic Loop	–	–	11 (35.5)	25 (15.7)	–
1995					
TRAVIS CO.					
Barton Creek	7 (14.3)	11 (15.1)	2 (4.1)	2 (3.2)	158 (22.3)
Bee Creek	3 (50.0)	3 (33.3)	1 (16.7)	1 (16.7)	30 (55.2)
Mt. Bonnell	0 (0.0)	0 (0.0)	3 (10.0)	3 (7.7)	3 (0.1)
Valburn	35 (31.0)	52 (26.4)	20 (17.7)	21 (14.5)	611 (27.7)
Mesa*	–	–	7 (13.0)	7 (9.0)	–
MEDINA CO.					
Lakeview	–	–	4 (16.7)	5 (7.8)	–
Scenic Loop	–	–	39 (16.5)	50 (7.6)	–
BEXAR CO.					
Eisenhower Park	–	–	4 (10.3)	7 (29.2)	–

* uncaged plots only

[†] includes cases where fruits were removed along with stem tissue

Table 2.8. Construction and results of the ANCOVA models comparing final above-ground biomass and number of seeds per plant between caged and uncaged plots. Initial stem basal diameter was used as the covariate. A separate model was run for each variable and each year. Model terms are listed in the order used in the design. Hierarchical sums of squares are presented.

Construction of the ANCOVA

Model term	F
COVariate	MS_{COV}/MS_{ERROR}
TREATment	$MS_{TREAT}/MS_{PLOT(TREAT)}$
PLOT (TREAT)	$MS_{PLOT(TREAT)}/MS_{ERROR}$
COV x TREAT	$MS_{COV\ x\ TREAT}/MS_{ERROR}$
COV x PLOT (TREAT)	$MS_{COV\ x\ PLOT(TREAT)}/MS_{ERROR}$
ERROR	

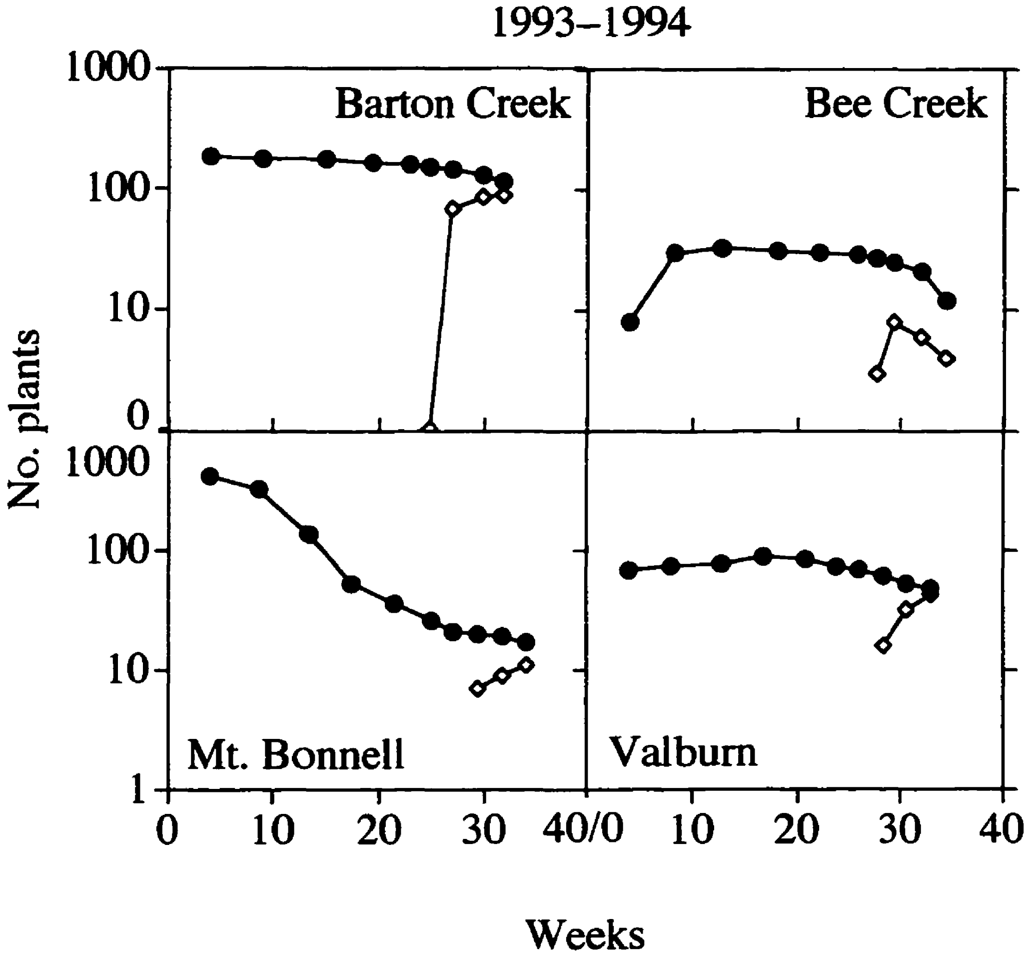
Results of the ANCOVA

	1994			1995		
	d.f	SS	F	d.f.	SS	F
biomass						
COVariate	1	23.91	124.5 ***	1	65.30	225.9 ***
TREATment	1	0.28	2.3 N.S.	1	5.03	19.8 ***
PLOT (TREAT)	10	1.21	0.6 N.S.	16	4.07	0.9 N.S.
COV x TREAT	1	0.01	0.1 N.S.	1	0.11	0.4 N.S.
COV x PLOT(TREAT)	9	0.17	0.1 N.S.	16	3.94	0.9 N.S.
ERROR	84	16.13		220	63.59	
seed number						
COVariate	1	7.47	54.6 ***	1	26.16	72.6 ***
TREATment	1	3.17	21.4 ***	1	1.39	2.0 N.S.
PLOT (TREAT)	10	1.48	1.1 N.S.	16	11.40	2.0 *
COV x TREAT	1	0.66	4.8 *	1	0.2	0.6 N.S.
COV x PLOT(TREAT)	6	0.79	1.0 N.S.	13	3.97	0.9 N.S.
ERROR	53	7.24		146	52.65	

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, N.S. = not significant

Figure 2.1. Population size (filled circles) and number of flowering or fruiting individuals (open diamonds) of *Streptanthus bracteatus* at four Travis County, TX, sites in (A) 1993–1994 and (B) 1994–1995. Censuses in 1993 began approximately one month later than in 1994. Note the log scale. Because most recruitment occurred during the first or second census interval, these curves closely resemble true survivorship curves.

A


1993–1994
Barton Creek
Bee Creek
Mt. Bonnell
Valburn
No. plants
1000
100
10
0
1000
100
10
1
0
10
20
30
40/0
10
20
30
40
Weeks

B

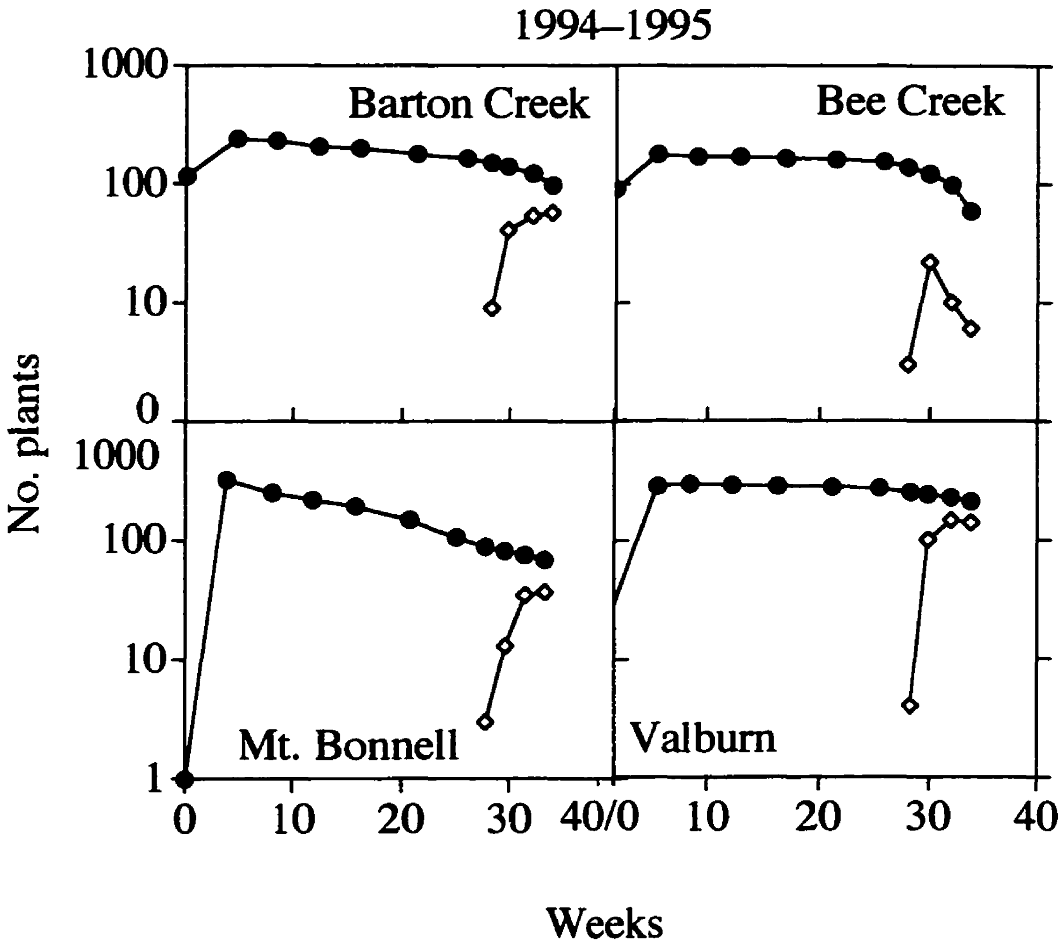
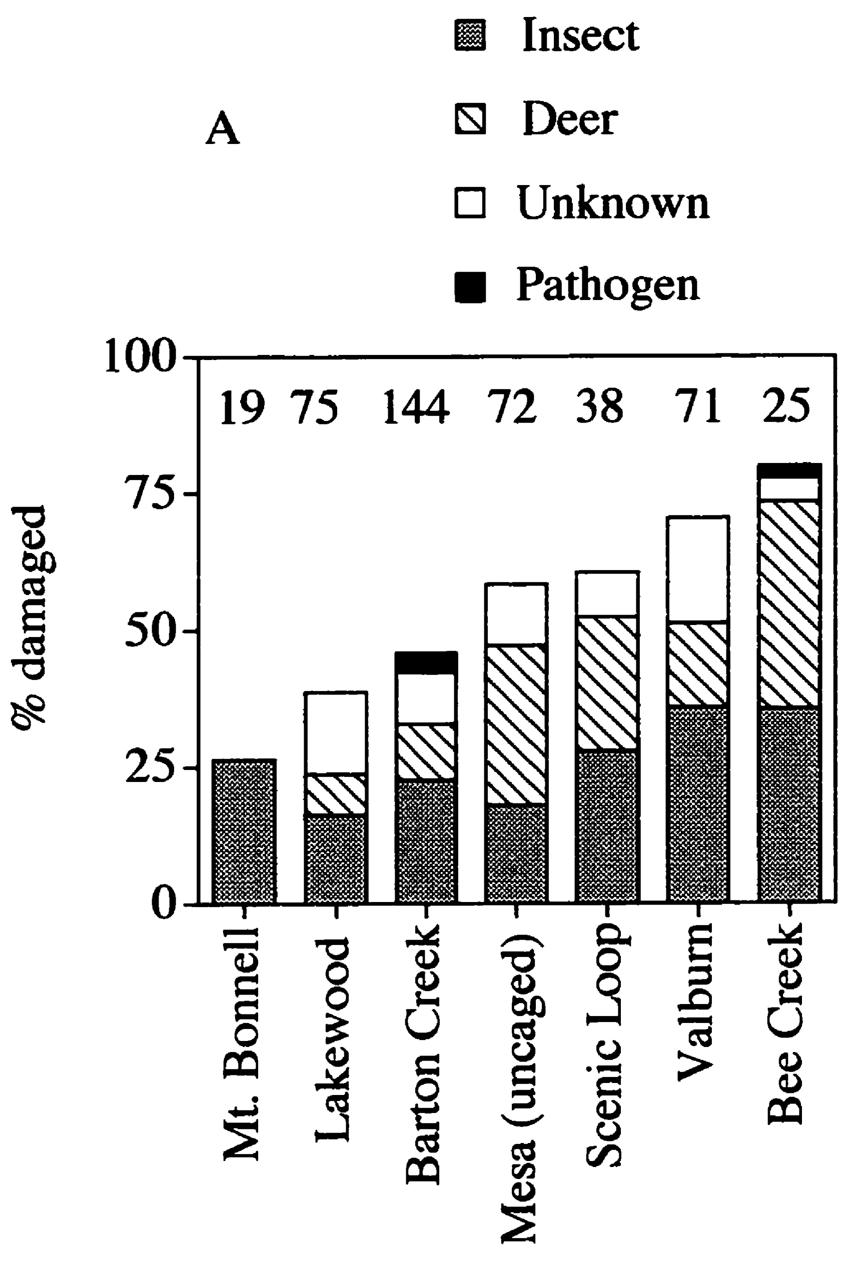

1994–1995
Barton Creek
Bee Creek
Mt. Bonnell
Valburn
No. plants
1000
100
10
0
1000
100
10
1
0
10
20
30
40/0
10
20
30
40
Weeks

Figure 2.2. Herbivory rates on *Streptanthus bracteatus* by site and herbivore type in (A) 1994 and (B) 1995. Bar height is the proportion of adults with their apical meristem eaten at least once in their lifetime. Because multiple herbivores often ate the same plant (and proportions would therefore not add to 100%), proportions within bars are based on the number of eaten stems. Sample sizes are given above each bar. Missing plants (< 10%) were assumed to be eaten by deer and insects at a 3:1 ratio.


A
Insect
Deer
Unknown
Pathogen
100
75
50
25
0
% damaged
19
75
144
72
38
71
25
Mt. Bonnell
Lakewood
Barton Creek
Mesa (uncaged)
Scenic Loop
Valburn
Bee Creek

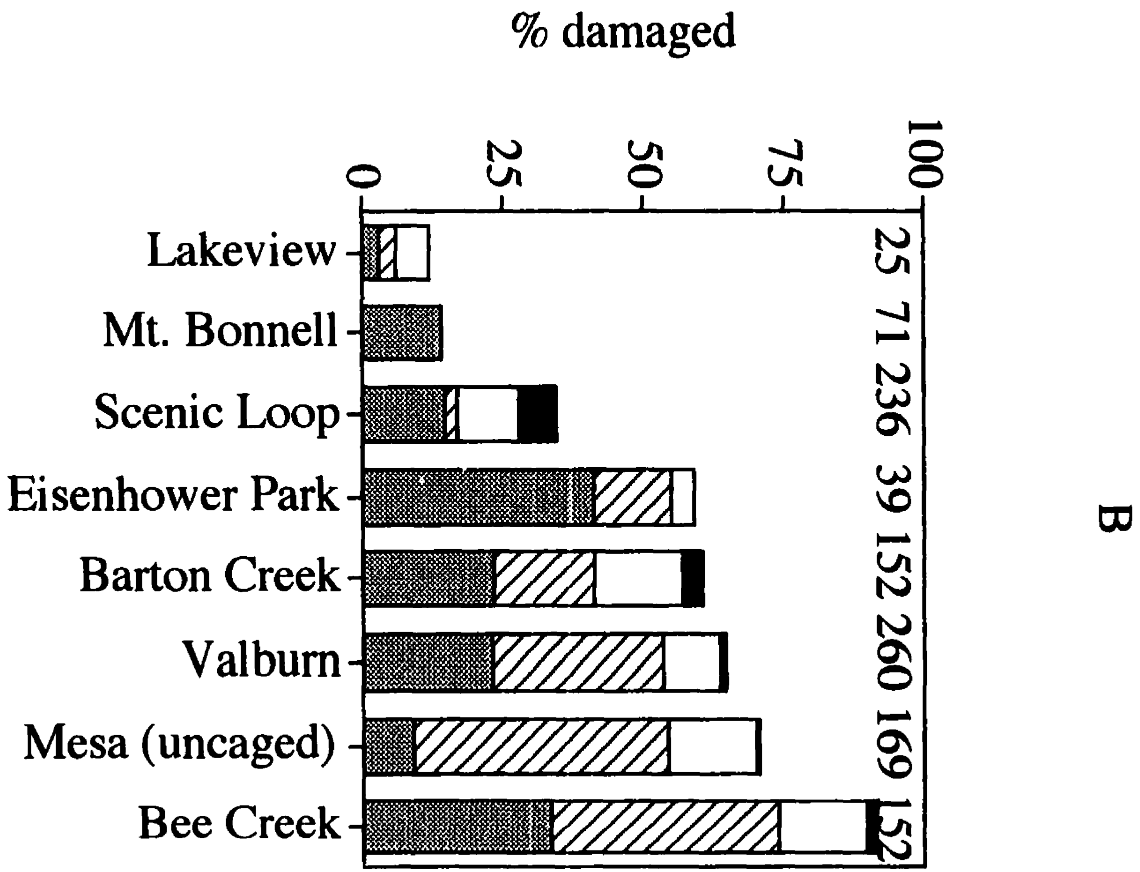
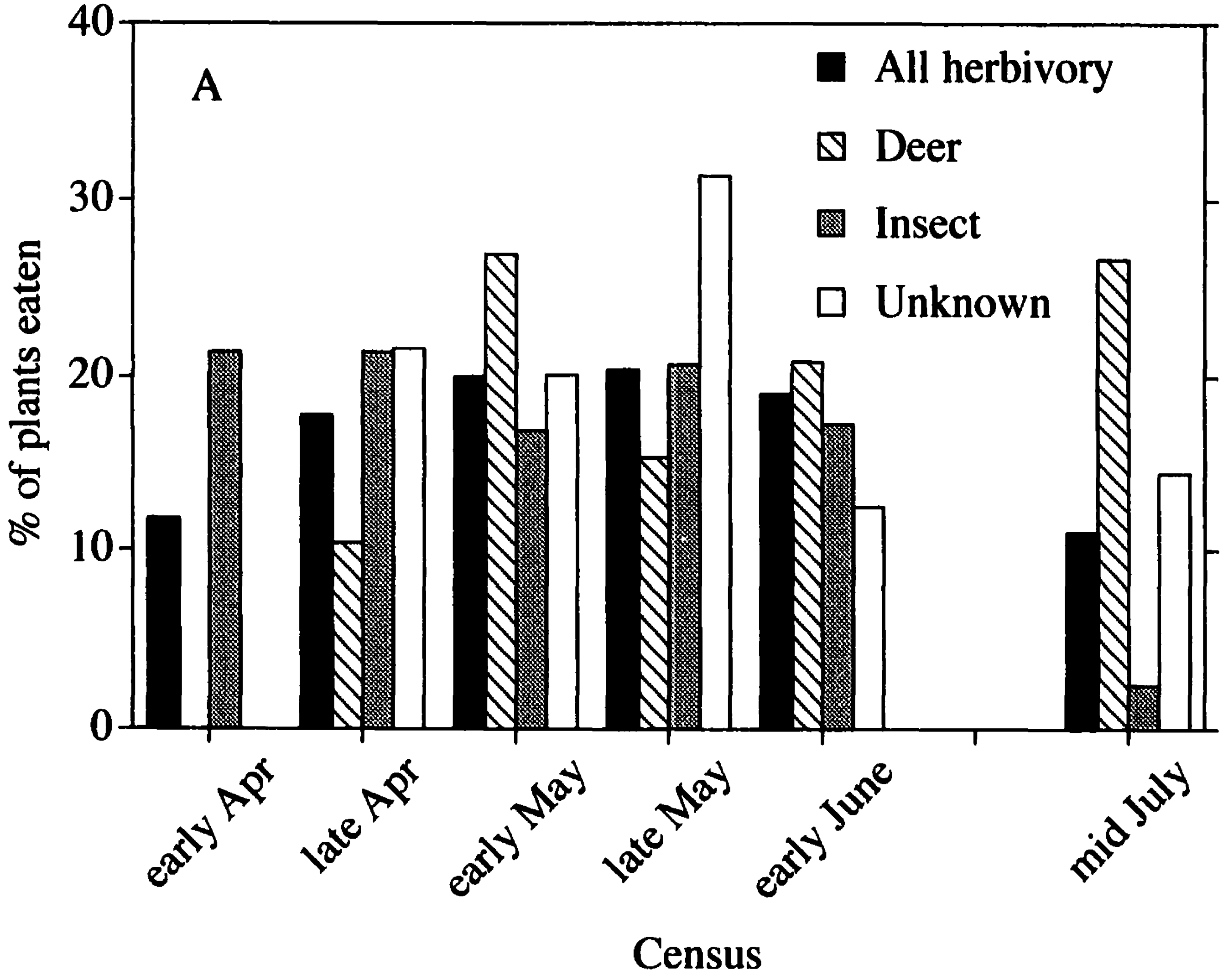

% damaged
0
25
50
75
100
Lakeview
Mt. Bonnell
Scenic Loop
Eisenhower Park
Barton Creek
Valburn
Mesa (uncaged)
Bee Creek
25
71
236
39
152
260
169
152
B

Figure 2.3. The timing of herbivory on adult *Streptanthus bracteatus* in (A) 1994 and (B) 1995. Data from the four intensively-sampled sites are pooled. Values are weighted by the population size at each census. Missing plants are assumed to be eaten by deer and insects at a 3:1 ratio. Plants attacked by pathogens are not included due to small sample size. The category 'All herbivory' is all three herbivore types pooled.


A
All herbivory
Deer
Insect
Unknown
% of plants eaten
0
10
20
30
40
early Apr
late Apr
early May
late May
early June
mid July
Census

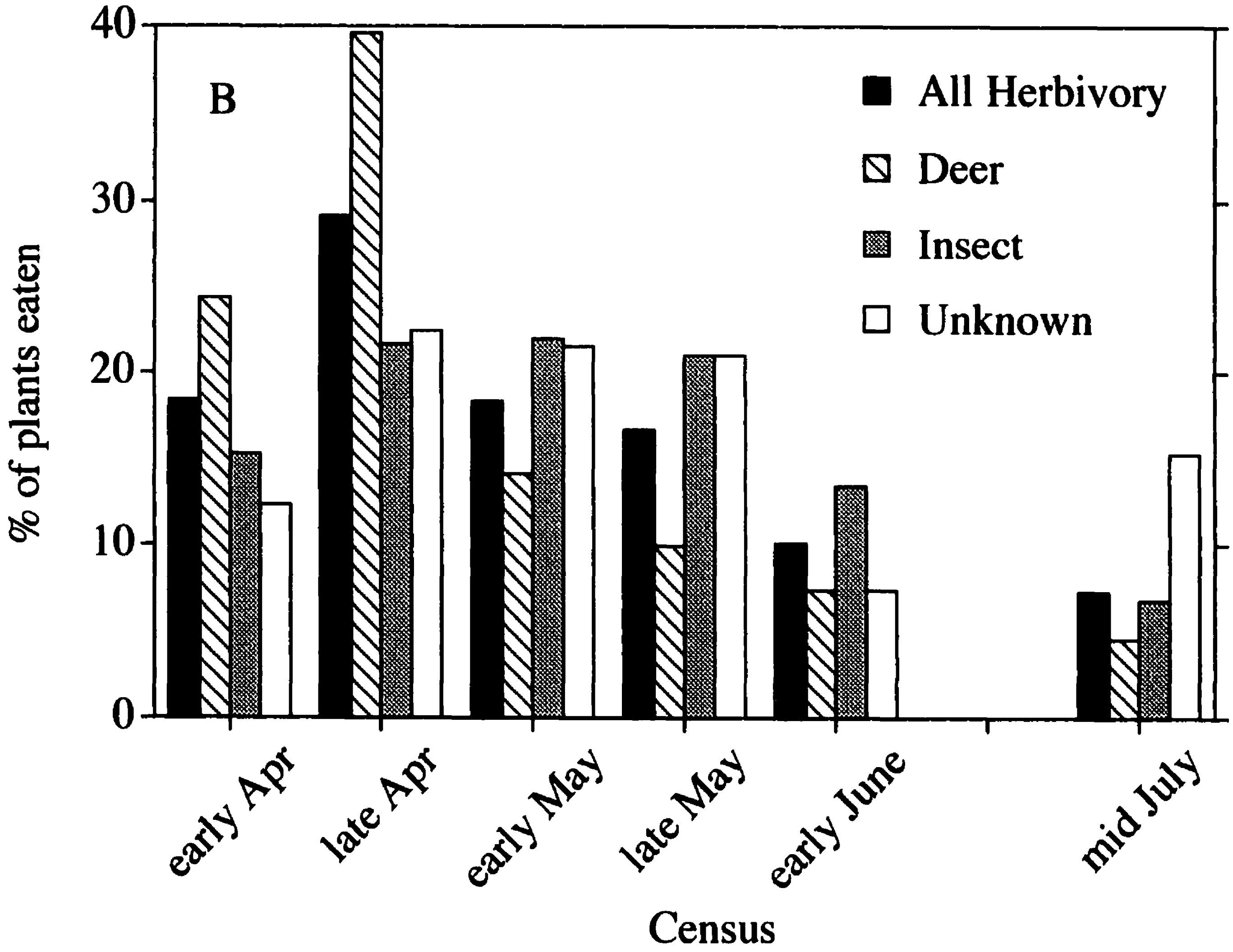

B
All Herbivory
Deer
Insect
Unknown
% of plants eaten
0
10
20
30
40
early Apr
late Apr
early May
late May
early June
mid July
Census

Figure 2.4. Herbivore size preference in 1994 and 1995. Data are pooled among sites. Values are means and standard errors of plant size for eaten plants (hatched or shaded bars) compared to a random sample of plants (open bars) paired by site and census. Only plants eaten for the first time and by a single herbivore were considered. Significance values are of paired t-tests performed separately for each herbivore type and each year. Sample sizes are given at the bottom of each bar.

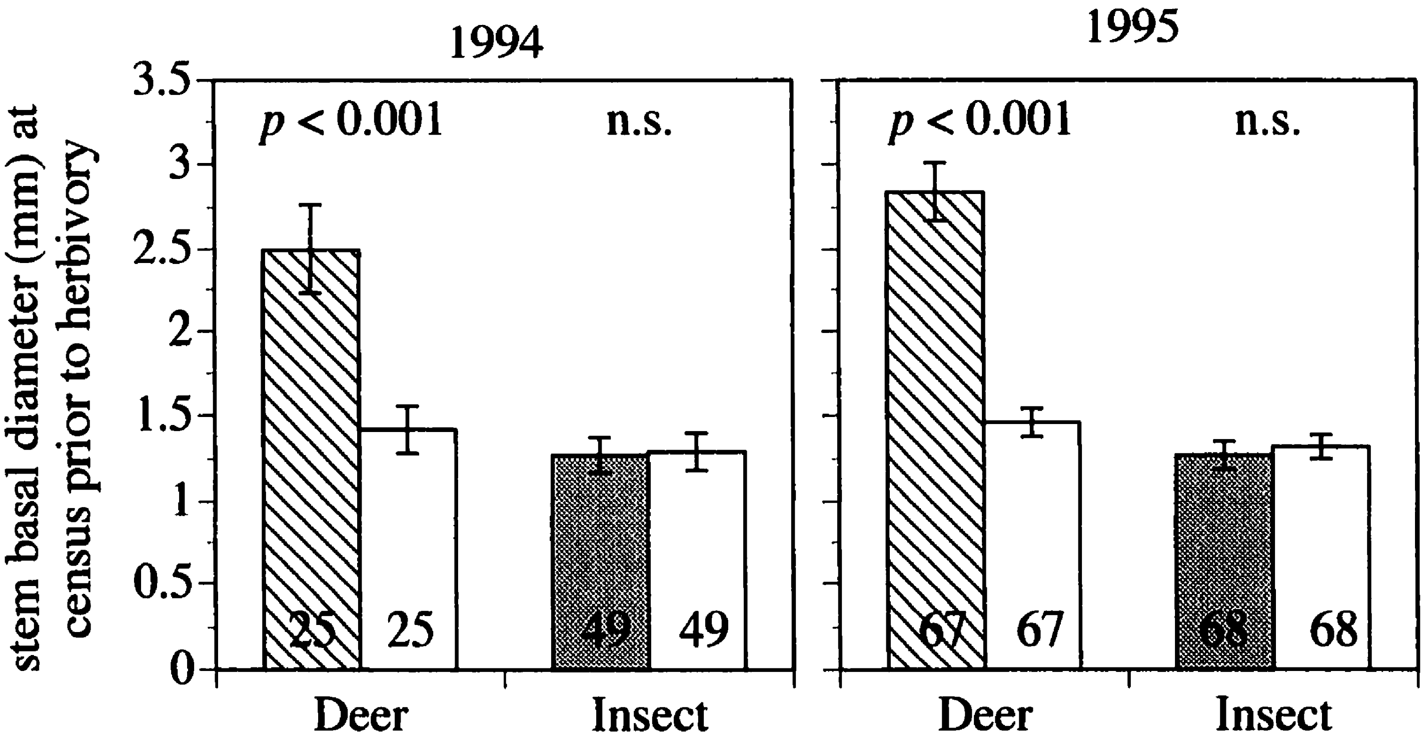
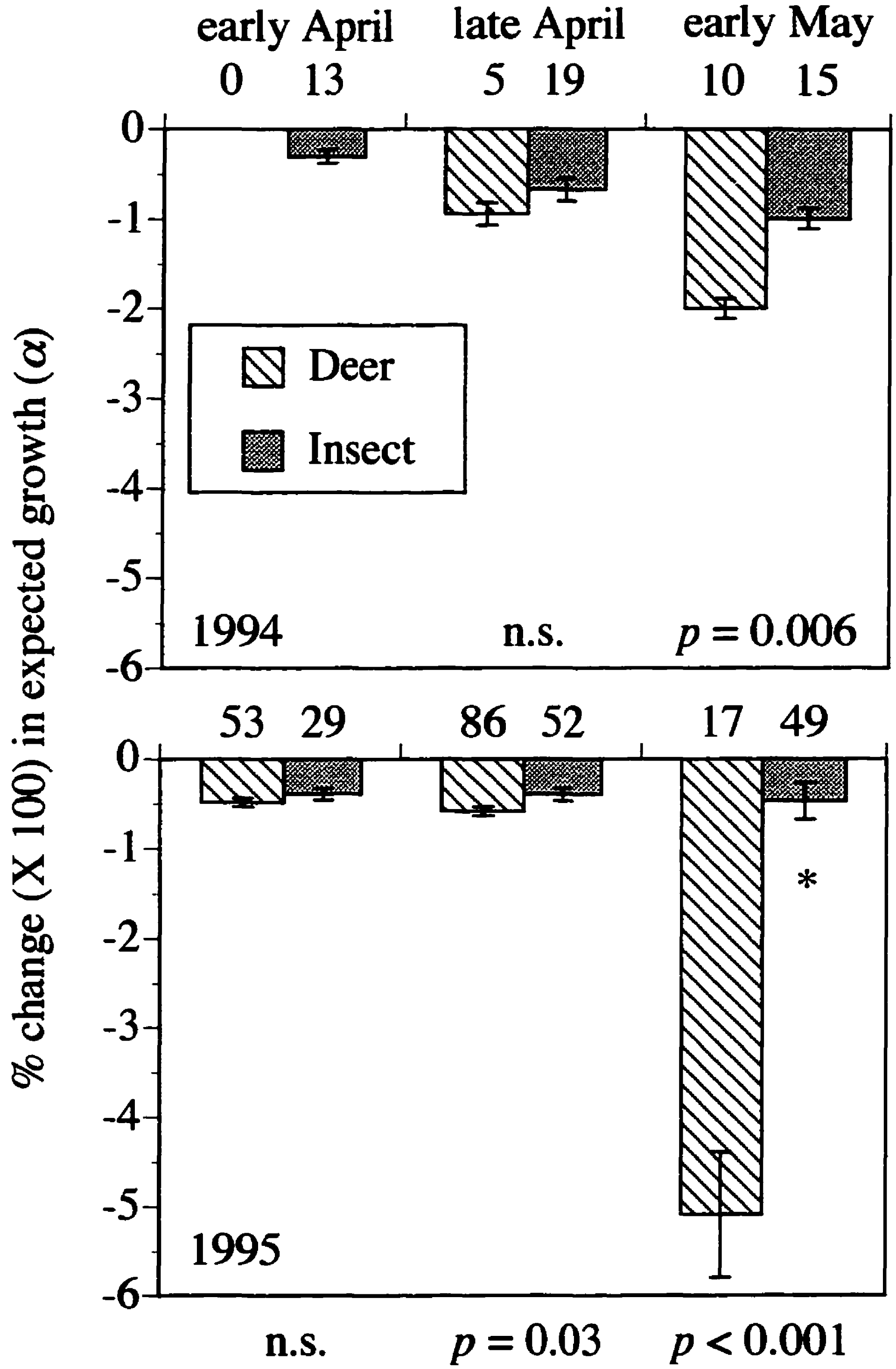
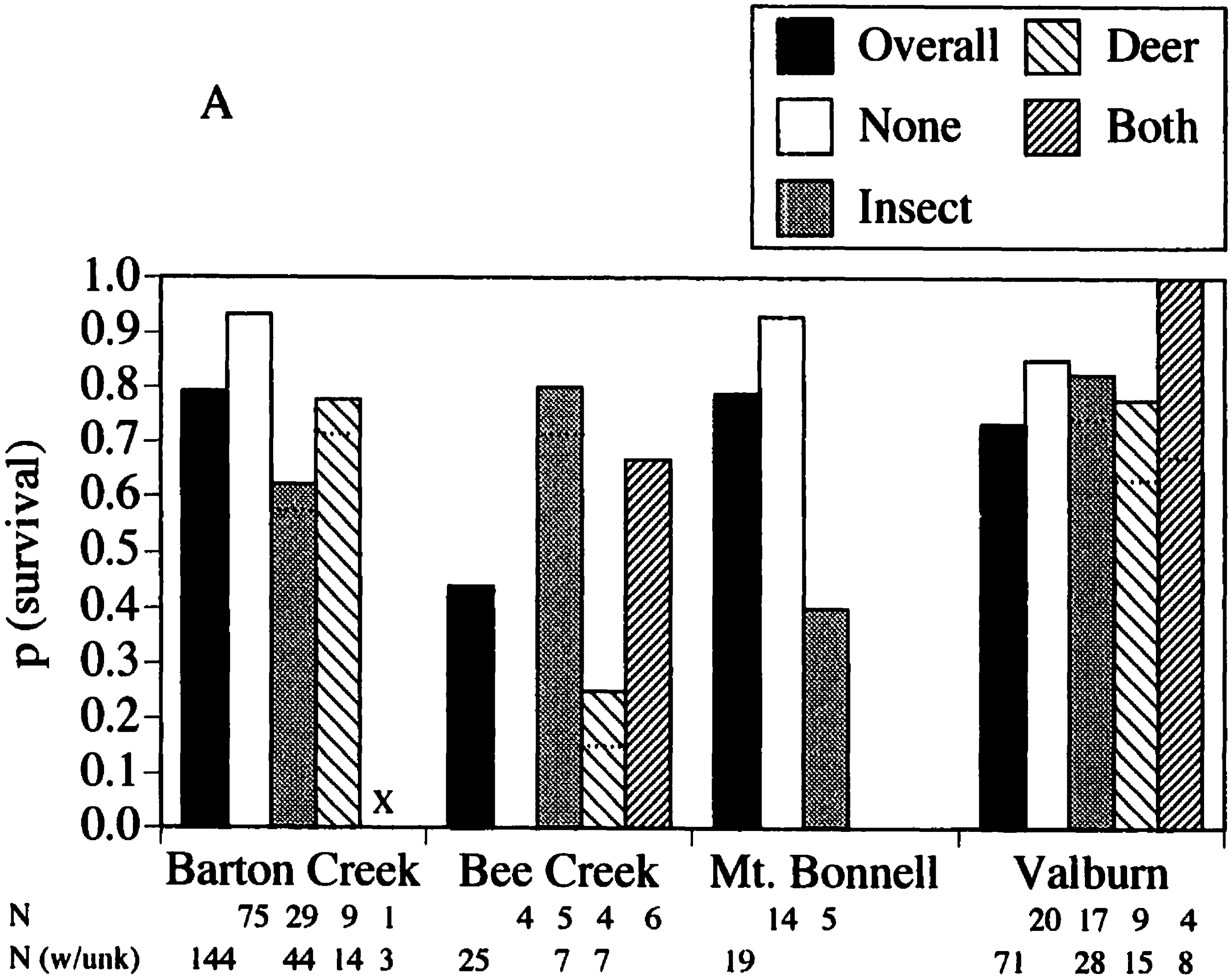

1994
1995
stem basal diameter (mm) at census prior to herbivory
3.5
3
2.5
2
1.5
1
0.5
0
$p < 0.001$
n.s.
$p < 0.001$
n.s.
25
25
49
49
67
67
68
68
Deer
Insect
Deer
Insect

Figure 2.5. Effect of herbivory on growth by herbivore type as measured by the difference between observed and expected (if uneaten) change in total stem length, pooled across sites, in the spring of 1994 and 1995. See Methods for details of these calculations. Values are means ± standard error. Significance values are from t-tests comparing the effects of deer and insects performed for each census interval and season. All means except for one (*) are significantly different from zero ($p < 0.05$). Sample sizes are given above the bars. More negative values indicate a stronger reduction in growth.



early April
late April
early May
0
13
5
19
10
15
0
-1
-2
-3
-4
-5
-6
Deer
Insect
1994
n.s.
$p = 0.006$
53
29
86
52
17
49
*
1995
n.s.
$p = 0.03$
$p < 0.001$
% change (X 100) in expected growth (α)

Figure 2.6. Adult survival of *S. bracteatus* by herbivory type in (A) 1994 and (B) 1995. Values are the probability of surviving to the last census. A pooled category, 'overall', includes all forms of herbivory. Sample sizes are given below each bar. If the value differed when 'unknown' and 'missing' cases were included, these values are shown by dotted lines and their corresponding sample sizes are given in the second line beneath the site names. Values of categories with an 'X' are not shown because of very small sample sizes.


A
Overall
Deer
None
Both
Insect
p (survival)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
X
Barton Creek
Bee Creek
Mt. Bonnell
Valburn
N
75 29 9 1
4 5 4 6
14 5
20 17 9 4
N (w/unk)
144 44 14 3
25 7 7
19
71 28 15 8

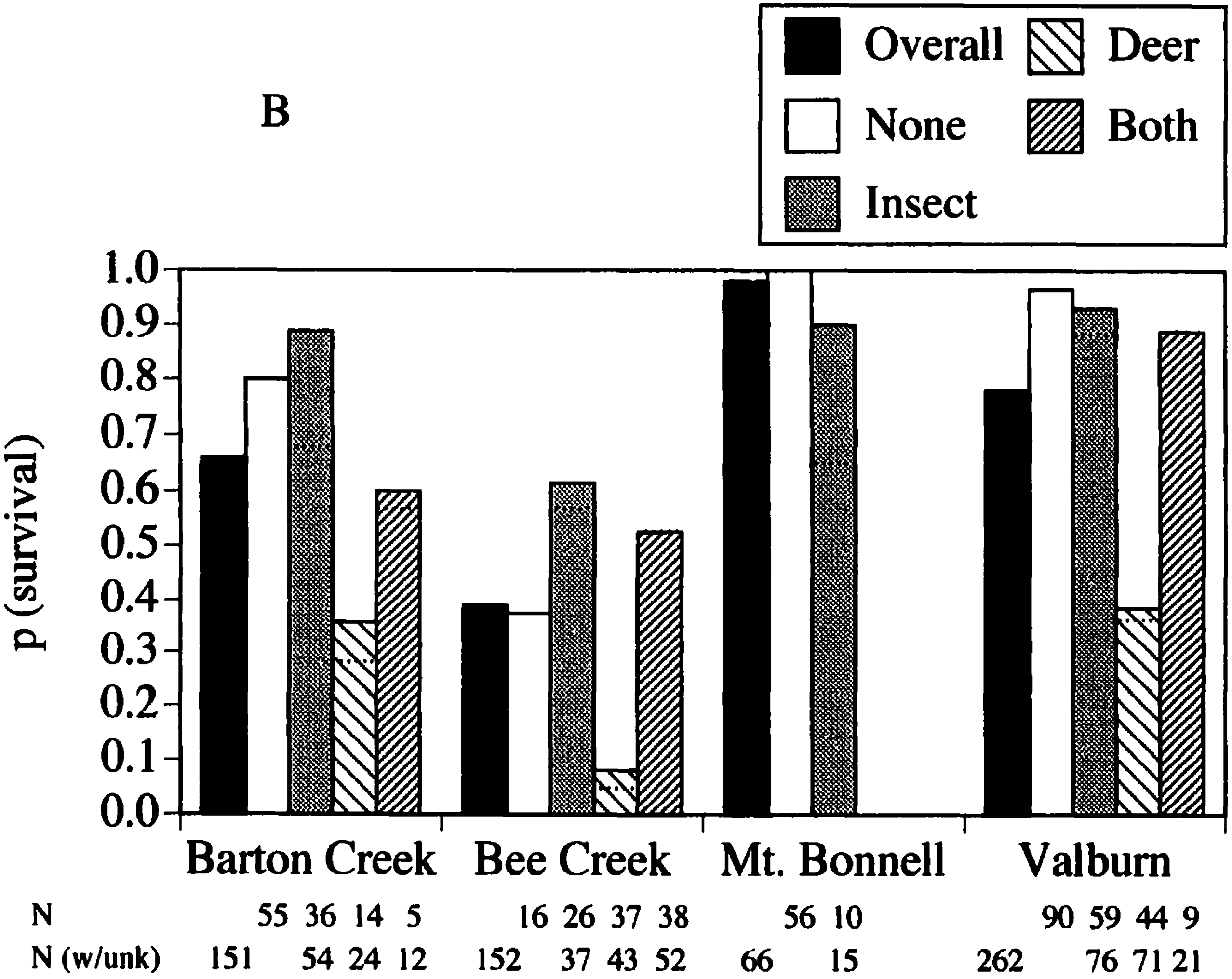
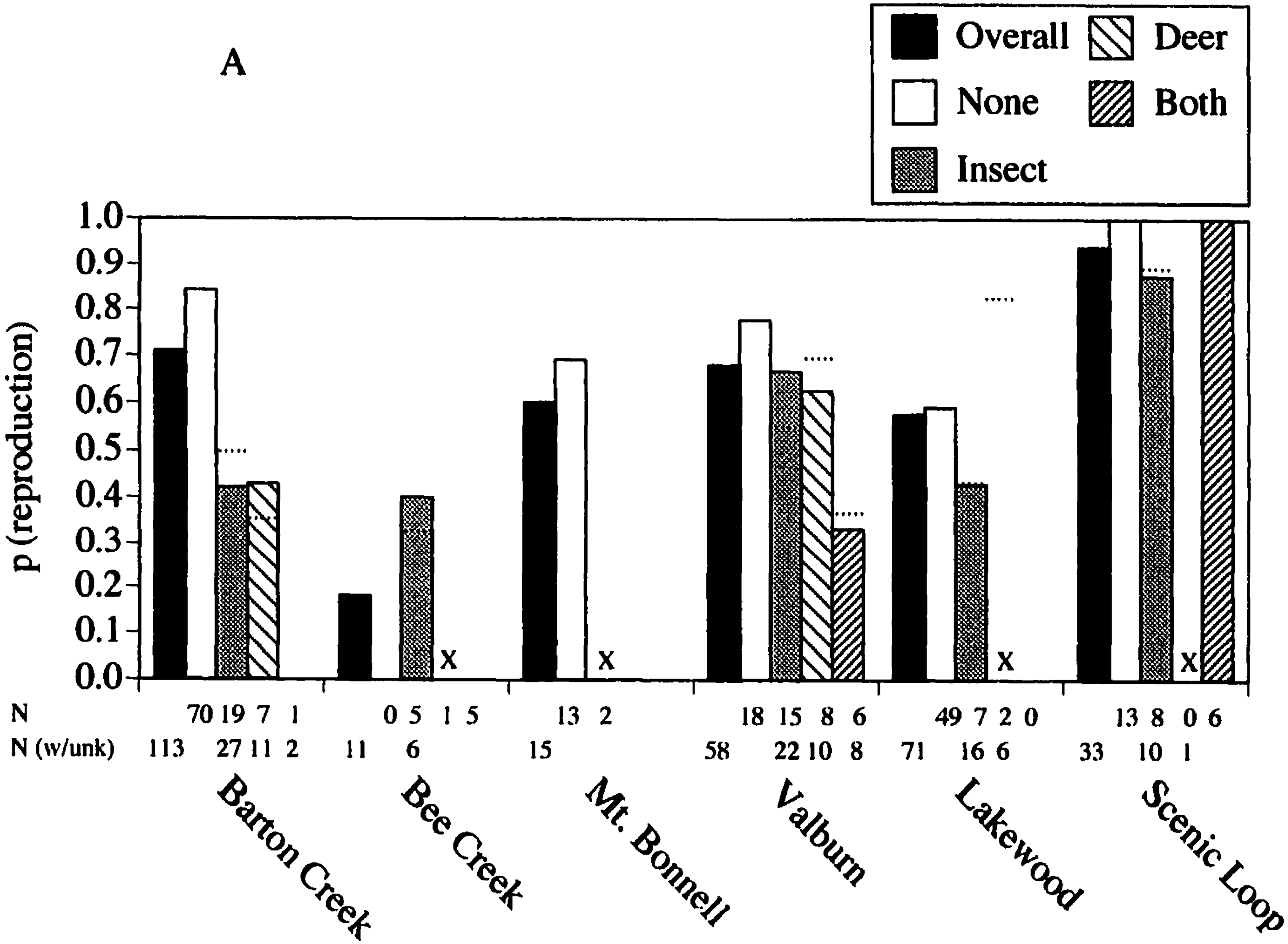

B
Overall
Deer
None
Both
Insect
p (survival)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Barton Creek
Bee Creek
Mt. Bonnell
Valburn
N 55 36 14 5 16 26 37 38 56 10 90 59 44 9
N (w/unk) 151 54 24 12 152 37 43 52 66 15 262 76 71 21

Figure 2.7. Probability of reproduction for (A) 1994 and (B) 1995. Data only include plants that survived to the final census. Format follows Figure 2.6.


A
Overall
None
Insect
Deer
Both
p (reproduction)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
X
N
N (w/unk)
70 19 7 1
113 27 11 2
0 5 1 5
11 6
13 2
15
18 15 8 6
58 22 10 8
49 7 2 0
71 16 6
13 8 0 6
33 10 1
Barton Creek
Bee Creek
Mt. Bonnell
Valburn
Lakewood
Scenic Loop

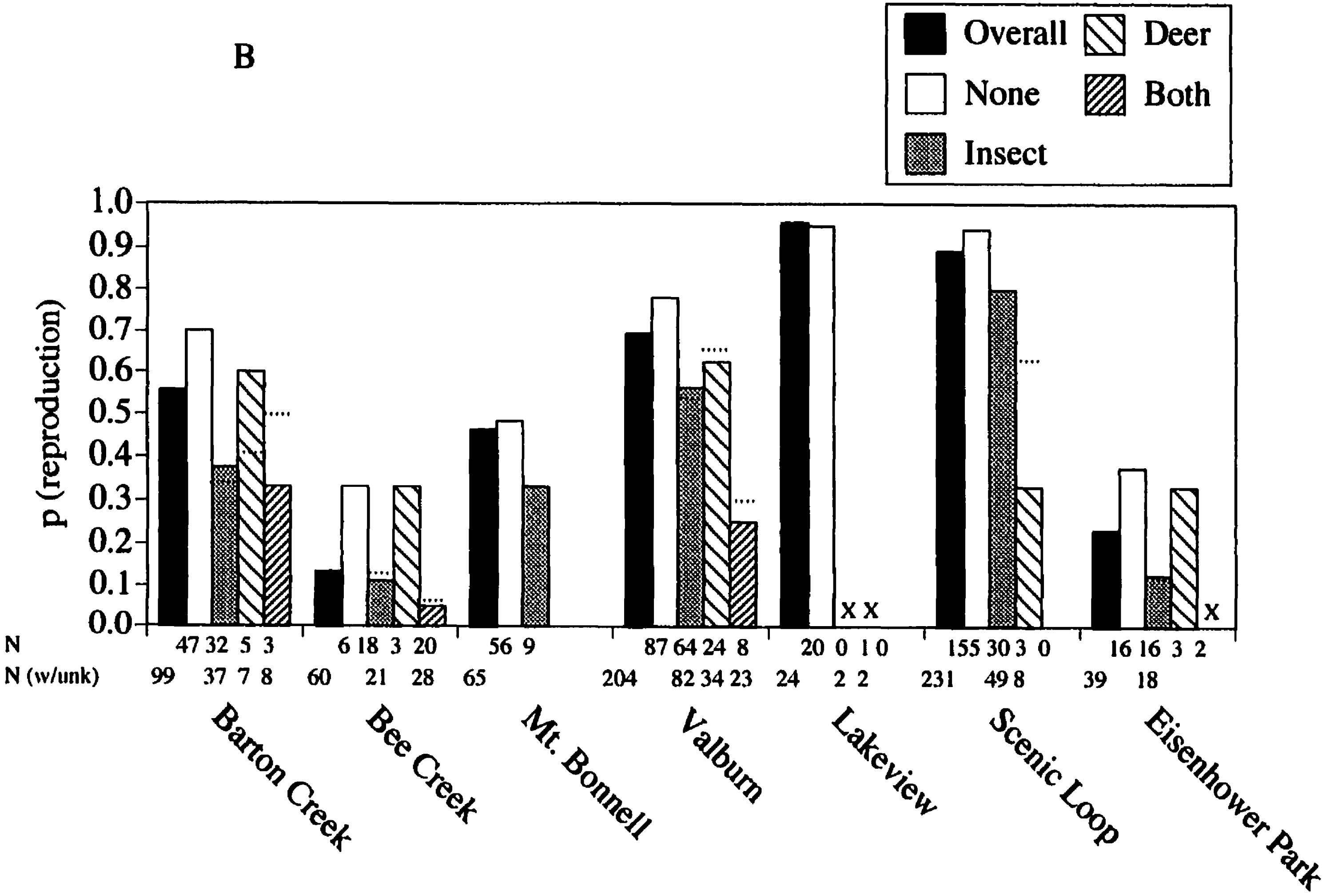

B
Overall
Deer
None
Both
Insect
p (reproduction)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
x x
x
N
47 32 5 3
6 18 3 20
56 9
87 64 24 8
20 0 1 0
155 30 3 0
16 16 3 2
N (w/unk)
99 37 7 8
60 21 28
65
204 82 34 23
24 2 2
231 49 8
39 18
Barton Creek
Bee Creek
Mt. Bonnell
Valburn
Lakeview
Scenic Loop
Eisenhower Park

Figure 2.8. The estimated probability of reproducing at Valburn in 1995 for uneaten plants (solid line) and plants eaten by insects (dashed line). Curves were derived from a logistic regression model.

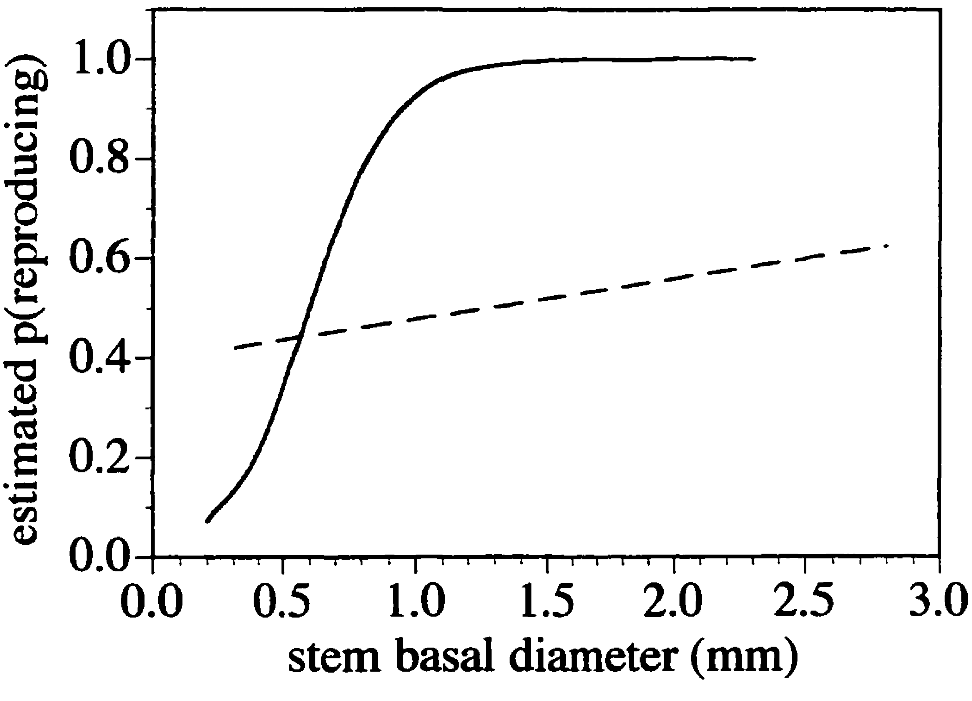


Figure 2.9. The effects of early-season herbivory on the fecundity of *Streptanthus bracteatus* in 1994 and 1995. Values were back-transformed from the ANCOVA for ease of interpretation. Different letters above the bars indicate significant differences among treatments. Sample sizes are given at the bottom of each bar.

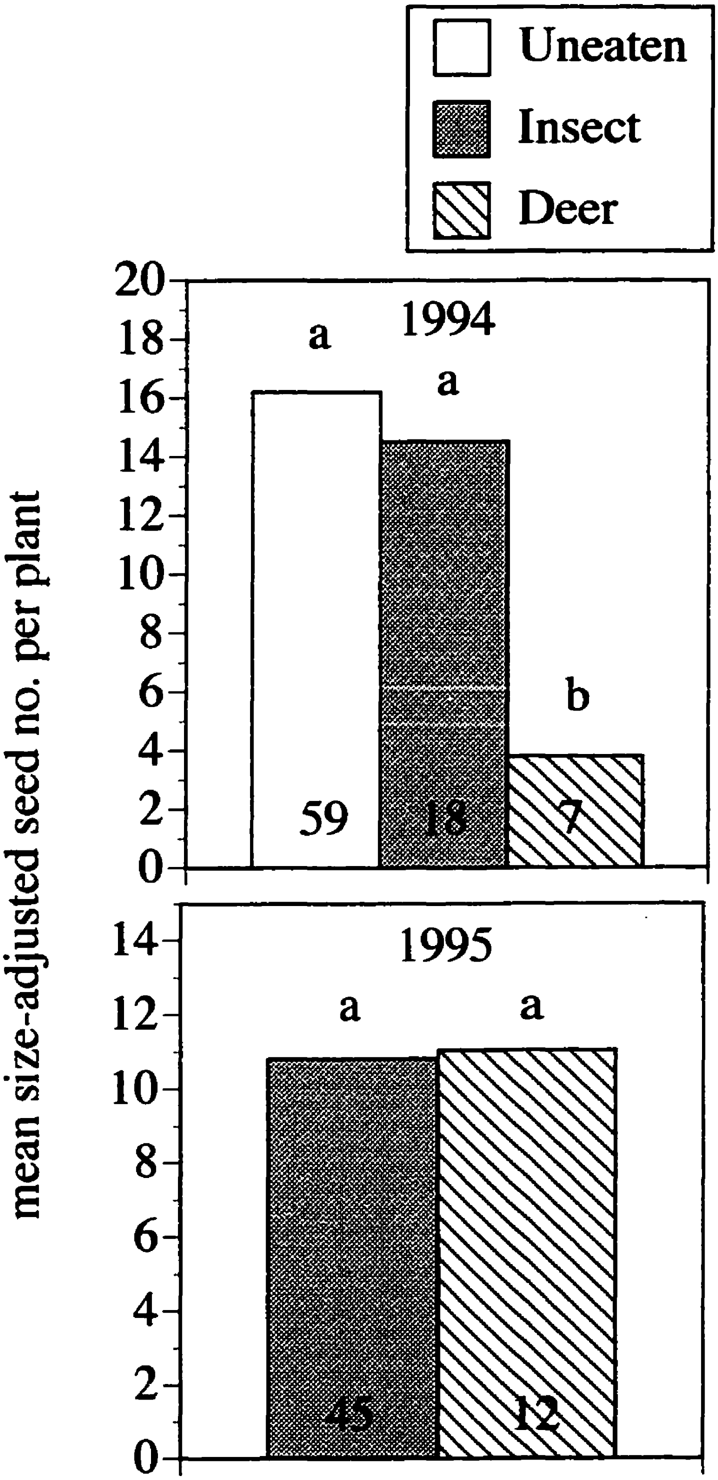
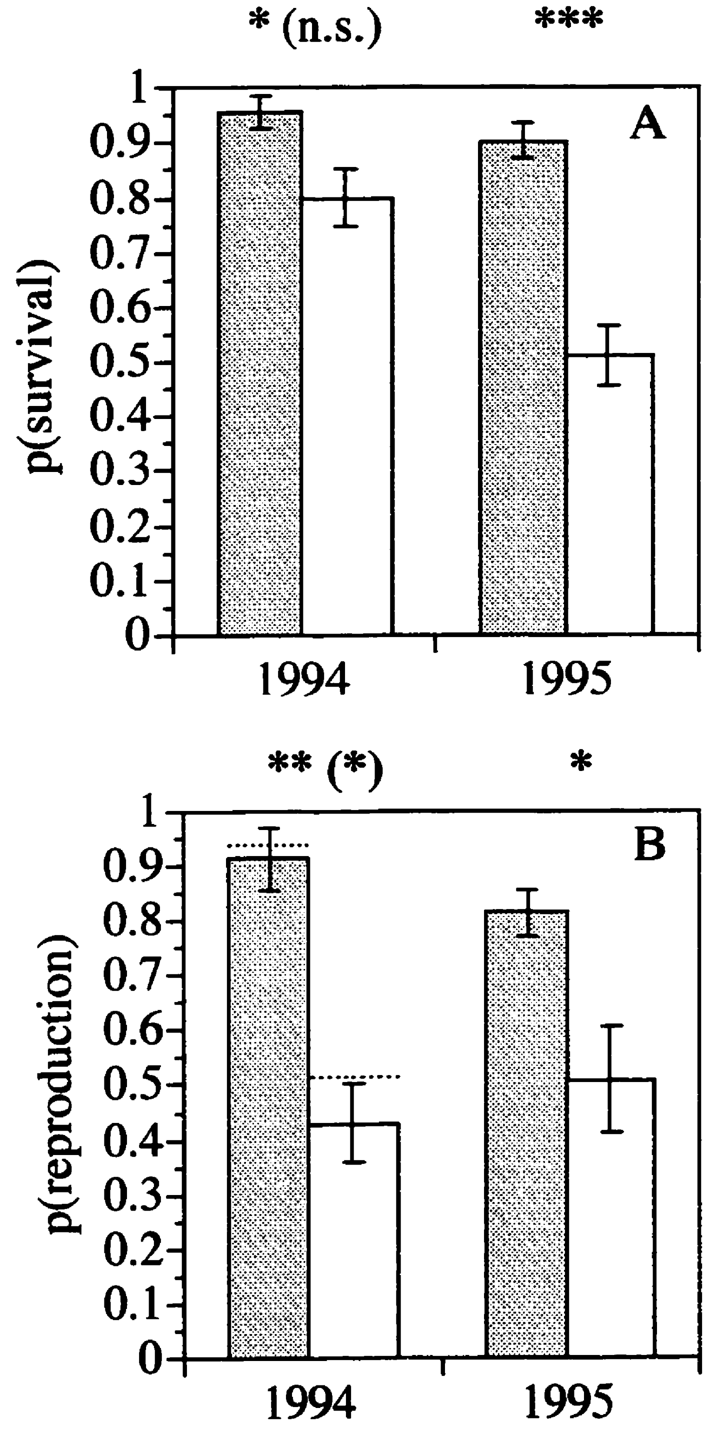

Uneaten
Insect
Deer
mean size-adjusted seed no. per plant
1994
20
18
16
14
12
10
8
6
4
2
0
a
a
b
59
18
7
1995
14
12
10
8
6
4
2
0
a
a
45
12

Figure 2.10. Results of caging experiments at Mesa during two seasons. Values are means and standard error of plot means (N = 6 in 1994; N = 9 in 1995) for (A) survival, (B) reproduction, (C) biomass, and (D) seed set. Shaded bars are of caged plots that excluded deer; open bars are of uncaged plots that allowed all herbivores. In 1994, means of the subset of plants uneaten before experiment installation, where they differed from values for all plants, are shown by a dotted line with significance values in parentheses. Significance values above bars in (A) and (B) are results of Mann-Whitney U tests. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. See Table 2.6 for test results of (C) and (D).


* (n.s.)
***
A
p(survival)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1994
1995
** (*)
*
B
p(reproduction)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1994
1995

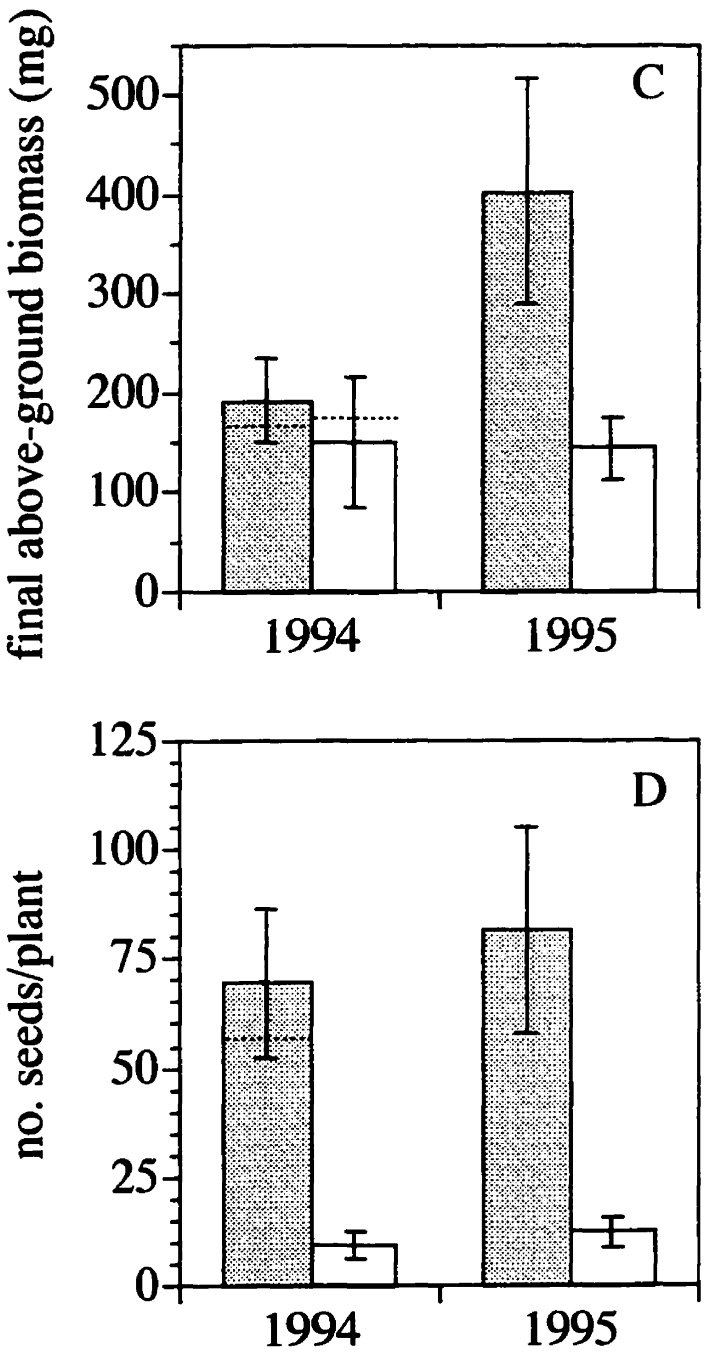
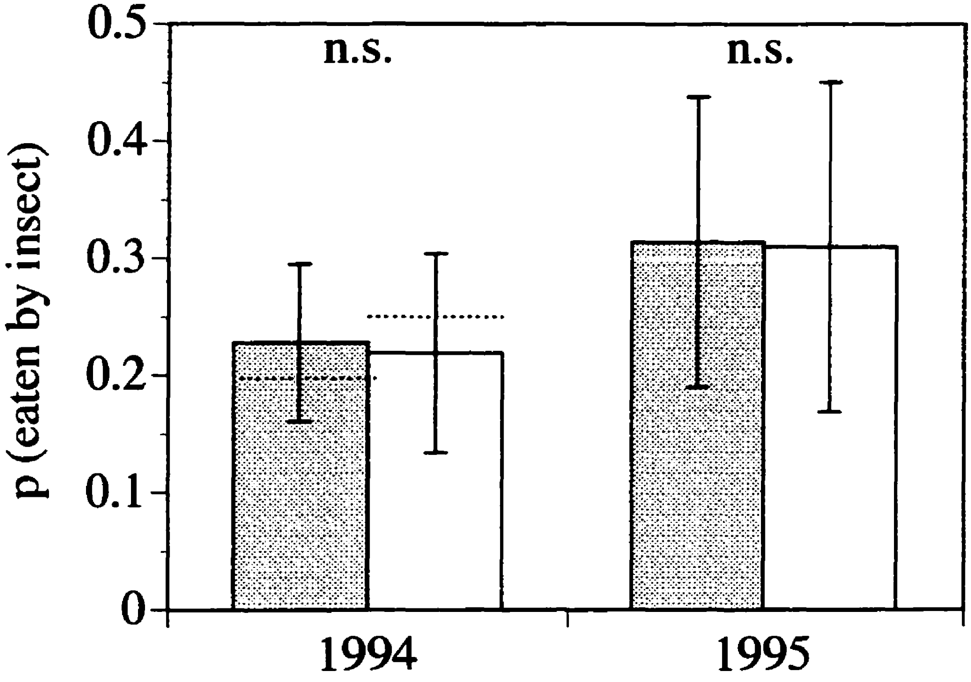

C
final above-ground biomass (mg)
0
100
200
300
400
500
1994
1995
D
no. seeds/plant
0
25
50
75
100
125
1994
1995

Figure 2.11. The effect of deer exclusion on the probability of insect attack. Values are means of plot means and standard errors. In 1994, dotted lines indicate values for the subset of plants uneaten before experiment installation. Significance values are from t-tests.



Chapter 3: The Role of Herbivory and Competition in Determining the Distribution of a Rare Plant: Experimental Evidence in Two Habitats

ABSTRACT

I investigate the separate and combined effects of insects and deer on a rare annual plant, the bracted twistflower (*Streptanthus bracteatus*; Brassicaceae). I hypothesize that white-tailed deer (*Odocoileus virginianus*) and insects reduce the survival, growth, and fecundity of this species. To test this hypothesis, I planted a population of *S. bracteatus* in a woodland site during two years, reducing either deer herbivory or both deer and insect herbivory. Despite an abundance of deer at the site, deer ate few plants. However, plants in caged plots had significantly higher survival and seed production than plants in uncaged plots. In contrast, the survival, biomass, and seed set of caged plants sprayed with insecticide were the same as caged plants sprayed with water. These results indicate that deer, not insects, have a negative effect on *S. bracteatus* at low browsing frequencies.

Unexpectedly, all plants in both years were much smaller and had lower survival than plants at natural populations. To generate hypotheses about the cause of this poor performance, I took measurements of soil and litter properties at this site and at five natural populations. These data suggest that a lack of soil nutrients may have caused the poor performance of *S. bracteatus*. Thus specific habitat requirements, in part, may have caused the rarity of this species.

Finally, I further investigate the habitat requirements of *S. bracteatus* by testing the following two hypotheses: (1) *S. bracteatus* favors a grassland habitat but is excluded from it by herbivory, and (2) *S. bracteatus* is excluded from grassland by competition. I tested these hypotheses by comparing germination, survival, and biomass in a woodland, the species' typical habitat, to that in a grassland. I also reduced competition and/or herbivory to determine if plant performance improved. I found that all plants in the grassland had significantly lower performance than in the woodland during both years. Furthermore, the poor performance of this species in the grassland was partially due to insect herbivory, but not due to competition or deer herbivory. Thus grassland is not a favorable habitat for *S. bracteatus*, at least at this site.

INTRODUCTION

Predicting the distribution and abundance of plants is a central goal of ecology. With regard to rare species, this goal is enhanced by a need to develop management and recovery strategies. However, it is often difficult to make such predictions for rare species. Because rare species often have few populations or few individuals within populations, problems of small sample size arise. For example, ecologists often describe the habitat requirements of rare species to aid management and recovery (e.g., Gehlbach and Polley 1982; Gawler et al. 1987). But if a species was once more widespread, remnant populations may not be found in optimal sites (Kruckeberg and Rabinowitz 1985). Rare species may be capable of occupying additional sites that are rather different from, and perhaps more favorable than, the sites to which they are currently limited. The traditional method of predicting the biotic and abiotic components of a species' habitat may not provide an accurate picture of the best habitat for a rare plant. Furthermore, it may lead to an attempt to maintain a species in sub-optimal habitat.

Streptanthus bracteatus (Brassicaceae) is an endemic of the Edwards Plateau of central Texas known from only eight populations (Appendix 1). The causes of its rarity remain unclear (McNeal 1989; Appendix 1). *S. bracteatus* may have a larger niche than is suggested by its current distribution in woodlands and woodland edges: *S. bracteatus* often grows larger in open shrublands adjacent to woodlands than in the shade of woodland understories (Appendix 1), suggesting that this species performs as well or better in high-light environments than it does in low-light environments. Furthermore, individuals of *S. bracteatus* grown from seed and planted in a grassland with neighboring plants clipped had higher survival, were larger, and produced more seeds than individuals planted in a woodland (D. Zippin, *unpublished data*). If grasslands are suitable habitat for *S. bracteatus*, its absence from this habitat may be due to herbivory or competition, or both.

Herbivory can affect the local distribution of plants (Parker and Root 1981; Boyd 1988; Louda and Rodman 1996). For example, insect herbivores exclude the crucifer *Cardamine cordifolia* from full-sun sites, restricting it to shaded sites under woody plant canopies (Louda and Rodman 1996). Herbivory on *Streptanthus bracteatus*, primarily by white-tailed deer (*Odocoileus virginianus*), reduces the survival of plants in woodlands (Chapter 2). Deer may reduce the survival of this species in grassland enough to exclude it from this habitat.

The dramatic increase in white-tailed deer populations in central Texas during the last 50 years (Leopold et al. 1947; Doughty 1983; Young and Richards

1994) may have led to herbivory pressures that excluded *S. bracteatus* from grasslands. Indeed, recent increases in herbivore populations have been acknowledged as a possible cause of rarity of many North American plants (Fiedler 1986; Alverson et al. 1988; Miller et al. 1992; Balgooyen and Waller 1995). *Streptanthus bracteatus* may also be excluded from grasslands by plant competition. Some rare species are also poor competitors (Morse 1981; Gawler et al. 1987; Watson et al. 1994), suggesting that competitive ability and rarity are inversely related.

In this chapter I address the following three hypotheses: (1) deer and insects reduce the survival, growth, and fecundity of *S. bracteatus* in its primary habitat, woodlands, (2) this species favors a grassland habitat but is excluded from it by herbivory, and (3) *S. bracteatus* is excluded from grassland by competition. To test these hypotheses, I performed a two-year field experiment using exclusion techniques. The results of these experiments support the hypothesis that deer but not insects negatively affect *S. bracteatus* in woodlands. My data do not support the hypotheses that this species favors grasslands but is excluded from it by either herbivory or competition.

METHODS

Study site and species

Because of the need to maintain natural populations in their undisturbed state, for both scientific and ethical reasons, I had to create a new population of *S. bracteatus* on which I could perform manipulative experiments. I chose a study site after an extensive survey of western Travis County, Texas. A site was deemed suitable if it met the following nine criteria: (1) close proximity (< 20 km) to extant *S. bracteatus* populations but without the species occurring on site (so that established seed banks would not interfere with experimental seed banks); (2) appropriate woodland habitat and grassland nearby, both of sufficient size to accommodate the experiment; (3) vehicular access to both habitats; (4) flat terrain or gentle to moderate slopes; (5) underlying geologic strata of the Edwards, Walnut, or Glen Rose formation (the strata under extant *S. bracteatus* sites); (6) limited or no public access; (7) a guarantee that land-use would not change within three years; (8) deer density similar to that at natural populations; and (9) relatively close to urban/suburban areas so that deer feeding behavior would be similar to that at extant sites. The only site that met all of these criteria was Emma Long Metropolitan Park, a 457-ha preserve adjacent to the Colorado River near Austin, Texas.

A general description of the climate, topography, and soils of the eastern Edwards Plateau is found in Chapter 2. Emma Long Park (ELP) supports a *Juniperus ashei — Quercus fusiformis* woodland and patchy areas of grassland that are typical of the Balcones Escarpment (Fowler and Dunlap 1986; Riskind and Diamond 1986, 1988; Van Auken 1988) and of extant locations of *S. bracteatus* (Appendix 1). The woodland overstory in the study area is dominated by *Juniperus ashei, Quercus fusiformis, Q. buckleyi,* and *Q. breviloba* var. *sinuata,* in that order. The understory is sparse (< 5% cover) and is dominated by graminoids such as *Carex planostachys*; shrubs were rare. The grassland is dense (75 to 95% cover) and is dominated by *Schizachyrium scoparium.* Scattered clusters (mottes) of

Quercus fusiformis and *Juniperus ashei* were also present. Both study sites had flat and gentle (< 10°) east-facing slopes. No livestock grazing has occurred in the park since at least 1939. A fire occurred in the late 1970's (C. Sexton, *personal communication*). Aerial photographs from 1940 reveal a denser woodland than existed in 1995. However, the relative extent of the grassland and woodland appeared unchanged.

Streptanthus bracteatus Gray (Brassicaceae) is a winter annual that produces a basal rosette of leaves before bolting in early spring, typically producing a single flowering stalk. *S. bracteatus* is found in moderate to deeply shaded understories of juniper-oak woodlands in the southern and eastern margins of the Edwards Plateau. More details of this species' distribution, habitat, and life-history are found in Chapter 2 and Appendix 1.

Abiotic factors

Although the vegetation and physical features of the Emma Long woodland appear to be similar to that of sites occupied by *S. bracteatus*, I still questioned whether the site was similar in important physical characters such as soil nutrient levels, soil pH, and litter composition. In order to evaluate this, I collected quantitative data on soil properties and soil surface features at Emma Long Park (ELP) and at five sites in Travis County with natural populations of *S. bracteatus*, and compared the results. The extant sites were Barton Creek, Bee Creek, Mesa, Mount Bonnell, and Valburn. Descriptions of these sites are found in Chapter 2 and Appendix 1.

I sampled soil and litter properties in April and May, 1996, within randomly selected 25 cm by 25 cm subplots. Subplot placement methods differed according to site. At ELP I randomly chose 30 circular plots that had been previously established for the experiments in the woodland (described below); within each I placed a single subplot. At the five extant sites, I randomly located 8 to 15 subplots within larger permanent monitoring plots established in 1993 and described in Chapter 2. I varied the sampling effort so that sample density per unit area was approximately equal among sites.

Within each subplot I estimated the cover of five categories of surface features: oak litter, juniper litter, other litter, rock, and bare ground. For each category I recorded one of six standard cover classes: absent, 1 to 5%, 6 to 25%, 26 to 50%, 51 to 75%, or 76 to 100%. I assessed litter depth at four points within each subplot by gently pushing a pin flag through the leaf litter until it stopped and measuring penetration depth to the nearest 0.5 cm.

On the Edwards Plateau, where litter is primarily of two types, conifer or oak, litter cover and depth may not adequately describe the important soil surface environment to which seedlings are exposed. For example, oak and other broadleaf litter is more of a barrier to seed germination than conifer litter (Ahlgren and Ahlgren 1981; Williams et al. 1990). Litter cover and depth measurements do not capture the proportion of these two litter types with the entire litter profile. To quantify these differences, I collected all surface leaf litter and woody debris from each subplot, and then sorted, dried, and weighed each sample. To remove fine soil and decomposed leaf particles (not considered as leaf litter), I first sifted each sample through a 1.0 mm sieve; material above this size was dried at 70° C for 2 d. I then sieved samples through a 5.0 mm mesh. I separated litter above this size into six types: oak leaves, juniper leaves, other leaves, woody debris, herbaceous material, and other material. Each type was then weighed separately. To separate rocks and soil from the remaining fine litter I submerged each sample in warm water and agitated it so that soil and rocks fell to the bottom. After removal with a slotted spoon, I dried and weighed the sub-sample. Fine litter in the majority of samples was composed mostly of a single type. In cases where composition was split between types, I divided the weight evenly among these types.

On the Edwards Plateau it is often difficult to assess soil depth in a way meaningful to plants. Roots are able to navigate around the abundant subsurface rocks, but soil corers and probes are not. Moreover, the caliche hardpan beneath this rocky surface layer is often patchy on the order of centimeters (D. Zippin, *personal observation*). As a result, a wide soil corer may overestimate the extent of the impenetrable portions of this layer. To assess how deep roots might be able to penetrate, I drove a 1 cm-diameter rebar stake into the ground with a hammer in two corners of each subplot to 50 cm or until it could not be driven further after four strikes. I recorded depths to the nearest 1 cm or as 'over 50 cm' for deep soil.

To provide a general picture of soil fertility, I measured the concentration of macronutrients and the more abundant micronutrients at each site. There are no records of unusual levels of heavy metals or other potentially toxic compounds on the eastern Edwards Plateau or in calcareous soils in general (Jeffrey 1987) that might produce high levels of edaphic endemism or rarity (Kruckeberg 1969;

Stebbins 1980). I collected 3 to 5 soil samples from each subplot in haphazard locations and combined them into a single composite sample. I could not sample at consistent locations within subplots because of the difficulty in extracting intact soil cores over 5 cm long.

Soil chemical and textural analysis was performed by the Texas A & M Soil Testing Lab (College Station, TX). Soil pH was measured with a standard glass combination electrode in a 2:1 mixture of soil:deionized water stirred 3 times over a 30-min period (Schofield and Taylor 1995). Soil nitrogen was measured as the concentration of its inorganic forms, primarily as ammonium and nitrate. An extraction with a 0.1M KCl solution was prepared and analyzed colorimetrically, a modification of a standard technique (Keeney and Nelson 1982). Phosphorous, potassium, calcium, magnesium, sodium, and sulfur were measured from a soil solution of 1.4 M NH_4OAc and 0.025 M EDTA at pH 4.2 (Hons et al. 1990). Organic matter content was determined using the Walkley-Black method (Walkley 1947). Soil salinity was determined by the Rhoades method (Rhoades 1982). Soil texture was quantified as the proportion of sand, silt, and clay particles using standard dispersion and fractionation techniques.

I evaluated statistically significant differences between ELP and the natural populations using a non-parametric Mann-Whitney U test of each variable. Despite data transformations, parametric tests could not be used because of violations of the assumptions of equal variance and a normal distribution. I pooled data from all occupied sites and performed the tests on untransformed data with an alpha value of $p = 0.001$ to minimize the chance of a Type II error.

Experimental design - woodland

I established 200 1 m^2 circular plots in the woodland in ELP. Plots were spaced at 8 m intervals along parallel transects spaced 8 m apart. I chose regular spacing to minimize the effects of neighboring plots and to maximize sample size within the limited habitat area. I discarded plots that fell in uncommon or inappropriate microsites, including exposed bedrock, woodland edges, dense patches of juniper seedlings, and those in which a tree trunk occupied over 25% of the plot surface.

In the first year (1993–1994) I planted four seedlings, propagated off-site, in each plot. Transplants were grown from seed collected from a first-generation greenhouse population that itself originated from the Valburn site (Chapter 2 and Appendix 1). The biomass of greenhouse-grown seed was not significantly different than seeds in harvested natural populations (mean = 1.3 mg, N = 100 randomly-chosen seed from each group; Student's $t = 0.70$, d.f. = 188, $p = 0.48$). Seeds were germinated in 2.5 x 16.4 cm plastic tubes (Cone-tainers®) in soil collected from a nearby woodland. Tubes were placed outdoors on the University of Texas campus to ensure cold hardening during early development. One month before planting I moved the seedlings to the field site, caged them, and sprayed them with insecticide periodically to minimize herbivory. I planted four seedlings in each plot, one at each cardinal direction 15 cm from the center, between 12 December and 6 January 1993. Seedlings were watered twice on the planting day, with at least 30 min between watering to allow for deep penetration. Because of low rainfall in the winter of 1993–1994 I applied supplemental water between rain events until 1 mo after planting. Seedling mortality during this time was as high as 23%. After approximately 1 mo, I replaced the dead transplants evenly among treatments until all of the extra material (N = 99) was used. Some plants could not be replaced because I lacked additional transplants.

I classified the microsite of all plots by litter type, slope, rockiness, and position relative to the tree dripline. I assigned plots in a stratified random manner by these microsite types to one of three treatments: (1) controls, (2) caged, or (3) caged and sprayed with insecticide. I could not use a complete factorial design (i.e., the inclusion of an insecticide-only treatment) because of the potential influence of the insecticide on deer feeding behavior. My original experimental design included six additional treatments that would have varied the timing, frequency, and intensity of simulated (i.e., clipping) herbivory within caged plots sprayed with insecticide. In order to maintain equal sample sizes among all treatments (N = 25 for each of the nine planned treatments), I assigned six times more plots to the caged and insecticide-sprayed treatment than to the control or caged-only treatments. However, because of the unexpectedly small size of plants in the first year of the study (see Results), I could not apply these six clipping treatments as planned. Therefore, by the end of the first season there were far more caged, sprayed plots (N = 150) than controls or caged-only plots (N = 25 plots each).

I hypothesized that the small size of adults in 1994 was due to either or both of: (1) the very low rainfall in the winter of 1993–1994, or (2) poor root development in the containers and in the field (i.e., transplant shock). In case my first hypothesis was correct, I chose to maintain the large number of caged and insecticide-sprayed plots in the second year in the event that winter rainfall increased and I could apply the six clipping treatments as originally planned.

To test the second hypothesis, in the second year I added another experimental factor, planting method, to every treatment. Plots were either planted with transplants using the same technique as the previous year or sown with seeds earlier in the season. I added 40 plots to compensate partially for this additional treatment. I assigned all of these plots to the seed addition and caged, insecticide-sprayed treatment to ensure an adequate sample size for the planned clipping treatments. I split the samples of all the other treatments into two groups and randomly assigned half to the seed addition method and the other half to the planting method (Figure 3.1A). For example, the 25 controls in the first year became in the second year 12 seeded control plots and 13 transplanted control plots.

To seed plots I buried seeds 0.5 to 1.0 cm below the leaf litter in a 15-cm radius from the central plot stake on 1 November 1994. I planted transplants for the second year between 12 and 19 December 1994 using the same method as the previous season. Because of ample rainfall in December 1994 and January 1995, transplants received no supplemental watering. Only three transplants (< 1%) died within 2 wk; all were replaced. Despite the high rainfall, transplants were still too small in the spring to be clipped as planned. Likewise, plants grown from seed were also too small for use in the clipping treatments. Thus, in 1995 sample sizes for the caged and insecticide-sprayed plots were still much greater (N = 73 and 115 for transplants and seeded plots, respectively) than the other treatments in the woodland (N = 13 for each).

Experimental design - grassland

I established 125 1 m^2 circular plots in the grassland in the same spacing arrangement as I used in the woodland. I discarded plots that fell on exposed bedrock, beneath shrubs, or within 5 m of a tree. I raised seedlings in soil collected from a nearby grassland and planted the transplants between 21 December and 17 January 1993 using the same technique as described for the woodland. After one month I replaced 35 transplants that had presumably died from transplant shock; all dead transplants were replaced in the grassland.

I assigned plots in a stratified random manner, equally by microsite type, to one of five treatments: (1) control, (2) caged and sprayed with insecticide, (3) vegetation cover reduced, (4) caged and vegetation cover reduced, or (5) caged, sprayed with insecticide, and vegetation cover reduced (Figure 3.1B). I included a vegetation reduction treatment because cover and biomass was particularly high in the grassland. I suspected that this condition was not typical of this habitat in the past. Grasslands and savannas on the Edwards Plateau used to undergo repeated burning and grazing (Smeins 1980; Doughty 1983; Fonteyn et al. 1988). The grassland at ELP burned very infrequently and was not grazed, and thus might not represent a habitat most favorable for the growth of herbs such as *S. bracteatus*. The vegetation reduction treatment consisted of clipping the herbaceous material to 5 cm of ground level twice during the year, once each in winter and spring.

In the second year, just as in the woodland, I split all treatments equally into two groups, transplants or seeded plots. I sowed seeds on 2 November 1994 in the same method as in the woodland. I planted transplants on 19 and 20 December 1994. As in the woodland, transplant death was initially low: only 17 transplants (5%) died within 2 wk; all were replaced.

Treatment application and census methods

Deer were excluded from both habitats with cages made of 14-gauge galvanized welded wire fabric (i.e., hardware cloth) with a mesh size of 5 x 10 cm, grounded with plastic tent stakes. All cages were 1.5 m tall cylinders that enclosed the 1 m^2 plots. I reduced insect herbivory by applying 70 ml m^{-2} of Ortho-Isotox® (8% Acephate and 0.5% Hexakis-distannoxane; Chevron Chemical Co.), a broad-spectrum systemic insecticide and miticide. I chose this commonly used insecticide for its low phytotoxicity and because it leaves a persistent surface residual (Louda 1983; Mills 1983). I applied it at the recommended concentration (30 ml per liter of water) with a hand-held polyethylene compressed air sprayer. On sunny days I applied the insecticide in the late afternoon to minimize evaporation. To control for spray effects, I applied an equal volume of water to the remaining plots with similar sprayers and at the same time as the insecticide application. In January 1994 I applied the insecticide to grassland plots at 3 d intervals. Once it became clear that the insecticide was just reducing herbivory and not eliminating it altogether, I reduced the frequency to the recommended interval of 2 wk. In the woodland, where insect herbivore damage was consistently lower, I applied the insecticide at

2 wk intervals throughout the 1993–1994 season. In the 1994–1995 season, I applied the insecticide at 1 wk and 2 wk intervals in the grassland and woodland, respectively. I ceased insecticide and water applications in early April to minimize damage to insect pollinators before flower emergence.

I censused all seedlings monthly to assess survival. I also censused seedlings at least twice during each winter to assess vigor and herbivory damage. At these censuses, I recorded the number of plants that showed any sign of wilting or leaf herbivory. I also made general qualitative notes about patterns of herbivory and leaf and stem damage. To assess treatment effects on winter rosette size, I measured the length of the longest leaf and counted the number of leaves on each plant in March 1994.

In the spring, at least one census was made in each habitat to assess plant size, reproduction, and herbivory. I measured the stem basal diameter using dial calipers and counted the number of fruits present. Data concerning stem herbivory formed the basis for quantifying the nature of herbivory on adults because this was its major form. I defined it as the removal of or damage to an apical or lateral meristem. I classified stem herbivory as due to either pathogen, insect, deer, or unknown. Assignment was based on stem morphology and other clues. For example, deer "cuts" tended to be jagged and perpendicular to the stem in cross-section and were often associated with epidermal tearing. In contrast, insect cuts tended to be smooth and diagonal in cross-section with little or no evidence of tearing. I classified eaten stems that could not be categorized unambiguously as ‘unknown’. I harvested all plants at the end of the season on multiple visits; each plant was removed as soon as its tissue had dried but before seed dispersal had occurred.

Analysis

The general experimental design is nested: plants nested within plots and plots nested within treatments. I was unable to perform analyses that incorporated all levels of this design because of the high variation in within-plot sample size. For example, plots often contained a single plant, especially later in the season. Small sample sizes within treatments (among plots) precluded the statistical comparison of many variables, especially of the probability of reproducing and of seed set. Three plots were omitted from analyses of the 1994–1995 data that involved the final censuses because of human disturbance to these plots late in the season. I performed all statistical analyses using SPSS (SPSS, Inc., Chicago, Illinois).

Whenever sample sizes were adequate and data could be transformed to meet assumptions of normality and homoscedasticity, I evaluated treatment effects using two separate tests. First, to compare the effects of herbivory treatment within and between sites in 1994, I performed a two-way analysis of variance (ANOVA) with site (woodland or grassland and clipped) and herbivory (control, caged, or caged and insecticide) as the main effects and an interaction term of site by herbivory. If significant differences were found among herbivory treatments, I performed a set of planned comparison to determine which treatments were responsible. For the 1995 data, I included an additional factor, planting type (transplants or seeded), in the models. Second, to evaluate the effects of the grassland vegetation removal and its potential interaction with herbivory, I performed two-way ANOVAs with main effects of competition treatment (clipped or unclipped) and two of the three herbivory treatments (caged plus insecticide or controls). Once again, I added a third factor, planting method, to the 1995 models.

Because of the much larger number of caged, insecticide-sprayed plots in the woodland, using the whole data set would have presented serious statistical problems including severely unbalanced designs and extreme heteroscedasticity. To minimize these problems, for each analysis I randomly chose caged, insecticide-sprayed woodland plots in equal numbers to the controls or caged-only plots, whichever number was larger.

To investigate the effects of each factor on survival, I ran separate analyses for each habitat, year, and, in 1995, planting treatment. Transplant data could only be analyzed as a categorical variable, because it took only five possible values. In order to maintain sufficiently large cell observation numbers, I categorized the proportion of plants surviving within these plots into two values. In the woodland, I classified survival as either 'high' (≥ 50%) or 'low' (< 50%). In the grassland, I classified survival as either 'zero' or 'some' (≥ 1 survivor). I compared treatment differences among transplant plots using Chi-square tests. For the seeded plots in 1995 I compared treatment effects with non-parametric Kruskal-Wallis tests for each habitat. When sample sizes permitted, I analyzed the proportion of plants reproducing with Kruskal-Wallis tests for each habitat, year, and planting treatment.

RESULTS

The effects of herbivory

Few adults that were eaten in the woodland survived to the final census (Table 3.1). This may have been due to a low abundance of insect herbivores but not to an absence of deer. The only insect herbivore seen feeding on *S. bracteatus* was the Alticid beetle *Phyllotreta* sp. (probably *P. prasina* Chittenden or *P. pusilla* Horn., Chrysomelidae; det. by E. Riley, Texas A & M University), a specialist on the Brassicaceae. The falcate orange-tip (*Anthocharis midea*; Pieridae), a common predator at extant *S. bracteatus* populations (Chapter 2), was not seen at the Emma Long Park (ELP) woodland as larvae or adults.

In contrast, white-tailed deer were abundant throughout the study site in both years (D. Zippin, *personal observation*). However, the only case of confirmed deer herbivory was on a single large plant that was leaning outside its cage. Herbivory rates were also similar between caged and uncaged plots in both years (Table 3.1), further suggesting that deer browsing was rare.

Despite the low frequency of deer herbivory, significantly more seeded plants died in the control plots than in the two herbivore-reduction treatments (Figure 3.2B; $X^2_2 = 17.06, p = 0.0002$). Herbivory tended to reduce the survival of transplants (Figures 3.2A and 3.3), but these differences were not significant in either year (1994: $X^2_2 = 2.18, p = 0.336$ and 1995: $X^2_2 = 0.62, p = 0.734$). There were no significant differences in plant survival between caged plants and plants caged and sprayed with insecticide.

There were no significant differences in biomass between herbivory treatments (Figure 3.4; 1994: $F_{2,47} = 1.49$, $p = 0.237$; 1995: $F_{2,57} = 0.79$, $p = 0.459$). However, mean biomass was larger in the two caged treatments than in the control plots in all three cases. In 1995, transplants were significantly larger than plants that originated from seed ($F_{1,57} = 4.78$, $p = 0.033$).

Transplants in caged plots in 1995 had significantly higher seed production than plants in uncaged plots (mean = 8 and 2, respectively; $F_{2,17} = 4.46$, $p = 0.028$). In 1994, plants in uncaged plots produced an average of less than one seed (because some plants produced empty fruits) while plants in the other treatments produced an average of four seeds. Herbivory also reduced the seed set of seeded plants (mean = 6 and 2 of each caged treatment and controls, respectively), although the low sample sizes precluded significance testing. Deer herbivory in the woodland appeared to reduce the chance of reproduction (Figure 3.5), although none of these differences were significant.

Woodland habitat suitability

Adults of *S. bracteatus* in the ELP woodland were much smaller than plants at natural populations (Figure 3.6). This was an unexpected result, since the timing of seedling emergence was similar to that in natural populations: 92 and 99% of seedlings emerged before 30 December 1994 in the grassland and woodland, respectively. In natural populations, 98% of recruitment occurred by that time (Appendix 1). Moreover, the soil and litter properties of the ELP woodland appeared similar in most respects to that of occupied sites (Table 3.2 and 3.3).

However, ELP woodland soil had a significantly lower clay content, nitrogen concentration, and phosphorous concentration than occupied sites. Soil calcium and sulfur concentrations were significantly higher than in soil in natural populations.

The condition of seedlings in the first season suggest a potential cause of the small size of ELP plants. In March 1994, 47 and 19% of the seedlings in the grassland and woodland, respectively, showed symptoms consistent with a nutrient-deficiency. These plants had stunted growth, reddish to deep-purple leaves, chlorotic leaves, the curling of leaf margins (usually upwards), or a combination of these symptoms.

Grassland habitat suitability

Grassland at ELP is not a suitable habitat for *Streptanthus bracteatus*. Recruitment in 1995 in seeded plots was significantly less in the grassland than in the woodland ($F_{1,69} = 66.33$, $p < 0.001$, Figure 3.7). Moreover, no seedlings emerged in 35% of the grassland plots while at least one seedling emerged in 99% of the woodland plots. The pattern of winter rosette size in 1994 was similar to that of recruitment in 1995. The mean length of the longest leaf (Figure 3.8A) was significantly larger in the woodland than in the clipped grassland plots ($F_{1,124} = 19.12$, $p < 0.001$). Likewise, the mean number of leaves (Figure 3.8B) was significantly larger in the woodland than in the grassland ($F_{1,132} = 6.91$, $p = 0.010$).

A much lower proportion of plants survived in the grassland than in the woodland in both years: 9 and 13% of transplants in the grassland (unclipped control plots) and 38 and 56% of transplants in the woodland (control plots) survived to the final census in 1994 and 1995, respectively. Likewise, reproduction in the grassland was extremely low: only 10 and 6 transplants reproduced in all plots in 1994 and 1995, respectively (2% of all transplants for each year), and only one seeded plant reproduced in 1995.

The experimental results suggest that the cause of this failure in all performance measures was not due to herbivory. There was no significant effect of the herbivory treatments on recruitment ($F_{2,69} = 0.79$, $p = 0.457$), mean number of winter rosette leaves ($F_{2,132} = 1.19$, $p = 0.307$) or mean length of the longest rosette leaf ($F_{2,124} = 1.53$, $p = 0.222$). Likewise, there was no effect of competition on final transplant biomass (comparing all five treatments: 1994: $X^2_4 = 2.68$, $p = 0.612$; 1995: $X^2_4 = 5.70$, $p = 0.222$). Sample sizes for seeded plots in the grassland were too low to be analyzed statistically.

The only significant effect of herbivory in the grassland was detected on survival. In 1994, a significantly higher proportion of transplants died in the caged plots and the control plots than in the caged and sprayed plots (Figure 3.9; $X^2_2 = 6.30$, $p = 0.043$). In 1995, a similar pattern was evident: spraying with insecticide appeared to improve survival more than caging did, except at the last census (Figure 3.10A; $X^2_2 = 0.65$, $p = 0.722$). Furthermore, in clipped and seeded grassland plots, more plants survived in caged and sprayed plots than in either caged or control plots (Figure 3.10B; $X^2_2 = 5.31$, $p = 0.070$).

In general, about twice as many seedlings and rosettes were damaged by herbivory in the grassland as in the woodland in both years (Tables 3.4 and 3.5). Likewise, in 1994 approximately twice as many plants were missing or were eaten during their lifetime in the grassland than in the woodland (Table 3.1).

Competition did not reduce plant performance in the grassland. There was no effect of reducing competition on either rosettes leaf length ($F_{1,82}$ = 3.04, p = 0.085) or rosette leaf number ($F_{1,87}$ = 0.02, p = 0.879). Moreover, in 1994, reducing vegetation competition did not significantly affect the survival of *S. bracteatus* transplants in either year (1994: X^2_3 = 6.60, p = 0.086, Figure 3.11; 1995: X^2_3 = 1.63, p = 0.803, Figure 3.12A). Because of high variances and small sample sizes, the effects of clipping on the survival of seeded plants was unclear (Figure 3.12B). Too few plants survived to the final census to analyze the effect of competition on reproduction or final biomass.

DISCUSSION

The role of herbivory and competition

In this study I show that plants in caged plots had significantly higher survival and seed production than plants in uncaged plots in the second, wetter year. Deer had no significant effect on the biomass of *Streptanthus bracteatus*, but the consistent trend in these data suggests that such an effect was not detected because of low sample size. Deer browsed relatively few plants despite their abundance at the site. Although the frequency of herbivory at Emma Long Park (ELP) was within the range of that seen at natural populations (Chapter 2), the inferred proportion of browsing due to deer was unusually low. In natural populations, deer have a strong preference for large plants of *S. bracteatus* (Chapter 2), so the small plants at ELP were probably not eaten because they were unattractive forage. Although remaining in a smaller size class was an effective escape from deer herbivory at this site, it is not a viable strategy for *S. bracteatus* because plant size and seed production are so highly correlated (Chapter 2).

Although deer were found to be an important herbivore at ELP in only one year, it is important to note that this result is still consistent with the results of Chapter 2. Deer in natural populations of *S. bracteatus* significantly reduce the survival and reproduction of *S. bracteatus*. Had plants been larger at ELP, they would almost certainly have been eaten by deer at a higher frequency and experienced greater reductions in plant performance. Moreover, the pattern of effects observed at ELP is consistent with those observed in natural populations. In both cases, the negative effects of deer were more substantial in the wet year than in the dry year. At ELP, effects in the dry year may have been at a level undetectable by this study.

I also found that plants in plots caged and sprayed with insecticide were not different from plants in plots that were only caged. This suggests that insects had no effect on *S. bracteatus* in the woodland. However, the effects of insect herbivory may have been underestimated. The insecticide treatment was relatively ineffective in reducing the proportion of seedlings, rosettes, and adults that were eaten. Either insects herbivores such as flea beetles and lepidopteran larvae were not affected by the treatment, or there were non-target herbivores at this site that were not seen in natural populations. For example, snails are important grassland predators on many herbaceous species (Dirzo and Harper 1980; Crawley 1989b; Rees and Brown 1992; Hanley et al. 1996; Hulme 1996). Because the insecticide did not have molluscicide properties, such herbivores would have been unaffected by this treatment. Despite these limitations, survival in the grassland was consistently higher in the caged and insecticide-sprayed plots than in the caged plots in the grassland, suggesting that insects have slight negative effects on *S. bracteatus* in this habitat.

Interestingly, the effects of herbivory in 1995 differed between transplants and plants established from seed. This may have been due to differences in phenology. Seeded plants of *S. bracteatus* were exposed to herbivory immediately upon emergence, while transplants were protected from herbivory until they were approximately two months old. Seedlings that emerge earlier often experience greater rates of herbivory and lower rates of survival than plants that emerge later (Thompson and Price 1977; Pyke 1987; Collinge and Louda 1989; Hanley et al. 1995).

Reducing above-ground competition from surrounding vegetation did not appear to affect the performance of *S. bracteatus* when herbivory was reduced. Theories of plant rarity often include the prediction that a species is rare because it is a poor competitor (Fiedler and Ahouse 1992). While there have been few empirical tests of this hypothesis, the results of the present study suggest that competition probably does not limit the abundance of *S. bracteatus* in grassland habitats.

Because I did not have a completely factorial design in the grassland that included all clipping and herbivory treatments, I could not address the interesting question of whether there was an interaction between herbivore type and plant competition (Bentley and Whittaker 1979; Archer and Detling 1984; Fowler and Rausher 1985; Bergelson 1990; McEvoy et al. 1993; Burger and Louda 1995). However, I was still able to address the cumulative effects of all types of herbivory (i.e., deer, insects, and everything else) and investigate their relationship to competition. Theoretical and empirical studies suggest that a plant's competitive ability depends primarily on morphological traits such as growth rate, total biomass, or plant architecture (for reviews see Goldberg 1990; Louda et al. 1990). Because herbivory often directly affects these traits, one would expect herbivory also to influence a plant's competitive ability.

The trend in survival rates in 1995 in the seeded plots suggests that the cumulative effects of all herbivory reduced the competitive ability of *S. bracteatus*. Furthermore, the rankings of the effects suggest that there may have been an interaction between herbivory and competition. However, these trends were not evident in transplants during the same year. In contrast, one study found that the effects of herbivory and competition on herbaceous plants was better described by a simple additive relationship (Fowler and Rausher 1985).

Habitat requirements

Streptanthus bracteatus has been found only in or near woodlands, but its high growth rate in woodland gaps and edges suggested that it might be successful in the high-light environment of grasslands (McNeal 1989, Chapter 2, Appendix 1). I hypothesized that white-tailed deer might be preventing this species from persisting in grasslands. White-tailed deer are a common herbivore that reduce the survival, growth, and fecundity of *S. bracteatus* in woodlands (Chapter 2). However, the experiments in this study show that grassland, at least at Emma Long Park (ELP), is not a favorable habitat for this species. Moreover, deer herbivory and plant competition are not responsible for its absence there.

The poorer plant performance in the grassland than in the woodland primarily reflected poor germination and winter seedling survival. Insect herbivory in February in control plots was more common in the grassland than in the woodland. This suggests that the greater mortality rate in the grassland was due, at least in part, to either larger populations of phytophagous insect or higher rates of insect herbivory there (Lincoln and Mooney 1983; Louda 1983; Louda and Rodman 1996). Furthermore, the reduced vigor of plants in the grassland at all stages of development (D. Zippin, *personal observation*) may have made these plants more attractive to insect herbivores. In studies of another crucifer, *Cardamine cordifolia*, plant stress levels were positively correlated to insect feeding rates (Louda and Collinge 1992; Louda and Rodman 1996). Germination rates in the grassland were one-third of those in the woodland. This result is consistent with other studies in which the germination success and survival of herbaceous plants were lower in an open grassland or an old-field than in a woodland (Winn 1985; Hoffman 1996).

Because deer herbivory rates were very low in the grassland, deer were not responsible for the failure of *S. bracteatus* in this habitat. This is consistent with the pattern of herbivory in natural populations in the winter, in which deer herbivory is very rare (Chapter 2). Furthermore, there was no significant difference in plant survival between caged and uncaged plots, suggesting that deer herbivory had little effect on survival.

Taken together, the results of the grassland experiment suggest that *Streptanthus bracteatus* is a true woodland species. Within the woodlands of the Edwards Plateau, this species appears to inhabit a diverse array of microsites (Appendix 1). However, its failure in the ELP woodland suggests that it may have specific woodland habitat requirements. Despite ELP's floristic and physiographic (e.g., topography, exposure, soil type, soil surface features) similarity to occupied sites, plants in the woodland had lower survival rates, they were much smaller, and they had much lower fecundity than did plants in natural populations. This pattern held even after the wet winter of 1994–1995. There are at least four possible explanations for this, one of which is reasonably likely.

First, herbivory rates were not unusually high and thus cannot explain the low survival of *S. bracteatus* in ELP woodlands. Indeed, there was a conspicuous absence of deer herbivory in both habitats, despite the frequent sightings of deer in both seasons. Because insect herbivores are generally less harmful than deer to *S. bracteatus* (Chapter 2), insect herbivory alone cannot explain its poor performance. Furthermore, uneaten plants were often as under-developed as eaten plants, strongly implicating a factor other than herbivory. Second, phenological differences cannot be responsible: in 1995 (when seeds were sown), *S. bracteatus* germinated, developed, and reproduced concurrently with natural populations.

Third, although there were some signs of water stress in the woodland seedlings in the dry year, soil water availability may not account for the poor performance of *S. bracteatus* in the ELP woodland. Unlike plants in natural populations, plants at ELP did not respond to the large amount of rainfall in the second year with increased growth, suggesting that water was not limiting at ELP. Furthermore, soil texture is a critical determinant of soil water availability (Jeffrey 1987; Killham 1994). Although clay content was much lower at ELP, water availability in clay soils is inversely proportional to the amount of clay present (Brady and Weil 1996), so soil water was probably more available at ELP than at occupied sites.

Finally, one probable explanation for the poor performance of *S. bracteatus* at ELP is that the woodland at ELP did not provide adequate growing conditions. For example, the ELP woodland site had much lower shrub cover than at any other site. Perhaps shrubs improve soil fertility or soil moisture availability. Recent work has shown that shrubs can facilitate the survival and reproduction of associated herbs through nutrient or water enrichment, shading, or reduced herbivory (Ellison 1987; Franco and Nobel 1989; Carlsson and Callaghan 1991; Callaway and D'Antonio 1992). Alternatively, shrubs simply may be an indicator of a site that already has higher (or certain kinds of) soil fertility.

Whether it is related to the absence of shrub cover or not, the low availability of one or more soil nutrients at ELP may have caused nutrient-deficiencies in *S. bracteatus* which led to reduced survival and growth. The prevalence of seedlings with leaf discoloration, leaf curling, or stunted growth strongly supports this hypothesis. These symptoms are consistent with deficiencies of nitrogen, phosphorous, or sulfur (Wallace 1961; Bergmann 1992). Because only nitrogen and phosphorous are present in low concentrations at ELP, deficiencies of these nutrients may have been responsible for the observed patterns.

On the Edwards Plateau, phosphorous may be more important than nitrogen in determining seedling survival. The limestone soils in this area, including at Emma Long Park, are slightly to moderately basic. At pH levels above neutral, pH is negatively correlated with phosphorous solubility and with its availability to plants (Grime 1965; Kinzel 1983; Jeffrey 1987; Rorison 1990). Moreover, in high pH calcareous soils, phosphorous is easily immobilized by calcium. The relatively high concentration of calcium at ELP suggests that phosphorous may be particularly difficult for plants to obtain at that site.

Conservation implications

In Appendix 1 I suggest that *S. bracteatus* does not have specific habitat requirements because soil surface features, soil types, and plant associates are similar between occupied and unoccupied sites. The results of this study contradict this hypothesis and suggest that *S. bracteatus* may have important habitat requirements related to soil fertility. Strong edaphic associations are known in other *Streptanthus* species (Kruckeberg 1954). Furthermore, the rarity of these soil types often explains the rarity of these species. If *S. bracteatus* is restricted to higher fertility soils and these soil types are uncommon on the Edwards Plateau, habitat specialization may also explain this species' rarity. However, the pattern of soil nutrients on sites unoccupied by *S. bracteatus* is not known, so it is unclear whether the rarity of *S. bracteatus* is related to the rarity of specific soil conditions.

In Appendix 1 I also suggest that the increase in woody cover on the Edwards Plateau over the last 150 years, primarily by *Juniperus ashei* (Buechner 1944; Johnston 1963; Weniger 1988), may have resulted in the loss of favorable habitat for *S. bracteatus* and thus caused its current limited distribution. This shift from commonness to rarity mirrors the constrictions in range of many species since the Pleistocene (Raven and Axelrod 1978), albeit over a much shorter time scale. In contrast, this study suggests the opposite pattern: that woodlands are better habitat for *S. bracteatus* than grasslands, and that the spread of woodland might favor this species. However, this would only be true if the increase in woodland cover were of a type suitable for *S. bracteatus*. Because many woodland types on the Edwards Plateau do not support this species, the challenge remains to find out what makes a woodland appropriate for *S. bracteatus*.

In the woodland in 1995, plants propagated by seed performed at least as well as those installed as transplants propagated off-site. These results have important implications for any future restoration efforts for *S. bracteatus*. One important decision in any reintroduction project is the type of plant material to use in the creation of the founding population (Guerrant 1996). Creating a population of *S. bracteatus* at ELP by sowing seeds took considerably less effort than planting seedlings. Seeding also resulted in more plants per plot. If a large initial seed stock is available, then seeding is clearly preferable to planting. Moreover, seeding begins the important process of building a soil seed bank at least one year earlier than planting would.

Assuming that no new populations of *S. bracteatus* are found, reintroduction or population augmentation may be required to ensure this species' long-term survival. If the experiments in this study were intended to create a self-sustaining population of *S. bracteatus* at ELP, they would have failed. Despite a careful site-selection process, the study site did not mimic conditions at natural populations of *S. bracteatus*. Choosing an appropriate reintroduction site is thus of paramount importance in ensuring the success of any restoration effort for this species. This is a general concern in plant restoration work. Indeed, a lack of care in selecting a site may help explain why so many plant reintroduction efforts fail (Hall 1986; Mehrhoff 1996). The use of a rigorous site-selection protocol combined with the use of well-designed planting techniques (e.g., Pavlik et al. 1993) will ensure the greatest chance of success.

CONCLUSIONS

Deer had a significant negative effect on *S. bracteatus* in the woodland site in one of the two years of this study. Insects, on the other hand, did not significantly affect this species in the woodland. The significant effect of deer is surprising given the relatively low browsing rates observed for both deer and insects. Furthermore, plants in both years were much smaller than plants at natural populations. Therefore, despite a preference for larger plants, deer appear to affect small plants even at low browsing frequencies, causing reductions in survival, fecundity, and possibly biomass.

The unusually small size of plants in the woodland may have been due to soil properties at the study site that were not typical of sites occupied by *S. bracteatus*. More specifically, a lack of soil nutrients, especially of phosphorous, may have caused the poor performance of *S. bracteatus*. If this species is restricted to a soil type that is itself rare, an edaphic adaptation may explain, in part, why *S. bracteatus* is rare.

Based on the experimental results of this study, shifts in the proportion of woodland and grassland habitat on the Edwards Plateau do not explain the rarity of *S. bracteatus*. Plant survival, growth, and fecundity were lower in the grassland than in the woodland. The poor performance of this species in the grassland was due primarily to abiotic conditions in the grassland and secondarily to insect herbivory. Its failure in the grassland was not due to competition or deer herbivory.

Table 3.1. Adult herbivory in the woodland and grassland in 1994 and 1995 by treatment with plots pooled. Values in 1995 are for planted plots only.

	1994[†]						1995					
			No. eaten by:						No. eaten by:			
Treatment	No. adults	No. (%) missing	deer	insects	unk.	Total no. (%) eaten[¥]	No. adults	No. (%) missing	deer	insects	unk.	Total no. (%) eaten[¥]
WOODLAND												
control	38	12 (32)	0	2	2	16 (42)	38	6 (16)	0	7	1	14 (37)
caged	51	14 (27)	--	5	1	20 (39)	38	3 (8)	--	9	0	12 (32)
caged + ins.*	333	79 (24)	--	30	2	111 (33)	225	28 (12)	--	37	11	76 (34)
GRASSLAND												
Clipped												
control	21	14 (67)	0	3	0	17 (81)	18	1 (6)	0	0	0	1 (6)
caged	20	12 (60)	--	3	0	15 (75)	25	0	--	1	1	2 (8)
caged + ins.	50	17 (34)	--	10	0	27 (54)	32	2 (6)	--	2	2	6 (19)
Unclipped												
control	28	16 (57)	0	2	1	19 (67)	18	2 (11)	0	1	1	4 (22)
caged + ins.	50	25 (50)	--	5	1	31 (62)	28	4 (14)	--	4	0	8 (29)

* insecticide

[†] data from three and two adult censuses, plus the final harvest each, for the woodland and grassland, respectively

[¥] includes missing plants

Table 3.2. Soil surface, physical, and chemical properties at five sites in Travis County occupied by *S. bracteatus* and at Emma Long in the woodland experimental site.

	OCCUPIED SITES						
Property	Barton Creek	Bee Creek	Mesa	Mt. Bonnell	Valburn	$p^{\dagger}$	Emma Long
sample date	15 May	9 May	21 May	21 May	6 May		6 May
sample area (m^2)	33	49	46	8	48		240^1
N	12	12	15	8	15		30
LITTER							
depth (cm)	4.7 ± 1.8	4.3 ± 1.7	4.5 ± 1.3	3.0 ± 1.4	4.5 ± 1.8	N.S.	3.5 ± 1.5
total biomass^1 (kg m^{-2})	1.5 ± 0.9	1.7 ± 0.8	2.1 ± 1.5	1.0 ± 0.7	2.2 ± 0.9	N.S.	1.7 ± 1.0
oak biomass^Y (kg m^{-2})	0.3 ± 0.6	0.6 ± 0.6	0.7 ± 0.5	0.7 ± 0.5	0.1 ± 0.1	N.S.	0.2 ± 0.5
juniper biomass^Y (kg m^{-2})	0.7 ± 0.6	0.7 ± 0.4	1.1 ± 1.7	--	1.9 ± 0.9	N.S.	1.3 ± 0.7
other spp. biomass^Y (kg m^{-2})	0.2 ± 0.2	--	0.1 ± 0.1	--	--		--
SOIL							
series$^{\&}$	Tarrant	Tarrant	Brackett	Brackett	Tarrant / Speck		Brackett
% sand	38.8 ± 4.7	35.5 ± 10.8	38.1 ± 10.0	48.3 ± 2.1	49.0 ± 11.4	**	52.0 ± 5.3
% clay	32.2 ± 5.1	27.0 ± 7.1	18.3 ± 3.6	21.4 ± 1.3	22.2 ± 3.4	**	13.8 ± 3.7
soil depth (cm)	26.8 ± 15.5	15.3 ± 12.3	21.5 ± 11.6	18.5 ± 6.2	15.6 ± 8.3	N.S.	18.0 ± 12.8
% organic matter	4.5 ± 0.5	5.2 ± 0.1	5.2 ± 0.2	4.2 ± 0.7	5.1 ± 0.2	N.S.	4.9 ± 0.3
pH	8.1 ± 0.1	7.7 ± 0.2	7.8 ± 0.3	8.1 ± 0.1	7.8 ± 0.1	N.S.	8.0 ± 0.1
N (ppm)	9.8 ± 10.1	34.5 ± 9.7	13.6 ± 8.6	5.9 ± 3.0	4.9 ± 3.5	**	1.8 ± 2.2

(continued on next page)

Table 3.2. continued.

	OCCUPIED SITES						
Property	Barton Creek	Bee Creek	Mesa	Mt. Bonnell	Valburn	$p^{\prime}$	Emma Long
SOIL (continued)							
P (ppm)	20.8 ± 6.5	18.1 ± 3.8	9.7 ± 5.1	19.5 ± 2.8	20.6 ± 7.0	*	13.4 ± 3.5
K (ppm)	248.8 ± 45.2	110.3 ± 26.6	360.4 ± 83.2	108.1 ± 22.3	159.3 ± 27.1	N.S.	166.8 ± 58.4
Na (ppm)	72.4 ± 13.3	23.9 ± 4.0	36.5 ± 18.9	58.2 ± 5.5	46.0 ± 7.5	N.S.	58.7 ± 14.0
Ca (ppt)	14.4 ± 2.1	16.2 ± 2.7	17.4 ± 1.9	16.3 ± 0.0	17.7 ± 0.7	**	21.1 ± 2.4
Mg (ppt)	1.4 ± 0.2	1.8 ± 0.9	0.7 ± 0.3	1.9 ± 0.1	1.2 ± 0.4	N.S.	1.0 ± 0.2
S (ppt)	1.4 ± 0.2	0.2 ± 0.1	0.7 ± 0.4	1.4 ± 0.2	0.2 ± 0.06	*	1.2 ± 0.3
salinity (g NaCl kg^{-1})	0.3 ± 0.2	0.6 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.3 ± 0.1	N.S.	1.2 ± 0.3

[′] * $p < 0.001$; ** $p < 0.0001$; N.S. = not significant

[†] The actual area over which sampling took place was much larger (approximately 0.9 ha) due to the wide spacing of permanent plots

[‡] Includes woody debris and other material

[¥] Leaf litter only

[&] Source: USDA (1974)

Table 3.3. Litter and soil surface cover at five sites occupied by *S. bracteatus* and the Emma Long Park woodland experimental site. Values are means (Avg) and standard deviations (s.d.) of cover class medians.

		Oak		Juniper		Other		Bare		Rock	
Sites	N	Avg	s.d.	Avg	s.d.	Avg	s.d.	Avg	s.d.	Avg	s.d.
Occupied											
Barton Creek	12	22	27	7	6	52	33	6	12	10	11
Bee Creek	12	56	30	17	19	9	10	4	7	10	17
Mesa	15	50	28	24	30	17	16	1	1	6	7
Mt. Bonnell	8	57	25	0	1	21	20	4	7	10	8
Valburn	15	10	23	50	27	15	11	3	6	20	23
Unoccupied											
Emma Long	30	34	35	54	35	5	8	3	8	5	9

Table 3.4. Woodland seedling herbivory in the winter of 1994 and 1995. Values are the total number of plants within treatment (plots pooled).

	early February		late March	
Treatment	N	No. (%) w/herbivory	N	No. (%) w/herbivory
1994				
Transplants				
controls	70	23 (33)	58	40 (69)
caged	75	17 (23)	59	38 (64)
caged, ins.*	441	77 (17)	379	216 (57)
1995				
Transplants				
controls	50	16 (32)	46	29 (63)
caged	55	16 (29)	51	25 (49)
caged, ins.	277	62 (22)	258	88 (34)
Seeded				
controls	59	29 (49)	58	36 (62)
caged	62	19 (31)	63	22 (35)
caged, ins.	632	137 (22)	626	160 (26)

* sprayed with insecticide

Table 3.5. Grassland seedling and rosette herbivory in the winter of 1994 and 1995. Values are the number of plants pooled across plots within a treatment. Numbers of plants were ± equal among plots (≈ 1/plot for seeded plots and ≈4/plot for transplanted plots).

	early February		March*	
Treatment	N	No. (%) w/herbivory	N	No. (%) w/herbivory
1994				
Transplants				
Clipped				
controls	79	43 (54)	46	38 (83)
caged	85	33 (39)	59	47 (80)
caged, ins.**	92	36 (39)	69	47 (68)
Unclipped				
controls	83	31 (37)	56	44 (79)
caged, ins.	84	37 (44)	67	47 (70)
1995				
Transplants				
Clipped				
controls	42	24 (57)	40	27 (67)
caged	44	26 (59)	43	28 (65)
caged, ins.	47	26 (55)	44	32 (73)
Unclipped				
controls	40	27 (67)	33	30 (91)
caged, ins.	44	24 (60)	43	31 (72)
Seeded				
Clipped				
controls	19	5 (26)	16	7 (44)
caged	9	5 (56)	10	5 (50)
caged, ins.	15	8 (53)	17	6 (35)
Unclipped				
controls	21	9 (43)	21	8 (38)
caged, ins.	7	2 (29)	7	4 (57)

* mid-March in 1994; early March in 1995

** sprayed with insecticide

Figure 3.1. Schematic of the experimental design and sample sizes in the (A) woodland and (B) grassland habitats, 1993 to 1995.

A

WOODLAND		1993–1994		1994–1995	
		uncaged	caged	uncaged	caged
TRANS-PLANTS	water spray	25	25	13	13
	insecticide	☒	150	☒	73
SEEDED	water spray			13	13
	insecticide			☒	115

B

GRASSLAND

Vegetation clipped

		1993–1994		1994–1995	
		uncaged	caged	uncaged	caged
TRANS-PLANTS	water spray	25	25	13	13
	insecticide	☒	25	☒	13
SEEDED	water spray			12	12
	insecticide			☒	12

Vegetation not clipped

		1993–1994		1994–1995	
		uncaged	caged	uncaged	caged
TRANS-PLANTS	water spray	25	—	13	—
	insecticide	☒	25	☒	13
SEEDED	water spray			12	—
	insecticide			☒	12

Figure 3.2. Survival of *S. bracteatus* in the woodland by treatment in 1995 of (A) transplants and (B) seeded plants. Values are means of plot means ± standard error.

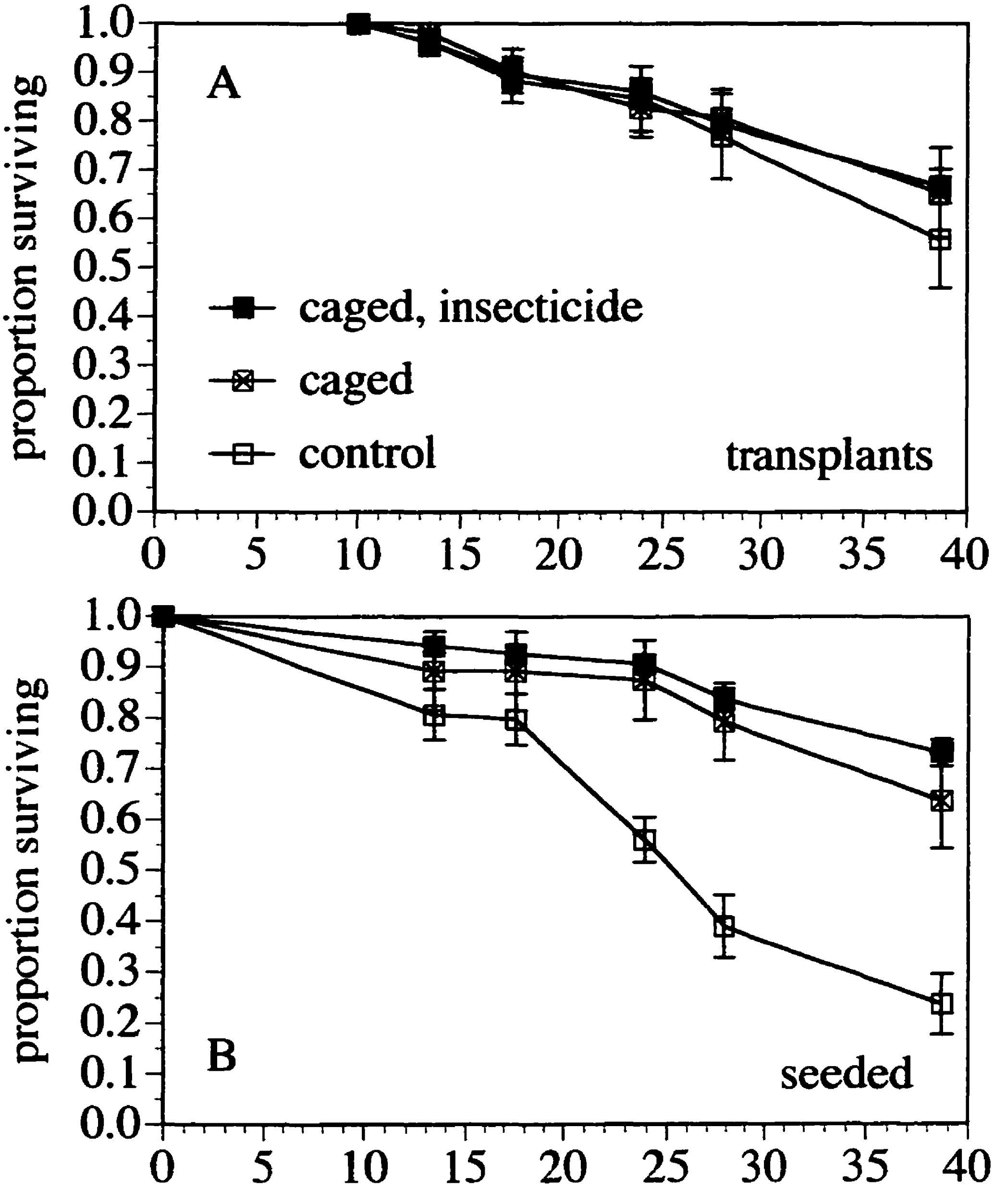

A
B
transplants
seeded
caged, insecticide
caged
control
proportion surviving
weeks after seed sowing
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
0
5
10
15
20
25
30
35
40

Figure 3.3. Survival of *S. bracteatus* in the woodland, by treatment, in 1994. Values are means of plot means ± standard error.

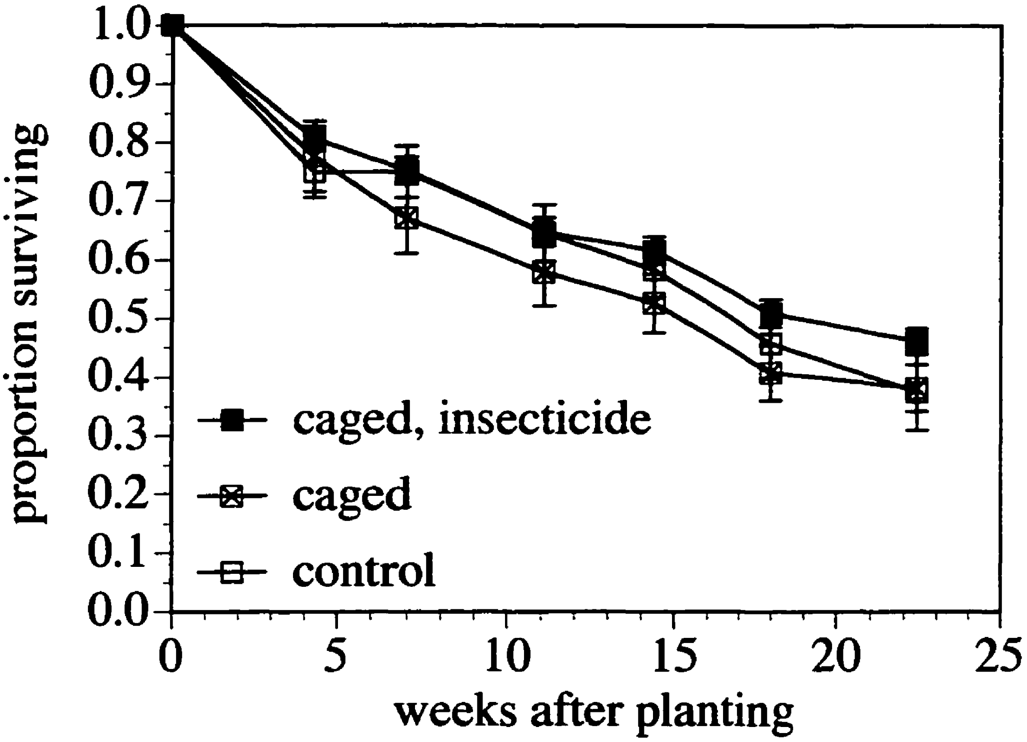


Figure 3.4. Mean above-ground biomass in the woodland by treatment. Values are means of plot means ± standard error. Sample sizes are shown at the base of each bar. One extreme outlier was omitted from each caged, insecticide treatment in each year.

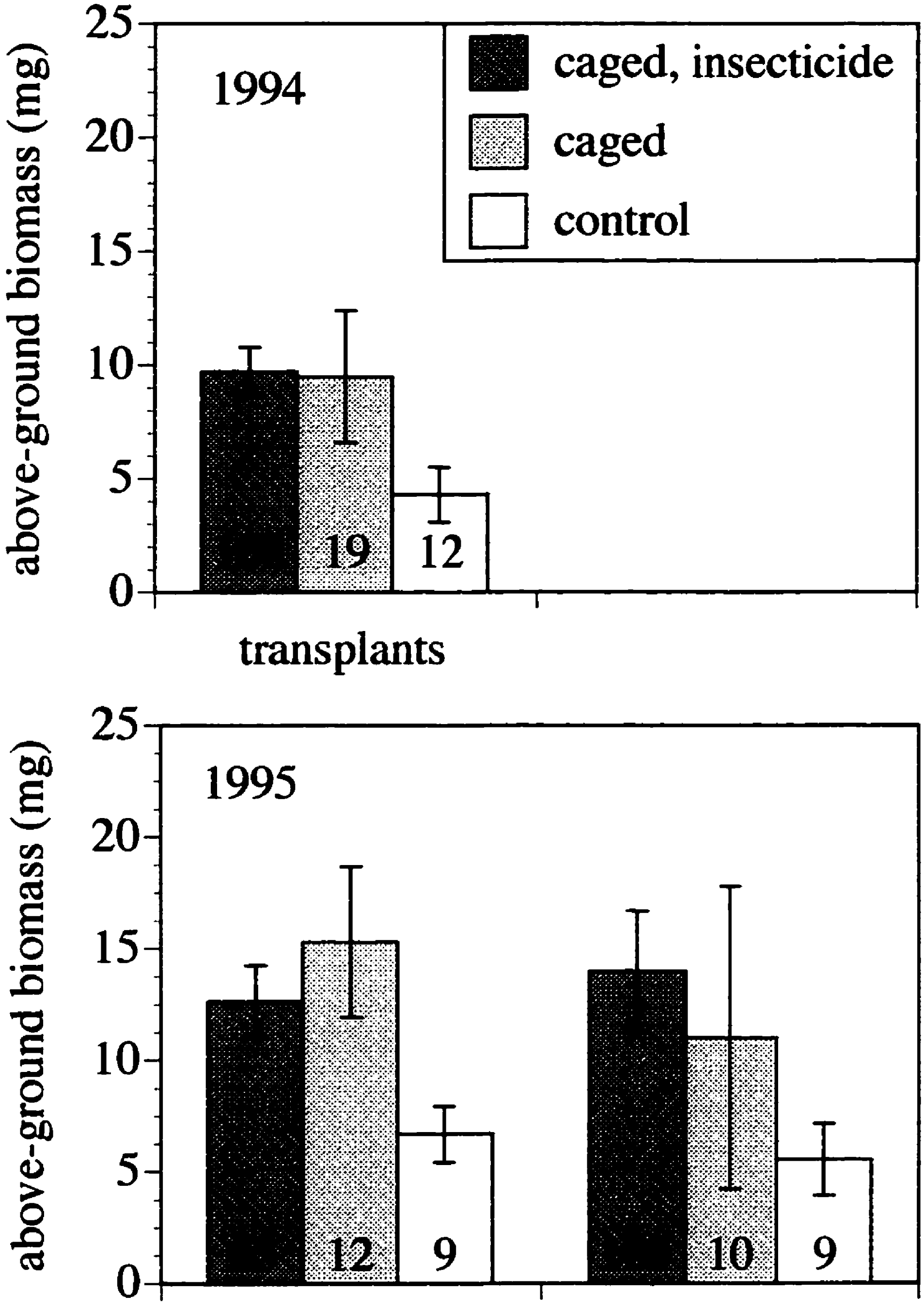

1994
caged, insecticide
caged
control
above-ground biomass (mg)
25
20
15
10
5
0
19
12
transplants
1995
above-ground biomass (mg)
25
20
15
10
5
0
12
9
10
9
transplants
seeded

Figure 3.5. Proportion of woodland plants surviving to the final census and reproducing, by treatment. Values are means of plot proportions ± standard error. Sample sizes are shown at the base of each bar.

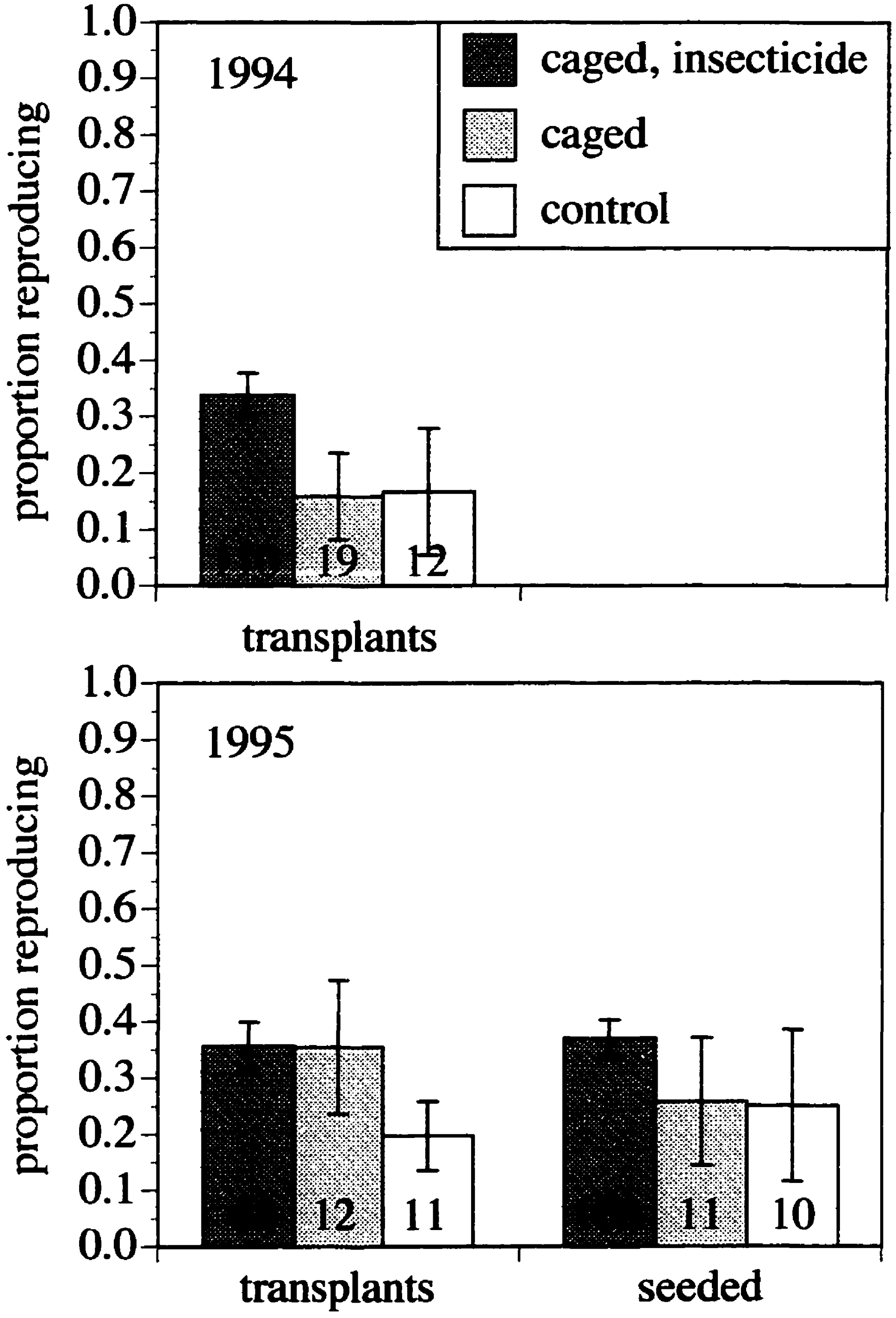
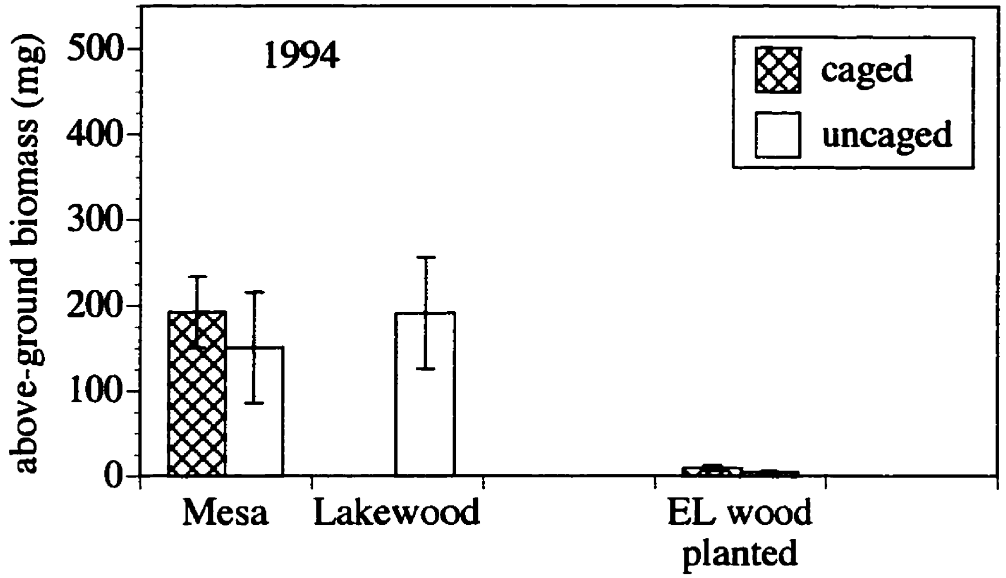

1994
caged, insecticide
caged
control
proportion reproducing
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
19
12
transplants
1995
proportion reproducing
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
12
11
11
10
transplants
seeded

Figure 3.6. Comparison of final biomass between the experimental site and three typical natural populations. Note that only two natural populations were harvested in each year. Values are means ± standard error. Values of caged plots at Emma Long Park (EL) are of plots sprayed with water.


1994
caged
uncaged
above-ground biomass (mg)
0
100
200
300
400
500
Mesa
Lakewood
EL wood planted

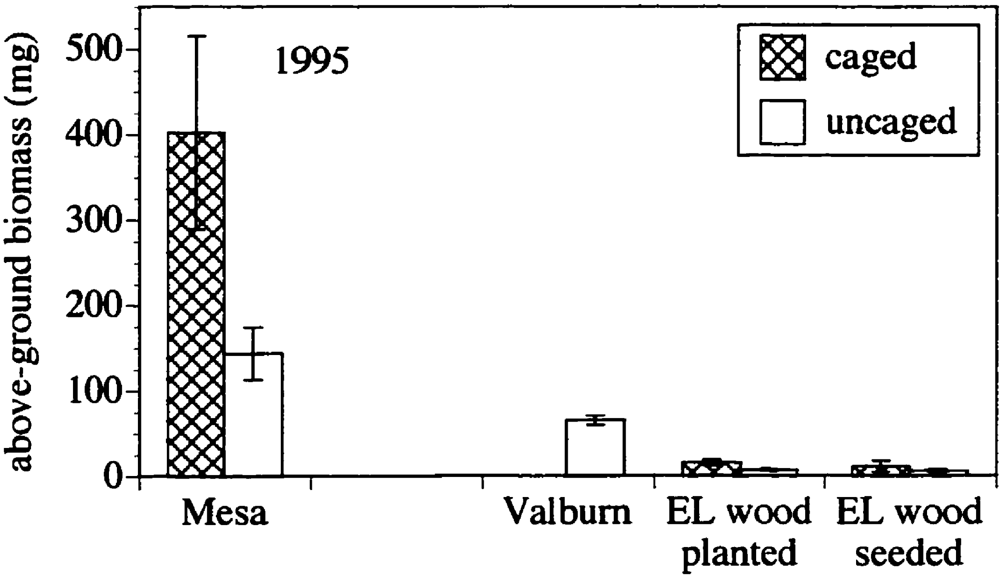

1995
caged
uncaged
above-ground biomass (mg)
0
100
200
300
400
500
Mesa
Valburn
EL wood planted
EL wood seeded

Figure 3.7. The proportion of seeds sown that produced seedlings, by treatment and habitat in 1994–1995. Values are means of plot proportions ± standard error. Sample sizes are shown below each bar.

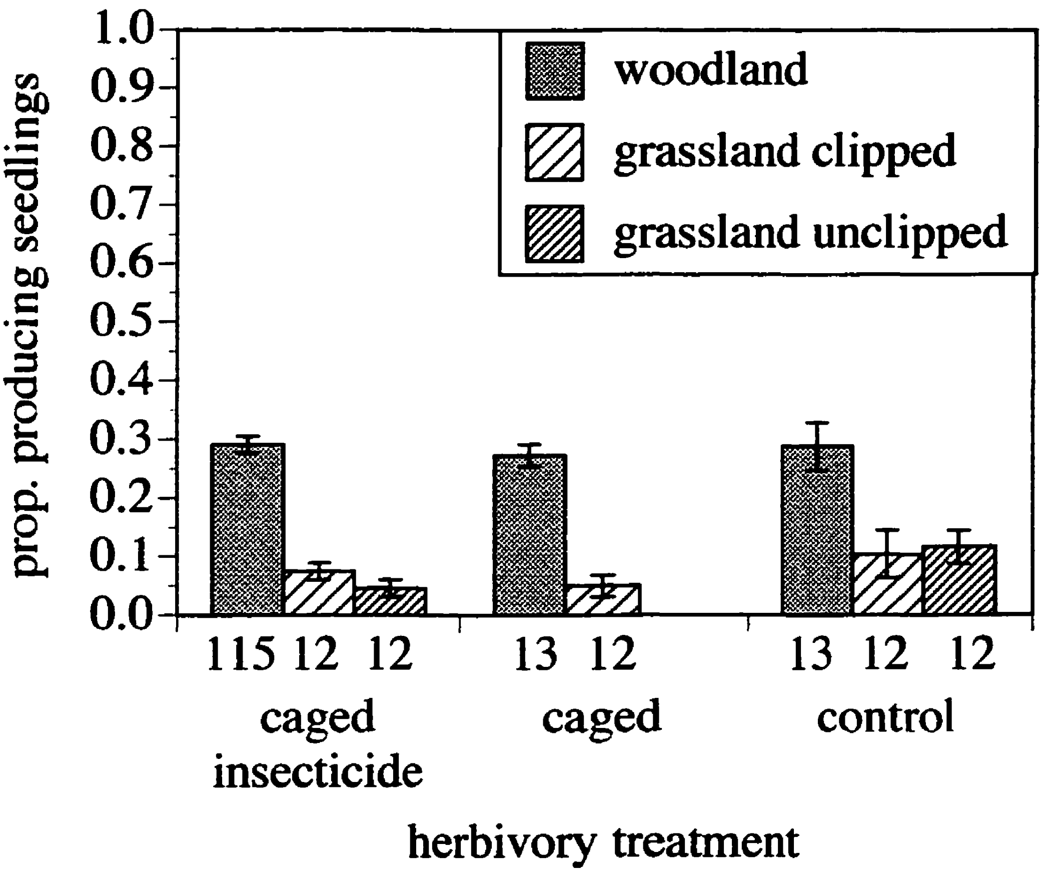
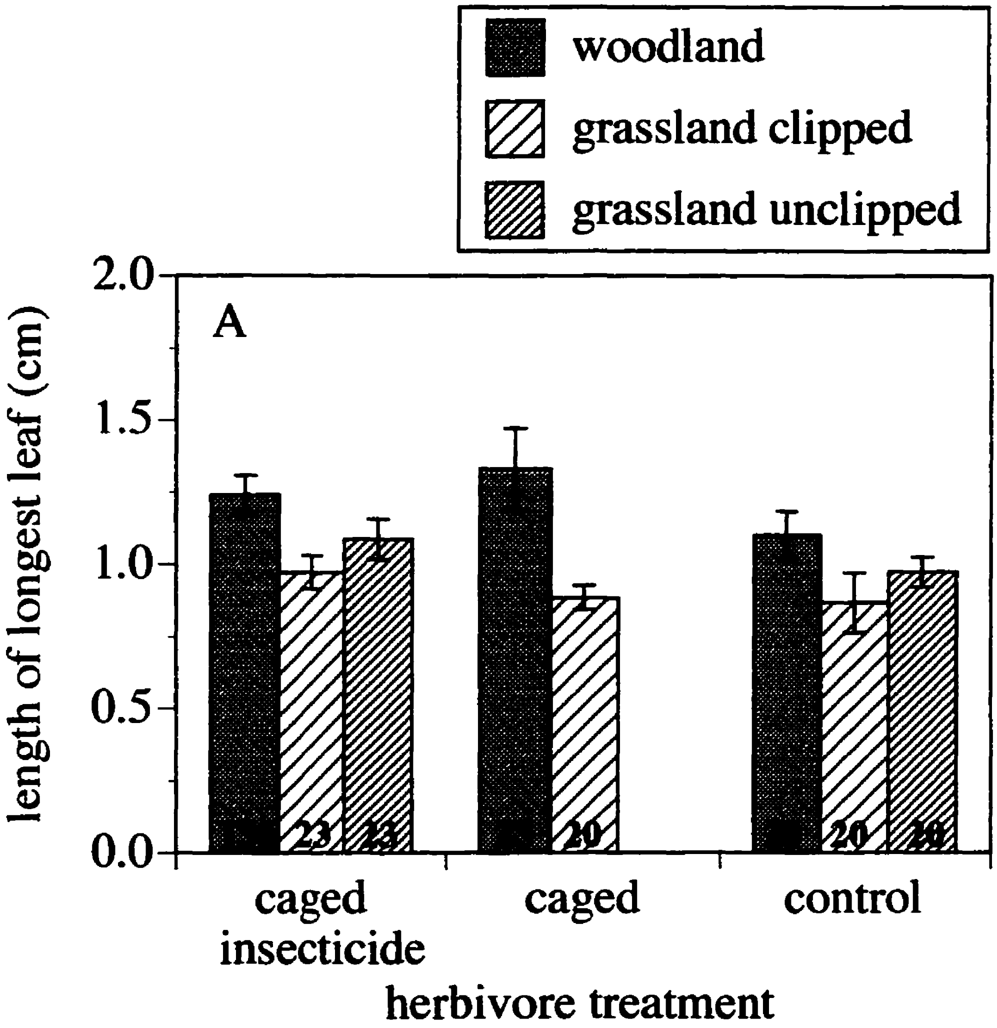


Figure 3.8. Winter rosette size by habitat and treatment in 1994. Values are means of plot means ± standard error of (A) the length of the longest leaf and (B) the number of leaves. Data are from surveys on 20 and 27 March in the grassland and woodland, respectively. Sample sizes are given at the base of each bar.


woodland
grassland clipped
grassland unclipped
A
length of longest leaf (cm)
2.0
1.5
1.0
0.5
0.0
23
23
20
20
caged
insecticide
caged
control
herbivore treatment

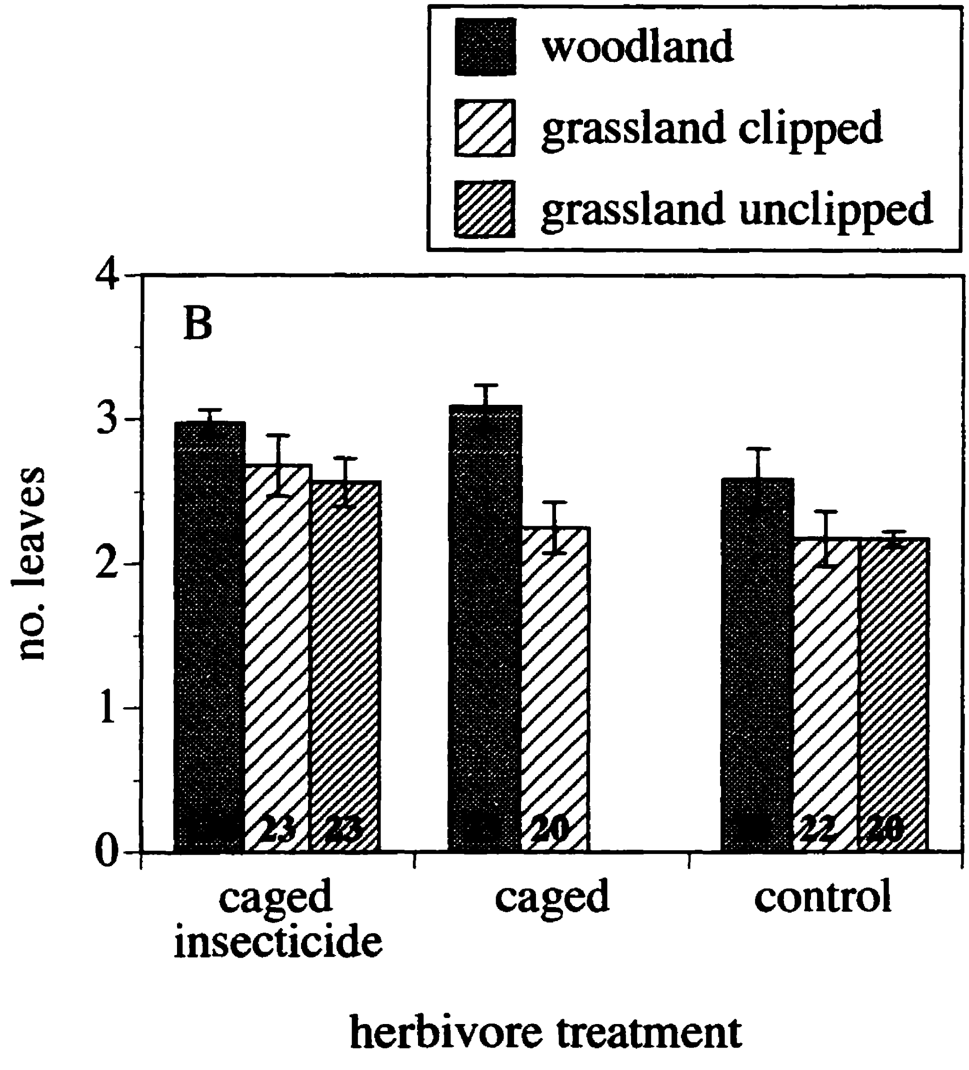

woodland
grassland clipped
grassland unclipped
B
4
3
2
1
0
no. leaves
23
23
20
22
20
caged insecticide
caged
control
herbivore treatment

Figure 3.9. Survival of *S. bracteatus* in clipped plots in the grassland in 1994 by treatment. Values are means of plot means ± standard error.

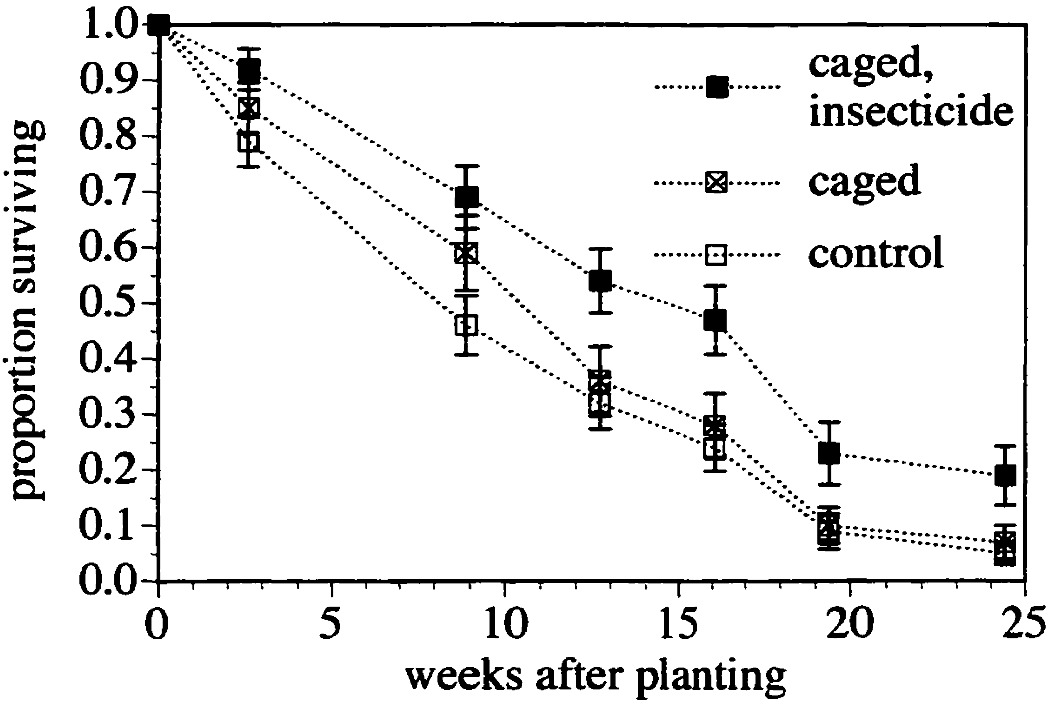


Figure 3.10. Survival of *S. bracteatus* in the grassland in 1995 comparing herbivory treatments within clipped plots of (A) transplants and (B) seeded plants. Values are means of plot means ± standard error.

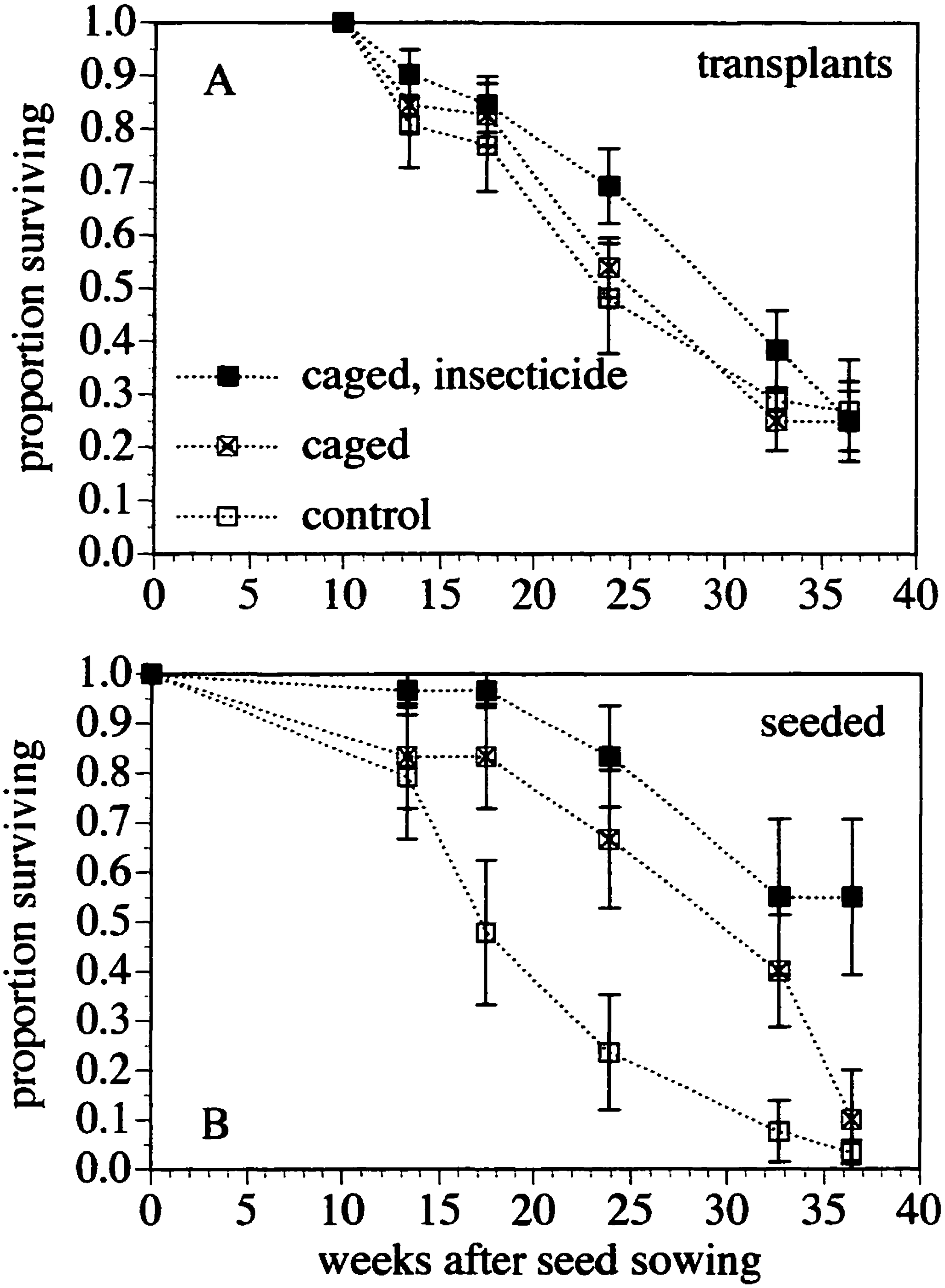

A
transplants
caged, insecticide
caged
control
proportion surviving
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
5
10
15
20
25
30
35
40
B
seeded
proportion surviving
weeks after seed sowing

Figure 3.11. Survival of *S. bracteatus* in the grassland in 1994 by vegetation removal and herbivory treatment. Values are means of plot means ± standard error.

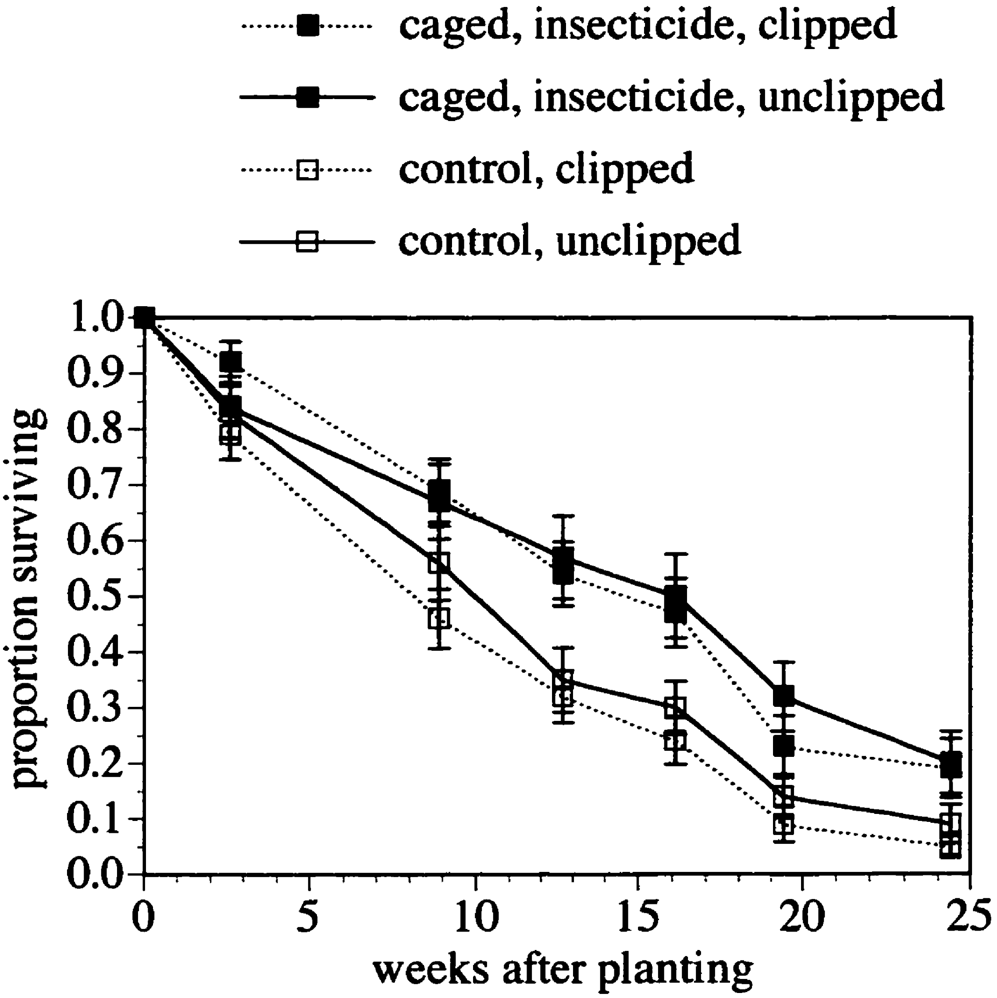
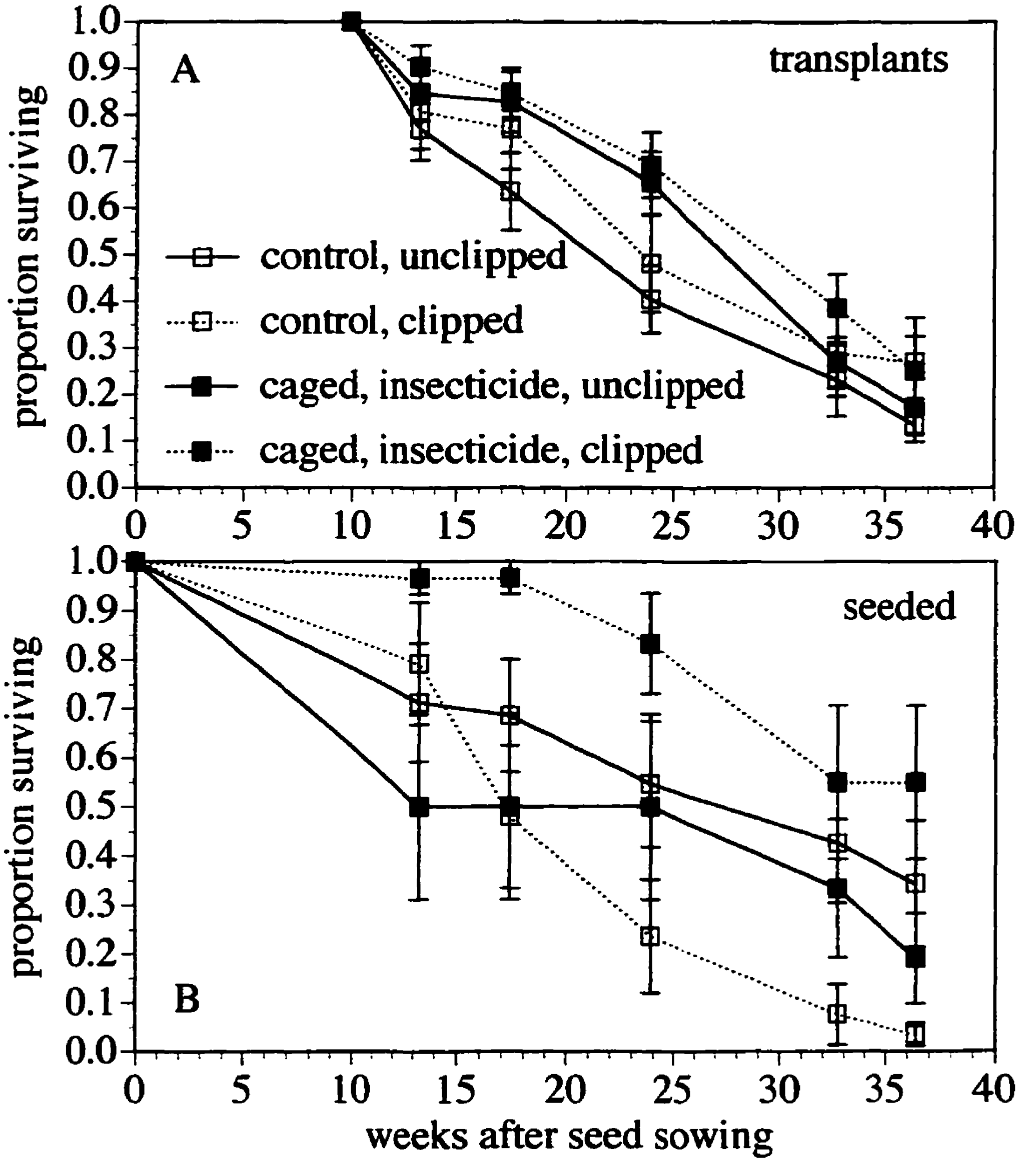


Figure 3.12. Survival of *S. bracteatus* in the grassland in 1995 by vegetation removal and herbivory treatments with (A) transplants and (B) seeded plants. Values are means of plot means ± standard error. Clipped treatments are shown by dotted lines, unclipped by solid lines; caged and insecticide-sprayed treatments are shown by solid symbols, controls by open symbols.


A
transplants
proportion surviving
control, unclipped
control, clipped
caged, insecticide, unclipped
caged, insecticide, clipped
B
seeded
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
5
10
15
20
25
30
35
40
weeks after seed sowing

Chapter 4: Herbivory and Seed Bank Effects on the Population Dynamics of a Rare Annual Plant: Projection Matrix and Elasticity Analysis

ABSTRACT

I investigate the effects of white-tailed deer (*Odocoileus virginianus*) on the population growth rate of three populations of a rare annual plant, *Streptanthus bracteatus* (Brassicaceae). I constructed projection matrix models derived from observational and experimental data. These data were collected during three years in five natural populations and in a planted seed bank.

With deer herbivory, two of three populations were probably stable or growing during at least one year. One population was probably in decline during two of the three years of the study. This population is forecast to become extinct within 50 years with a probability of over 50% because of high variance in its population growth rate. Without deer herbivory, all the models predict that the population growth rate of *S. bracteatus* should increase, sometimes substantially.

Using elasticity analysis, I investigate the relative importance of each life-stage of *S. bracteatus* to the population growth rate. I found that combining elasticity with the natural variation in demographic parameters provides a better estimate of each life-stage's relative importance than does each value alone. The life-stage transition that contributed most to the population growth rate differed according to population and year.

INTRODUCTION

It is now well-documented that herbivory can affect all aspects of individual plant growth, development, and reproduction. The effects of herbivory on population dynamics, however, remain unclear. Demographic parameters such as survival and fecundity are the basis for estimates of a key aspect of population dynamics, population growth rate. If herbivores have effects on one or more of these demographic parameters, it follows that they might also be affecting the population growth rate. For example, herbivores can substantially reduce the fecundity of some species (e.g., Crawley 1983; Hendrix 1984; Kinsman and Platt 1984; Brown et al. 1987; Louda et al. 1990; Bergelson and Crawley 1992). We might expect that this also reduces the growth rate of these populations. However, changes in particular demographic parameters are not necessarily proportional to or correlated with changes in population growth rates (Kalisz and McPeek 1992; Silvertown et al. 1993). Thus in order to predict the effects of herbivory on population dynamics, one must directly estimate or measure a population's response to herbivory (Doak 1992; Bastrenta et al. 1995; Ehrlén 1995b; Bullock et al. 1996).

Population projection matrices are a powerful set of models used to predict population dynamics (Caswell 1989). These models have been used to investigate the effects on population growth rate of fire (Silva et al. 1991), commercial harvesting (Olmsted and Alvarez-Buylla 1995), spatial and temporal heterogeneity (Moloney 1988; Kalisz and McPeek 1992; Bengtsson 1993; Oostermeijer et al. 1996), and herbivory (Doak 1992; Ehrlén 1995b; Bullock et al. 1996). In this study I predict the effects of herbivory on the population growth rate of a rare annual plant, *Streptanthus bracteatus* (Brassicaceae).

Although there are many examples of models being used to predict population persistence (i.e., time to extinction) of rare animal species (Lande 1987; Schemske et al. 1994) and at least one rare plant (Menges 1990), models using population projection matrices have not been widely been used for conservation purposes or to investigate rare species (but see Oostermeijer et al. 1996). Some have used such models to predict the effects of management practices (e.g., Crouse et al. 1987; Menges 1990; Olmsted and Alvarez-Buylla 1995).

In this chapter I predict the effects of excluding white-tailed deer (*Odocoileus virginianus*) from populations of a rare annual plant, *Streptanthus bracteatus*. In chapters 2 and 3, I found that white-tailed deer have significant negative effects on the growth, survival, and fecundity of *S. bracteatus*. However, the effects of white-tailed deer on the population dynamics of *S. bracteatus* are unknown. White-tailed deer have large negative effects on the individual plant performance of other plant species (e.g., Allison 1990b; Canham et al. 1994; Gedge and Maun 1994). Moreover, anecdotal evidence suggests that they similarly affect many rare plants (Miller et al. 1992). If individual plant performance is correlated with population growth, white-tailed deer may be dramatically reducing the population growth of many plants. In this chapter I test the hypothesis that deer are reducing the growth rate of populations of *Streptanthus bracteatus*. I used data from chapter 2 and from an experimental seed bank to construct population projection matrix models. These models suggest that deer reduce the population growth rate of *S. bracteatus* at all sites, sometimes substantially.

METHODS

Study species

Streptanthus bracteatus (Brassicaceae), the bracted twistflower, is an annual herb that is restricted to limestone-derived soils of the eastern and southern margins of the Edwards Plateau of central Texas (Appendix 1). It is known from eight populations, all of which are found in and adjacent to evergreen woodlands dominated by *Juniperus ashei* and *Quercus fusiformis*. Many of these populations experience high rates of herbivory, primarily by white-tailed deer (hereafter referred to as 'deer') and the larvae of the falcate orange-tip butterfly (*Anthocharis midea*: Pieridae). In some populations, herbivory reduces the survival, chance of reproduction, and fecundity of adult plants (Chapters 2 and 3).

Experimental seed bank

To determine the population dynamics of most annual plants one must have knowledge of the dynamics of the soil seed bank (Harper 1977). I quantified the persistence of *S. bracteatus* seeds by creating two experimental seed banks, one each in 1993 ('experiment 1') and 1994 ('experiment 2'). In order to prevent the mixing of natural and artificial seeds, I established these experiments at a site in which *S. bracteatus* was not known to occur. The study site, Emma Long

Metropolitan Park in Travis County, Texas, had vegetation and physical characteristics similar to sites occupied by *S. bracteatus* elsewhere in Travis County (Chapter 3).

In experiment 1, I collected seeds from a second-generation greenhouse population originally from Valburn (Chapter 2; Appendix 1). I sorted seeds that were not obviously inviable into 50 groups of 100 seeds each for a total of 5000 seeds. To ensure that this seed stock was representative of wild stocks, I weighed 100 randomly-chosen seeds and compared them to 100 randomly-chosen seeds that were collected in the spring of 1993 from a wild population.

At the study site I established ten 1 m-diameter circular plots, each of which was caged to minimize disturbance. Cages were 1.5 m tall and were constructed of 14-gauge galvanized welded wire. In each plot, I placed five 10 cm-diameter subplots in a 15 cm-radius circle around the central stake and equidistant from each other. Each plot was then randomly assigned to one of five harvesting dates: (1) 1 week, (2) 12 months, (3) 18 months, (4) 24 months, and (5) 32 months after installation. The first harvest was used to determine the expected recovery rate. On 27 October 1993, I removed the top 1 cm of leaf litter and soil within each subplot and then sowed each group of 100 seeds (100 seeds * 5 subplots per plot * 10 plots = 5,000 seeds) evenly on the exposed soil surface. Afterwards I replaced the original topsoil and litter and lightly packed the soil surface.

Within one month of installation of experiment 1, most of the seeds germinated (see Results). This left few seeds in the soil with which to estimate long-term viability. I hypothesized that the unexpectedly high germination rates were due to one or both of two factors: (1) Because seeds of *Streptanthus bracteatus* typically disperse in July and August (D. Zippin, *personal observation*), the later sowing date in experiment 1 may have reduced the time available for dormancy to become established; (2) because seeds of *S. bracteatus* may require exposure to high temperatures on the soil surface in order to induce dormancy, seed burial may have reduced this exposure and thus prevented the establishment of dormancy.

To test these hypotheses, I established a second experiment in 1994 of ten additional plots (but containing four subplots each instead of five: 100 seeds * 4 subplots per plot * 10 plots = 4,000 seeds). I used the procedure of experiment 1 except for two modifications that better mimicked the natural pattern of seed dispersal. First, I sowed seeds two months earlier, on 30 August 1994. Second, instead of burying the seeds, I spread them on the soil surface and left rocks and plant material intact. The latter technique introduced the problem of how to keep the seeds in place so that they could be retrieved up to two years later. To hold the seeds within each subplot, I constructed 2 cm-high "fences" of nylon mesh, 10 cm in diameter. The four treatments of 10 subplots each were harvested 2 wk, 6 mo, 12 mo, and 24 mo after installation, respectively. The first harvest was delayed due to heavy rains.

Seed viability testing

I tested seed viability for each treatment in three stages: field germination, incubator germination, and chemical testing. First, I assessed field germination by performing censuses for newly emerged seedlings at irregular intervals, approximately one week after each major rain. Seedlings were immediately removed after they were counted. Despite the nylon fences, some seedlings in experiment 2 emerged outside of their subplots (but always within or close to their plots); these seedlings were assigned to the nearest subplot.

Second, I harvested each seed bank at the assigned interval to assess germination in an incubator. I removed the top 6 cm of soil within each of the ten subplots, 2 cm beyond the subplot boundary, and then filled the hole with nearby soil. Samples were stored in a plastic bag at room temperature until the incubator tests were performed. Before incubation, I mixed the sample with 300 ml of fine vermiculite (< 2 mm particle size) and spread this mixture in a plastic flat that was lined with a nylon mesh to prevent soil and seed loss but allow drainage. Flats were watered in an incubator at 29° C on a 12-hour light cycle, conditions that were determined optimal for germination of *Streptanthus bracteatus* in previous experiments (D. Zippin and J. Fritz, *unpublished data*).

Seedlings of *S. bracteatus* that emerged in the incubator were removed and classified as having 'weak dormancy' (i.e., requiring only watering to break dormancy). After recruitment ceased (after 2 to 3 weeks), I attempted to break dormancy in the remaining seeds by adding 1.5 liters of a 0.5 gram-per-liter solution of gibberellic acid and water. Seedlings that emerged after this point were scored as having 'moderate dormancy'. Once germination ceased again, I sifted each sample through a series of sieves in order to find every remaining seed. Seeds that were partially eaten were scored as 'inviable due to predation'.

Finally, to determine the viability of the remaining intact seeds, I immersed them in 5 ml of a buffer solution (pH 7.41) and allowed them to imbibe. I then added 5 ml of a solution of 2, 3, 5-triphenyl tetrazolium chloride and distilled water (10 mg ml^{-1}) to each sample in a petri dish and covered them with aluminum foil to prevent photochemical reactions. After 48 hours, I scored each seed as having 'strong dormancy' if it was red or pink and 'inviable' if there was no color change. Such effects are reliable indicators of biological activity (Smith and Thornberry 1951). In summary, I categorized the fate of seeds into six categories: (1) field germination, (2) weak dormancy, (3) moderate dormancy, (4) strong dormancy, (5) inviability, or (6) predation.

Seed fate calculations

Because only a subset of seeds was recovered at each harvest, the proportion of seeds in each fate category after field germination had to be adjusted by a "recovery rate" in order to estimate the fate of the original cohort. I estimated the recovery rate by calculating the mean fraction of seeds recovered from the first treatment using the formula: $(I + S) / (100 - F - P)$, where I = incubator germination (weakly and moderately dormant seeds), S = sifted seeds, F = field germination, and P = predation. This method assumes that there was no seed predation or decomposition between installation and the first harvest. Original seeds unaccounted for by the six categories once the recovery rate was taken into account were assumed to be missing due to predation or decomposition.

From these data I derived three parameters in each year that were used in the construction of the population dynamics models (Figure 4.1): (1) g_{seed}, the fraction of seeds that germinated from seed just dispersed from the parent, (2) g_{dorm}, the fraction of one-year-old seed that germinated from the seed bank, and (3) q_{dorm}, the mortality of seeds in the soil in their first year of dormancy. I calculated dormant seed mortality (q_{dorm}) as the sum of the mean fractions of inviable seeds and those missing due to predation and decomposition. I estimated the germination fraction of new seed in each year (g_{seed}) as the mean proportion of field germinants (mean of treatment means) within the first season of the experiment. The germination fraction of dormant seeds (g_{dorm}) was estimated as proportion of field germinants after one year of dormancy, adjusted for germination and mortality in the previous year.

Unfortunately, separate seed bank experiments could not be performed at each of the four natural population. This was due, in part, to the potential of contamination from an existing seed bank. Thus the same estimates of *S. bracteatus* seed bank dynamics were used in the model for each natural population.

Population models

Models of the population dynamics of *Streptanthus bracteatus* above-ground were based on demographic data collected in two seasons (November 1993 to August 1994 and October 1994 to August 1995) at four populations in Travis County, Texas. Censuses occurred monthly in the winter and bi-weekly in the spring and early summer (Chapter 2; Appendix 1). Additional surveys not described previously were conducted in the spring of 1993, in which adult survival and fecundity were assessed at three of the four sites.

I distinguished four stage classes in plants above-ground: (1) seedlings, (2) rosettes, (3) pre-reproductive adults, and (4) reproductive adults. I defined rosettes as having at least four leaves, two of which were larger than the cotyledonous leaves. A rosette became a pre-reproductive adult after bolting and as soon as the basal diameter of a stem could be measured with dial calipers. Reproductive adults had fruits just before seed dispersal. Using this structure, I estimated for each site and each year the probability of survival, p, between each of four stages and the mean fecundity, m (Figure 4.1). In this model, adult 'survival', p_{pra}, was equivalent to the product of the probability of adult survival and the probability of reproduction (Chapter 2).

In the first season monitoring began in the spring, so survival data were incomplete. To fill in the gap I assumed that the survival of seedlings and rosettes was the mean of the values in the next two years. Rainfall during the first season was intermediate between that of the next two years (Figure 4.2). Moreover, rainfall appears to be strongly correlated with the probability of germination and survival of *S. bracteatus* (Appendix 1). Given the pattern of rainfall during the three seasons of this study, I hereafter refer to these seasons as the 'average', 'dry', and 'wet' year, respectively.

To estimate the growth rates of *Streptanthus bracteatus*, I constructed a population projection matrix model of each population in each year. In such models, the time at which the annual cycle ends is somewhat arbitrary. I chose as the end point of the annual cycle the final census in August, which is the time just before reproductive adults dispersed their seeds (Figure 4.1). Each matrix contained annual transition probabilities between the two major life-history stages of *S. bracteatus*, dormant seeds and adults with mature seeds. Dormant seeds of *S. bracteatus* live more than one year, so this species is not a true annual (Appendix 1; this chapter). Thus, more than one annual stage ought to be included in a projection matrix model of this species. Kalisz and McPeek (1992) constructed such a model of an annual plant with a seed bank. They incorporated several dormant seed stages, each of progressively older age. In contrast, I used only one dormant seed stage. Differences in the germination rates of seeds of *S. bracteatus* among years was likely due to the high variation in rainfall among years rather than to differences in seed age. Indeed, in some weeds the rate of dormant seed mortality is known to be age-independent and constant (Roberts and Feast 1973; Warnes and Andersen 1984). Thus for *S. bracteatus* it made more biological sense to incorporate the variation in seed bank dynamics into models of environmental stochasticity (described below) rather than to increase the number of stages in the matrix models.

The matrix models were constructed in the form:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$$

where **n** is a vector that contains the number of individuals in each stage at time t. To obtain the number of individuals after one year, one multiplies $\mathbf{n}(t)$ by **A**, the population projection matrix (van Groenendael et al. 1988; Caswell 1989), where

$$A = \begin{bmatrix} s_{11} & a_{12} \\ s_{21} & a_{22} \end{bmatrix}.$$

Each element of **A** is an annual transition probability from the jth (column) stage to the ith (row) stage. The elements in column one describe the transitions from the dormant seed stage, s, and the elements in column two describe the transitions from the reproductive adult stage, a (Figure 4.3). The four transition elements were calculated from the terms in the annual life-cycle diagram by the following formulas:

1) $s_{11} = (1-g_{dorm})\,(1-q_{dorm})$ = the probability of a dormant seed remaining a dormant seed and surviving one year.
2) $s_{21} = g_{dorm}\, p_{seedling}\, p_{ros}\, p_{pra}$ = the chance of a dormant seed germinating and surviving to become a reproductive adult.
3) $a_{12} = m\,(1- g_{seed})\,(1-q_{dorm})$ = the probability of a reproductive adult producing a seed that enters the seed bank and survives until the following year.
4) $a_{22} = m\, g_{seed} p_{seedling}\, p_{ros}\, p_{pra}$ = the probability of a reproductive adult producing a seed that germinates within the next season and survives to become a reproductive adult.

The final element, a_{22}, describes seeds that do not enter the seed bank but germinate in the fall within several months after dispersal from the parent. This component is often missing from matrices of annuals with or without persistent seed banks (Caswell 1989; Silvertown et al. 1993). Its omission results in an underestimate of the population growth rate. Note that both values of a are composite terms of survival and fecundity and thus can take values greater than one. Values of s are strictly survival probabilities and will always be between zero and one. The potential growth rate of each population, λ, is the dominant eigenvalue of its corresponding projection matrix (Caswell 1989). Values of λ greater than one indicate a population that is growing; values less than one indicate a population in decline.

For each population with a negative growth rate I estimated the time to extinction assuming constant environmental conditions. In essence, this measure forecasts what will happen if current conditions remain constant. However, there is an important distinction between a forecast and a prediction. Because constant environmental conditions are clearly not realistic, time to extinction does not predict what *might* happen to a population (Caswell 1989). To add more realism to these estimates, I calculated time to extinction for each site assuming that environmental conditions varied randomly. The transition matrix was chosen with equal probability from among the dry, wet, and average year matrices.

It is also useful to calculate how sensitive λ is to small changes in individual elements of the projection matrix. Such values provide information about several aspects of population biology and about the construction of the model. For example, if an element has a large sensitivity, it indicates that small errors in the measurement of that value will produce relatively large errors in the estimate of λ. In biological terms, changing a sensitive transition element by a small amount through deliberate manipulation can potentially change the population growth rate by a large amount. Thus sensitivity is a particularly useful measure to managers interested in increasing population growth rates. I calculated values of sensitivity using the formula:

$$\frac{\partial \lambda}{\partial x_{ij}} = \frac{v_i w_j}{\langle \mathrm{w}, \mathrm{v} \rangle}$$

where v_i is the *i*th element of the left eigenvector, and w_j is the *j*th element of the right eigenvector of **A** (Caswell 1989). The denominator is the scalar product of the two eigenvectors. These eigenvectors are also of biological interest: the right eigenvector is the stable stage distribution and the left eigenvector is the reproductive value, or the relative contribution of each stage to reproduction.

A major limitation of sensitivity is that it is an absolute measure. Because some transition elements are always less than one and other elements can be much larger than one, it is difficult to compare sensitivities among elements. An alternative measure, elasticity, has been developed. It describes the effects on λ of proportional changes in transition elements (De Kroon et al. 1986). Here I calculate the elasticity, e_{ij}, of each transition element in each projection matrix to describe the contribution of changes in each transition element to changes in λ by:

$$e_{ij} = \frac{x_{ij}}{\lambda}\frac{\partial \lambda}{\partial x_{ij}}$$

where x_{ij} is the projection matrix element in the *i*th column and *j*th row. Elasticities within a matrix also have the desirable property of adding to one (Mesterton-Gibbons 1993). Thus one can compare values among matrices with the same dimensions.

Deer exclusion models

To estimate the effects of deer exclusion on the population growth rate, I constructed projection matrices for each site except Mt. Bonnell (where deer were not present naturally). These models were equivalent in structure to those described above, but contained transition probabilities that would be expected in the absence of deer. The effects of deer were not quantified in the first season, so I constructed these matrices for the wet and dry year only. I estimated the expected transitions by first calculating the expected adult survival and fecundity of plants in the absence of deer (survival and fecundity were components of three of the four transition elements). I assumed that the transition from dormant seed to dormant seed (s_{11}) was not affected by herbivory. I also assumed that the seedling and rosette stages were unaffected by deer (Chapters 2 and 3). Another important assumption of these models was that the effects of insect herbivory would not change. This assumption is supported by the results of deer exclusion experiments in which insect feeding rates and the effects of insects were the same whether deer were present or not (Chapters 2 and 3).

The ideal method with which to derive expected transition probabilities in the absence of deer is to exclude deer from a portion of a population and compare the performance of these plants to that of unmanipulated plants. This was not possible at most natural populations, for reasons described in chapter 2. Instead, the effects of deer on individuals of *S. bracteatus* were estimated by comparing the performance of eaten plants to uneaten plants. Although I was careful to account for size-based preference in these analyses, these estimates lacked the strength of the results that manipulative experiments provide. I performed exclusion experiments at a fifth natural population, Mesa, that addressed this concern (Chapter 2). I estimated the effects of deer on survival and fecundity using three sets of models.

'MESA' models: experimental data. Conditions at Mesa were similar to those at other populations in both years: the intensity of deer herbivory at Mesa was greater than average, but it was less than that of Bee Creek (Chapter 2); above-ground plant size was average (Appendix 1); and the transition probabilities of adults outside of cages were nearly identical to those of other populations (Chapter 2). However, because deer herbivory rates were higher at Mesa than at most other sites, the effects of deer exclusion were probably greater there than at other sites. This model assumed that survival probabilities were equivalent to those of plants inside cages at Mesa in each year. To obtain estimates of fecundity in the absence of deer, I multiplied fecundity with deer by the proportional increase in the fecundity of plants in cages at Mesa relative to caged plants. The next two models, ‘POOLED’ and ‘SITE’, were constructed from observational data in three natural populations that experienced deer herbivory.

‘POOLED’ models. Because of problems of small sample size in some populations in some years, I constructed models in which transition probabilities in the absence of deer were estimated from the three sites pooled in each year. Probabilities of survival and reproduction in the absence of deer were estimated by using values for uneaten plants in place of plants eaten by deer. I used values for insect-eaten plants in place of plants eaten by both insects and deer. Because deer have a preference for larger plants (Chapter 2), I took plant size into account by assigning plants to one of two size classes: ‘small’ (< 1.5 mm stem basal diameter) or ‘large’ (≥ 1.5 mm). Survival and reproduction probabilities were estimated jointly to increase sample size. Surprisingly, calculations based on only one size class yielded results that were nearly identical to those based on two size classes; I present only the results of the analysis using two size classes. Increases in fecundity due to deer exclusion were estimated for each plant using the regression equations described in Chapter 2. For plants not eaten by deer I used regression equations in which the sum of fruit lengths per plant predicted seed number ($R^2 = 0.74$ and 0.73 for 1994 and 1995, respectively). For plants that were eaten by deer, I used regression equations of the effect of herbivory on fecundity before fruit set (called the ‘indirect’ effect on fecundity in Chapter 2). In these models, stem basal diameter at the first adult census predicted seed set ($R^2 = 0.64$ and 0.65 for 1994 and 1995, respectively). Separate equations for each year, and in some cases, herbivory type, were used.

'SITE' models. Because there were considerable site-to-site differences in individual plant performance (Chapter 2; Appendix 1), important spatial variation in the effects of deer would go undetected in the POOLED models. In the SITE models I estimated the changes in survival and fecundity in the absence by deer by substituting probabilities in the same manner as in the POOLED models, but for each site separately. Due to small sample sizes, regression models to predict fecundity could not be developed for each site. Instead, the same regression models used in the POOLED models were used for each site in the SITE models.

RESULTS

Seed bank dynamics

Seeds in the seed bank experiment had the same mean weight as seeds collected from natural populations (Student's $t = -0.70$, d.f. = 199, $p = 0.48$). Within two months of the installation of experiment 1, an average of 77% of the seeds of *Streptanthus bracteatus* (s.d. = 8.1) had already germinated in the field. 72% of the seeds were recovered in the first treatment and the inviability of the original seed stock was estimated to have been 8%. Given these values, only 4% of the original seeds would have remained in the soil after the next treatment extraction, thus leaving too few seeds from which to draw conclusions about the demography of the seed bank. Indeed, this prediction held true: after three years, the final treatment of experiment 1 had an average of only 2% additional field germination.

In contrast, average field germination after the first two months of the experiment 2 was 19%, despite more than six times more rainfall during this period than in the same interval in the previous year (albeit one month earlier). This strongly suggests that the sowing method was more important than the earlier sowing date in establishing dormancy. Inviability of the original seed stock of the second experiment was 5%. Because of the small sample size of experiment 1, all data reported below are from experiment 2, unless otherwise noted.

As predicted, some seeds dispersed outside the subplot fences and, in some cases, outside the plot cages. Most of these recruits were less than 30 cm away from the subplot, but some recruits emerged up to 80 cm away. Dispersal was also surprisingly rapid: an average of 6% of the seeds germinated outside of the subplots within the first two weeks of the experiment, some as far as 20 cm away. This suggests that a single rain event is capable of causing substantial seed movement. The recovery rate was lower in experiment 2 (59%) than in the experiment 1, probably due to this dispersal. The timing of germination in both experiments was consistent with observations of wild sites (Appendix 1): over 90% of recruitment occurred in September or October.

87% of seeds showed some type of dormancy at the beginning of the study, declining to 25% after two years (Figure 4.4). Most of this dormancy was of the strong type, not broken by incubator conditions or the addition of a hormone. The weakest form of dormancy was most evident at the beginning of the study and was later replaced by moderate dormancy, suggesting that dormancy is acquired gradually after seed dispersal. Field germination was actually assessed more frequently than the intervals shown in Figure 4.4. An average of 19% (s.d. = 4.1) of the seeds germinated every six months. If decomposition played an important role in seed mortality, one would expect to see filled seeds in varying stages of decay. Instead, filled seeds sifted from the soil from all of the treatments showed almost no sign of decay, indicating that missing seeds (40% after two years) were removed by predators rather than by decomposition.

Given these results, a very large seed bank of *S. bracteatus* during successive dry years should persist for up to 100 years without replenishment (Table 4.1). In contrast, the seed bank would decline rapidly in successive wet years due to higher germination and mortality rates. If environmental conditions varied randomly, the longevity of the seed bank without replenishment is still quite short, less than 22 years.

Population dynamics with and without deer

Except during the wet year, populations of *Streptanthus bracteatus* under natural conditions had either stable or growing populations (Table 4.2). Three of four populations were increasing in size, but the estimates of λ were greater than 1.0 in all three years of the study at only one site. On average, population growth rates were lowest in the wet year. The variance in the estimate of λ was much higher at Bee Creek than at any other site. These estimates of λ undoubtedly differ from the true underlying values. Furthermore, the accuracy of these estimates cannot be judged because I did not estimate their associated confidence limits.

In all cases, and especially in the wet year, the models simulating deer exclusion predicted that population growth rates would probably increase in the absence of deer (Table 4.2). Models based on the experimental data at Mesa predicted that the increase in λ may be dramatic: λ may increase up to almost 7-fold, regardless of the site or year. In contrast, the models based on observational data predicted increases in λ of up to 61%. Overall, all but one of these models predicted that populations may be near stability or may be growing.

At every site in all three years, the models of unmanipulated populations predict that, once at a stable stage distribution, most individuals would be seeds (Table 4.3). In many cases, especially in the dry year, < 2% of individuals would be adults. Deer exclusion increased the evenness of the stage distribution only in the wet years, suggesting that populations above-ground would be much larger proportion of the population in the wet years than in the dry years.

The time to extinction of populations of *S. bracteatus* varied substantially according to site, year, and whether environmental conditions were held constant or varied randomly (Table 4.4). In contrast, variation in model initial conditions made little difference in the outcome of the simulation. Differences of three orders of magnitude in initial conditions changed the results by a maximum of only 46%. Given the assumptions of the simulation, the Bee Creek population is forecast to go extinct within 50 years with a probability of at least 54% and with near certainty within 100 years. Although Mt. Bonnell had a lower mean growth rate than Bee Creek, the variance in its growth rate was also lower. At larger initial sizes the population at Mt. Bonnell appears to have less chance of extinction than the Bee

Creek population. This suggests that variation in λ is more important than the mean of λ in determining the chance of population extinction.

The relative importance of the four transitions to the population growth rate (i.e., elasticity) are shown superimposed onto the matrix model diagram (Figure 4.5). In the dry year, the transition from seed to seed consistently had the largest effect on λ (Figure 4.5A). This suggests that seed survival rates in the soil are critical determinants of population carry-over in dry years. In the average and wet year (Figures 4.5B, C), the importance of each stage transition was less clear. In general, the a_{12} and s_{21} elements were moderately important, while the s_{11} and the a_{22} elements were more and less important, respectively. The elasticity of the a_{12} and s_{21} elements were always equal because this is a general property of a 2 x 2 matrix of this type. All model terms and elasticities are given in Tables 4.5A–C.

DISCUSSION

Seeds of *Streptanthus bracteatus* have the capacity to germinate within one to two months of dispersal from the parent plant. Thus seeds are not born dormant but must acquire physiological dormancy, a state known as either induced dormancy (Harper 1977; Symonides 1988) or conditional dormancy (Baskin and Baskin 1989). *S. bracteatus* seeds sown on the soil surface had a much lower germination rate than seeds buried just below the surface. This suggests that the acquisition of dormancy is related to conditions at the soil surface such as temperature or light quality (Baskin and Baskin 1986). This process must occur within the first 3–6 months of exposure, because after this time most seeds became buried in the soil or leaf litter, where environmental conditions are likely very different. The replacement of weak dormancy with moderate dormancy after six months suggests that the acquisition of physiological dormancy is a gradual process.

The pattern of germination and dormancy in *S. bracteatus* appears to mimic that of other obligate winter annuals in which seeds undergo annual cycles of dormancy (Baskin and Baskin 1983; Baskin and Baskin 1984; Baskin and Baskin 1989). In these species, some seeds germinate soon after dispersal if environmental conditions are favorable. If conditions are not favorable, seeds gradually enter dormancy, reaching a peak in late-winter or spring at which dormancy is strongest. After this period, the strength of dormancy gradually declines until the fall, when germination will occur once again if conditions are favorable.

The presence of a persistent seed bank has several important implications for the population dynamics of *S. bracteatus*. The seed bank plays a critical role in buffering populations against periods of low recruitment from droughts. This pattern is also seen in desert annuals (Kemp 1989; Pake and Venable 1996). Under severe drought conditions such as those seen in the winter of 1995, recruitment of *S. bracteatus* approaches zero (Appendix 1). During such a catastrophic event, the seed bank ensures that populations will not go extinct. Indeed, persistent seed banks are common adaptations to improve the fitness of plants in highly variable and unpredictable environments (Cohen 1966; Silvertown 1988; Venable and Brown 1988; Pake and Venable 1996).

The seed bank also buffers populations against high adult mortality and low fecundity from herbivory (Chapter 2). In some cases, herbivory may be severe enough to reduce the seed production of *S. bracteatus* to near zero. For example, fecundity at Bee Creek in the spring of 1995 was extremely low (Chapter 2; Appendix 1), causing the next year's recruits to come almost exclusively from the seed bank.

Elasticity analysis showed that variation in dormant seed survival had a larger effect on population growth rate than did the same variation in any other matrix element, especially in the dry year. However, this result should be interpreted with caution. The matrix models were constructed using the same values of seed bank transitions in each year. Moreover, the seed bank experiment was conducted at a site unoccupied by *S. bracteatus*. The morphology of seeds excavated from the seed bank suggests that seed predation is largely responsible for the mortality of dormant seeds. Most dormant seeds probably reside in the leaf litter (Chapter 3; D. Zippin, *personal observation*), so a huge variety of seed predators may be causing this mortality. Post-dispersal seed predation dramatically influences the demography of many plants (Harper 1977; Crawley 1983; Louda 1989). It seems to play an important role in *S. bracteatus* dynamics as well.

The importance of the seed bank to the population dynamics of *S. bracteatus* has implications for the restoration of extirpated populations. A critical step in establishing a new population of a rare plant is ensuring that favorable conditions are present (Pavlik et al. 1993; Primack 1996). For *S. bracteatus*, such conditions occur only once every few years. A newly established population of *S. bracteatus* will persist only if it has a mechanism to survive through the unfavorable years. Thus a reintroduction effort of *S. bracteatus* must quickly establish a persistent seed bank if it is to succeed without frequent re-seeding. The choice of seed sowing method appears to strongly influence how fast such a seed bank is created in this species (Chapter 3).

Theoretical models of annuals with a seed bank appear to contradict the elasticity values of this study. According to these models, λ should not be sensitive to changes in dormant seed survival or to the probability of germination from the seed bank (Schmidt and Lawlor 1983). These predictions have been generally supported by empirical studies of perennial herbs (Silvertown et al. 1993; Ehrlén 1995b; Bullock et al. 1996) and by a study of at least one annual herb (Kalisz and McPeek 1992). This discrepancy may reflect a bias in the literature in which most studies focus on plants in mesic environments that experience relatively little variation in environmental conditions. Germination in *S. bracteatus* is highly variable (Appendix 1) and appears to be correlated with the variation in fall and winter rainfall. In dry years, when few or no seeds germinate, the only transition that affects population growth is the one within the seed bank, so in those years one should expect this transition to have the largest effect on λ.

The stable stage distribution of *S. bracteatus* suggests that the individuals seen above-ground are just a fraction of the total population size. The observed reproductive adult population sizes (Chapter 2) are consistent with a concurrent seed population of 40 to 4000, depending on the site and year. This implies that no seed bank is of sufficient size to buffer a population against a lack of seed input for more than 15 years, and probably much less.

Variation in population dynamics

Surprisingly, the spatial variation in population growth (i.e., among sites within years) in *S. bracteatus* was approximately equaled by the temporal variation (i.e., among years within sites) in population growth. Annual plants, especially those in arid environments, often exhibit high temporal variation in population growth rates but do not always exhibit similarly high spatial variation in growth rates (e.g., Epling et al. 1960; Harper 1977; Mack and Pyke 1983; Kalisz and McPeek 1992). Interestingly, the pattern and magnitude of temporal and spatial variation in λ of *S. bracteatus* was very similar to the small-scale variation in λ seen in the perennial grass *Danthonia sericea* (Moloney 1988). The high site-to-site differences in population dynamics of *S. bracteatus* may be related to the high variation in herbivore activity and in herbivore effects among sites (Chapter 2). For example, in 1995 the proportion of plants attacked by herbivores at Mt. Bonnell was approximately 15% while at Bee Creek it was over 90% and these rates appeared to be positively correlated with the magnitude of herbivore effects (Chapter 2).

Because the models used in this study were density-independent, they may have underestimated the actual time to extinction under these specific environmental conditions. My models do not take into account extinction risk factors that are unique to very small populations. For example, small populations are susceptible to sudden extinction from catastrophic events such as drought, storms, or other regional disturbances that affect the entire population at once (Gilpin and Soulé 1986; Menges 1990; Lande 1993; Mangel and Tier 1994). A potential catastrophe for *S. bracteatus* might be consecutive years in which a wet winter was followed by a dry spring. In such a scenario, three factors that reduce population growth rate would coincide: (1) in the winter the seed bank would be depleted quickly by high germination rates and high seed mortality rates, (2) herbivory frequency and intensity would be greater; and 3) the lack of spring rainfall would greatly reduce the ability of adults to recover from more intensive herbivory.

Another limitation of the models in this study is their equal treatment of all individuals. When populations size is large, the results of models that calculate individual responses are often identical to the results of models that use mean responses. However, in a small population, if birth and death rates were calculated on a individual basis, the chance of extinction would rise dramatically. This process, known as demographic stochasticity (Shaffer 1981; Gilpin and Soulé 1986; Lande 1988; Lande 1993), describes how, just by chance, the remaining individuals in a small population may all die or not reproduce, causing a sudden extinction. Taken together, these theoretical predictions about the demographic behavior of small populations strongly suggest that the extinction forecasts presented here are underestimates of the true values. Populations of *S. bracteatus* with declining populations (Mt. Bonnell and Bee Creek) and/or a high variance in population growth rates (Bee Creek) may be in serious danger of extinction within the next 50 years.

The effects of deer

My results predict that the exclusion of deer may increase the population growth rate of *S. bracteatus*, possibly substantially. The predicted increases in population growth rate based on observational data (POOLED and SITE models) are much lower than the predictions based on the experimental data (MESA models). For several reasons, I believe that the former models underestimate the effects of deer. The values of survival that were substituted (i.e., uneaten or insect-eaten plants) were often based on relatively few individuals, producing potentailly substantial sampling error. For example, at Bee Creek almost all plants were eaten in both years. All of the uneaten plants in 1994 and 88% of the uneaten plants in 1995 did not survive. This resulted in estimates of adult survival in the absence of deer that seemed unreasonably low.

It should be noted that the values of λ presented here are only estimates that may differ substantially from the actual values of λ. Furthermore, the accuracy of these estimates is unknown because I did not estimate confidence limits. Sources of error in these estimates of λ include sampling error, which arises from small sample sizes. In models in which sites are pooled, error also arises from the variation among sites. Variation among years may introduce error for two reasons: (1) the estimates of λ rely on only three years of data, and (2) the assumption that 'dry', 'wet', and 'average' years occur with equal frequency may not be true. There may also be error due to the variation in the interaction between site and year. Finally, most of these sources of variation probably include both genetically-based and non-genetic variation among plants (Pease and Fowler 1997). The same caveats apply to the estimates of population persistence time and to extinction probabilities.

These sources of variation in the estimates of λ or of population persistence time could potentially be modeled. From these models one could estimate the distributions of these estimates and, ultimately, derive confidence limits for them. However, such modeling is beyond the scope of this chapter.

The effects of herbivory on population growth using a matrix projection approach has been studied in only a small number of perennial herbs (Doak 1992; Bastrenta et al. 1995; Ehrlén 1995b; Bullock et al. 1996). Thus generalizations across taxa or functional groups about the effects of herbivory on λ are premature, especially for annuals. In the unpalatable perennial *Cirsium vulgare*, sheep grazing was found to have a significant positive effect on λ (Bullock et al. 1996) through selective herbivory on plant competitors. The intensity of grazing was positively correlated with the effect on the population growth rate.

In a study of *Anthyllis vulneraria* (Bastrenta et al. 1995), sheep grazing reduced population growth, and these effects were especially pronounced in wet years, when seed production in ungrazed plots was over 100 times higher than in ungrazed plots in dry years. In this species, herbivory "dampened" population growth by reducing the temporal variation in fecundity. A similar pattern appears to occur in *S. bracteatus* in which herbivory had greater effects in the wet year than in the dry year. However, this result requires confirmation with monitoring data over several dry and wet years. This may not be a general phenomenon because there must be enough temporal variation on which herbivory can act. Such temporal variation may not be present in all species (Law 1981; Ehrlén 1995b; Bullock et al. 1996).

Beyond elasticity

Elasticity has been used as a guide to which life-stage transitions (either age- or stage-based) are most important for population growth (Silvertown et al. 1993). Conservation biologists are beginning to use this measure to guide management decisions aimed at increasing the population growth of rare species (Oostermeijer et al. 1996). Elasticity analysis has promise as a conservation tool, but actions based solely on elasticity may not have the desired intent (Oostermeijer et al. 1996; Silvertown et al. 1996). I concur with this cautionary note. As I argue below, another factor besides elasticity should be considered if one wants to maximize the change in population growth rate of changes in life-stage transitions.

A change in the magnitude of one transition element in a population projection matrix will cause a substantial change in λ only if (1) a change in the magnitude of the element causes a substantial change in λ (i.e., the elasticity is large enough) and (2) there is substantial natural variation in the element (i.e., the change in the element is large enough). Thus a large elasticity is irrelevant if there is little variation in the matrix element. Likewise, deliberate manipulations, whether for experimental or management purposes, will only have a substantial effect on λ if both the change in the magnitude of the element and the magnitude of the corresponding elasticity are large enough. To illustrate this point I calculate the temporal variation in the four elements of my matrices for nine combinations of site and year (Figure 4.6). The expected variation in λ due to a change in a matrix element is simply the product of this temporal variation in the matrix element and the elasticity of that element.

The s_{11} element always had little variation (although this is, in part, due to the way dormant seed germination was measured). In several instances, s_{21}, a_{12}, and/or a_{22} were highly variable. For this reason, the expected variation in λ is poorly predicted by the elasticities in these instances (Bee Creek, dry and wet years; Valburn, dry and average years). On the other hand, the actual variation in the matrix elements is not a good predictor of the expected variation in λ either. Note also that the relative importance of the four matrix elements in the expected variation in λ is not consistent among either sites or years, but appears to be specific to individual site-year combinations.

Elasticity may be a poor guide to the "importance" of matrix elements for several other reasons. Elasticity analysis makes predictions about changes in λ under stable conditions. The actual changes will be affected by the existing stage structure. The actual changes in population growth rate would be the same as those predicted by this analysis only if the actual stage structure of the population is the same as the stable stage distribution. This is an unlikely situation.

Furthermore, the individual matrix elements often do not represent separate parts of the life cycle, especially if the species is an 'annual' with a persistent seed bank (Caswell 1989; Kalisz and McPeek 1992). Most of the elements are composites of several different life-cycle stages. For example, the a_{22} element in my models is the product of seedling, juvenile, and adult survival, adult fecundity, and the probability of germination. Moreover, there is often overlap among the terms used to calculate each matrix element. For example, germination probability in my models also contributes to the other three elements of each matrix. Therefore both natural environmental fluctuations and deliberate manipulations will tend to affect more than one matrix element. Deer exclusion from *Streptanthus bracteatus*, for example, affects adult survival (thus affecting the s_{21} and a_{22} matrix elements) and fecundity (thus affecting the a_{12} and a_{22} matrix elements). Because the matrix elements are often composites of several terms, the variation in these elements may arise primarily from variation in one or two individual terms. For example, in *S. bracteatus* at Bee Creek, the high variation in the a_{12}, and/or a_{22} elements in the dry and wet years was largely due to the high variation in just two of their component terms, pre-reproductive adult survival and fecundity (Table 4.6).

CONCLUSIONS

Matrix models suggest that the exclusion of deer from one population, Bee Creek, will substantially improve adult survival, fecundity, and the population growth rate. This may also substantially reduce that population's risk of extinction. At two other sites at which deer were present, populations appeared to be either stable or increasing in size during this study. However, because of the uncertainty in the estimates of λ, and because this species appears to experience large temporal fluctuations in population size above-ground, these values should be interpreted with caution. Most populations of *S. bracteatus* have lower rates of deer herbivory than at the three sites for which predictive models were developed (Chapter 2).

Therefore, deer exclusion will probably improve the population size of this species only at some sites.

These matrix models also suggest that the vast majority of the population of *S. bracteatus* resides in the leaf litter or soil as dormant seed. The survival of these dormant seeds plays an important role in determining the population growth rate. Post-dispersal seed predation may strongly influence the survival of seeds in the soil and requires further study. The natural variation in demographic traits suggests that at some site in some years, changes in adult survival and fecundity have much larger effects on the population growth rate. By combining elasticity values with the natural variation in demographic parameters, one can predict the relative importance of each life-cycle transition with greater accuracy.

I have shown in Chapter 2 that deer substantially reduce the survival and fecundity of *Streptanthus bracteatus* at some sites. This study confirms the expectation that these effects also reduce the population growth rate at these sites. Although deer can have important negative effects upon some populations in some years, urban development has the greatest negative impact to this species because it eliminates entire populations (Appendix 1).

Table 4.1. Estimated longevity of the seed bank of *Streptanthus bracteatus*. Values are the years from seed dispersal until the population size = 1, without germination or additional seed input. Values are based on the results of experimental seed banks at Emma Long Park.

			randomly varying annual rainfall[†]		
Initial seed bank size	consecutive dry years	consecutive wet years	mean ± s.d.	min	max
10	20.1	2.4	5.3 ± 1.5	3	14
100	40.2	4.8	9.3 ± 2.3	5	18
1,000	60.3	7.1	13.6 ± 3.0	9	25
10,000	80.4	9.5	17.8 ± 3.4	10	29
100,000	100.4	11.9	22.0 ± 3.8	13	36

[†] 1,000 runs of a simulation that randomly chose dry or wet years with equal probability

Table 4.2. Estimated annual population growth rates (λ) at a stable stage distribution. Values are given for four populations of *Streptanthus bracteatus* in three years with deer herbivory and without deer herbivory under several models. In all deer-absent models it is assumed that there is no compensation by insect herbivores. Values are based on a two-stage growth model.

		deer exclusion models		
Site and year	natural conditions	MESA[3]	POOLED[3]	SITE[3]
Dry (1993–94)				
Barton Creek	1.27	3.74	1.38	1.36
Bee Creek	0.92	2.37	1.14	0.94
Mt. Bonnell[2]	0.94	—	—	—
Valburn	1.12	2.95	1.24	1.34
Mean (± s.d.)	1.06 ± 0.16	3.02 ± 0.69	1.25 ± 0.12	1.21 ± 0.24
Avg (1992–93)				
Barton Creek[1]	0.98	—	—	—
Bee Creek[1]	2.10	—	—	—
Valburn[1]	1.21	—	—	—
Mean (± s.d.)	1.43 ± 0.59	—	—	—
Wet (1994–95)				
Barton Creek	0.99	6.79	1.39	1.28
Bee Creek	0.43	3.53	0.91	0.68
Mt. Bonnell[2]	0.73	—	—	—
Valburn	1.60	10.85	1.95	2.58
Mean (± s.d.)	0.94 ± 0.50	7.06 ± 3.67	1.42 ± 0.52	1.51 ± 0.97

[1] effects of deer were not estimated in this year

[2] deer were not present at this site

[3] see Methods for an explanation of model construction

Table 4.3. The stable stage distribution of four populations of *Streptanthus bracteatus* in three years with deer herbivory and without deer herbivory under several models. Values on the left of each pair are the proportion (%) of plants in the seed stage; values on the right are the proportion in the adult stage.

		deer exclusion models		
Site and year	natural conditions	MESA[3]	POOLED[3]	SITE[3]
Dry (1993–94)				
Barton Creek	98/02	97/03	97/03	97/03
Bee Creek	99/01	97/03	98/02	99/01
Mt. Bonnell[2]	99/01	—	—	—
Valburn	98/02	97/03	98/02	98/02
Avg (1992–93)				
Barton Creek[1]	95/05	—	—	—
Bee Creek[1]	96/04	—	—	—
Valburn[1]	95/05	—	—	—
Wet (1994–95)				
Barton Creek	90/10	85/15	88/12	88/12
Bee Creek	98/02	83/17	86/14	97/03
Mt. Bonnell[2]	95/05	—	—	—
Valburn	85/15	81/19	85/15	80/20

[1] effects of deer were not estimated in this year

[2] deer were not present at this site

[3] see Methods for an explanation of model construction

Table 4.4. Estimated time to extinction and the probability of extinction of three populations of *Streptanthus bracteatus*. Presented are two-stage growth models under deterministic or stochastic conditions.

	Initial conditions (N_0)[1]		Yrs to extinction under contant or stochastic environmental conditions				p(extinction): stochastic models[2]	
			constant					
Site	seeds	adults	wet	average	dry	stochastic[2]	100 yrs	50 yrs
Barton Creek[3]	100	100	448	310	--[†]	> 1,000	0.00	0.00
	1,000	100	468	332	--	> 1,000	0.00	0.00
	10,000	100	555	404	--	> 1,000	0.00	0.00
	100	1,000	600	413	--	> 1,000	0.00	0.00
	1,000	1,000	603	415	--	> 1,000	0.00	0.00
	10,000	1,000	624	437	--	> 1,000	0.00	0.00
Bee Creek[3]	100	100	8	--[†]	84	41 ± 0.7	0.97	0.75
	1,000	100	9	--	92	42 ± 0.7	0.97	0.73
	10,000	100	11	--	113	48 ± 0.7	0.97	0.64
	100	1,000	10	--	111	50 ± 0.8	0.96	0.60
	1,000	1,000	10	--	112	54 ± 0.8	0.95	0.61
	10,000	1,000	11	--	120	60 ± 0.8	0.93	0.54
Mt. Bonnell[4]	100	100	17	--[*]	140	43 ± 0.2	1.00	0.84
	1,000	100	18	--	143	44 ± 0.2	1.00	0.82
	10,000	100	21	--	160	51 ± 0.2	1.00	0.51
	100	1,000	22	--	178	55 ± 0.3	1.00	0.27
	1,000	1,000	23	--	179	56 ± 0.3	1.00	0.28
	10,000	1,000	23	--	182	57 ± 0.3	1.00	0.21

[1] biologically reasonable initial conditions were chosen; [2] mean ± s.e. of 1000 simulations

[3] wet, average, and dry years were chosen randomly with equal probability

[4] simulations used data from wet and dry years only

[†] not calculated because λ was always > 1; [*] not calculated because of missing data

Table 4.5A. Values used in the models of population growth in 1993–1994 ('dry' year).

	Site			
Variable	Barton Creek	Bee Creek	Mt. Bonnell	Valburn
multistate transitions: natural conditions				
g_{dorm}	0.075	0.075	0.075	0.075
q_{dorm}	0.036	0.036	0.036	0.036
g_{seed}	0.040	0.040	0.040	0.040
$p_{seedling}$[1]	0.634	0.610	0.039	0.537
p_{ros}[1]	1.000	1.000	1.000	1.000
p_{pra}	0.521	0.080	0.474	0.431
m	17.453	8.500	38.667	14.160
projection matrix transitions				
s_{11}	0.892	0.892	0.892	0.892
s_{21}	0.025	0.004	0.001	0.017
a_{12}	16.159	7.870	35.800	13.110
a_{22}	0.228	0.016	0.028	0.130
elasticity				
e_{11}	0.512	0.933	0.892	0.646
e_{21}	0.220	0.033	0.053	0.166
e_{12}	0.220	0.033	0.053	0.166
e_{22}	0.048	0.001	0.002	0.022
no deer models: MESA				
p_{pra}	0.889	0.889	--	0.889
m	103.643	50.476	--	84.086
POOLED model				
p_{pra}	0.550	0.550	--	0.550
m	21.886	10.659	--	17.757
SITE model				
p_{pra}	0.586	0.107	--	0.556
m	19.652	8.763	--	22.826

[1] $l_{seedling}$ estimates both $l_{seedling}$ and l_{ros}

Table 4.5B. Values used in the models of population growth in 1994–1995 ('wet' year).

	Site			
Variable	Barton Creek	Bee Creek	Mt. Bonnell	Valburn
multistate transitions: natural conditions				
g_{dorm}	0.377	0.377	0.377	0.377
q_{dorm}	0.390	0.390	0.390	0.390
g_{seed}	0.199	0.199	0.199	0.199
$p_{seedling}$	0.750	0.720	0.249	0.848
p_{ros}	0.724	0.809	0.763	0.881
p_{pra}	0.322	0.039	0.423	0.446
m	11.286	4.833	12.633	13.750
projection matrix transitions				
s_{11}	0.380	0.380	0.380	0.380
s_{21}	0.066	0.009	0.030	0.126
a_{12}	5.514	2.362	6.173	6.718
a_{22}	0.393	0.022	0.202	0.913
elasticity				
e_{11}	0.190	0.787	0.312	0.086
e_{21}	0.305	0.104	0.289	0.275
e_{12}	0.305	0.104	0.289	0.275
e_{22}	0.201	0.006	0.110	0.364
no deer models: MESA				
p_{pra}	0.733	0.733	--	0.733
m	74.943	32.096	--	91.307
POOLED model				
p_{pra}	0.447	0.447	--	0.447
m	15.100	6.467	--	18.397
SITE model				
p_{pra}	0.413	0.084	--	0.671
m	14.085	17.240	--	18.177

Table 4.5C. Values used in the models of population growth in 1992–1993 ('average' year).

	Site		
Variable	Barton Creek	Bee Creek	Valburn
multistate transitions: natural conditions			
g_{dorm}[1]	0.266	0.266	0.266
q_{dorm}[1]	0.213	0.213	0.213
g_{seed}[1,2]	0.119	0.119	0.119
$p_{seedling}$[1,2]	0.589	0.596	0.642
p_{ros}	1.000	1.000	1.000
p_{pra}	0.331	0.291	0.289
m	9.383	53.812	17.240
projection matrix transitions			
s_{11}	0.609	0.693	0.693
s_{21}	0.044	0.039	0.042
a_{12}	6.504	37.298	11.949
a_{22}	0.218	1.113	0.382
elasticity			
e_{11}	0.416	0.116	0.291
e_{21}	0.256	0.282	0.288
e_{12}	0.256	0.282	0.288
e_{22}	0.073	0.320	0.133

---

[1] value is the mean of values in the wet and dry year

[2] $l_{seedling}$ estimates both $l_{seedling}$ and l_{ros}

Table 4.6. Temporal variation in individual terms of the matrix model, by site. Values are the standard deviation of each model term divided by the mean of each term (= coefficient of variation).

	Site		
Model term[1]	Barton Creek	Bee Creek	Valburn
g_{dorm}	0.668	0.668	0.668
q_{dorm}	0.831	0.831	0.831
g_{seed}	0.668	0.668	0.668
$p_{seedling}$	0.126	0.106	0.234
p_{ros}	0.176	0.118	0.071
p_{pra}	0.286	0.987	0.223
m	0.332	1.129	0.127

[1] see methods section for key to model terms

Figure 4.1. Life-cycle diagram of *Streptanthus bracteatus* used to construct the population projection models. Variables above the arrows represent the transition probability between two stages. The timing of important life stages is shown on the top line. The vertical dotted line indicates the point in time at which the matrix models begin and end.

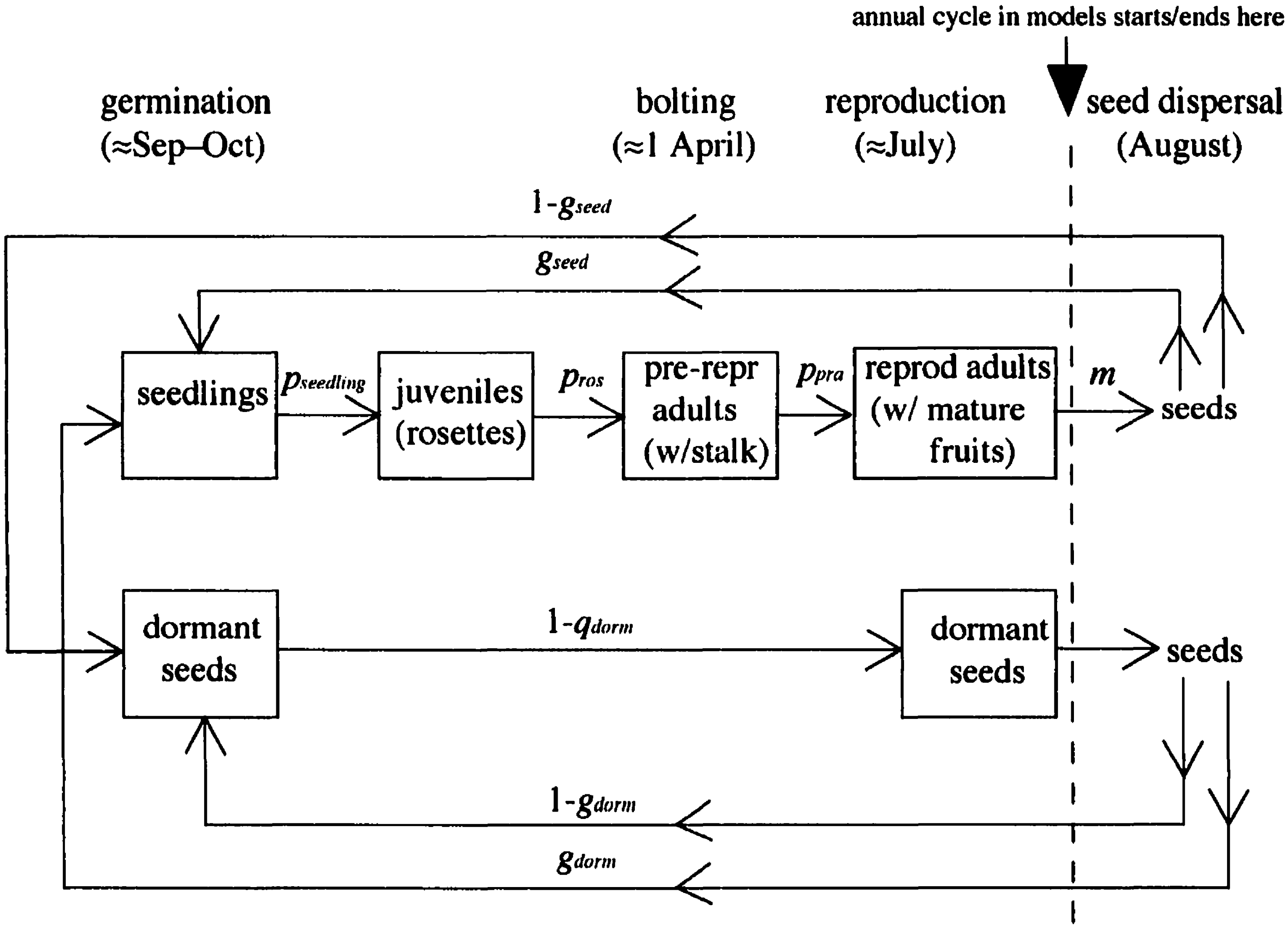

annual cycle in models starts/ends here
germination
(≈Sep–Oct)
bolting
(≈1 April)
reproduction
(≈July)
seed dispersal
(August)
1-g_{seed}
g_{seed}
seedlings
$p_{seedling}$
juveniles
(rosettes)
p_{ros}
pre-repr
adults
(w/stalk)
p_{pra}
reprod adults
(w/ mature
fruits)
m
seeds
dormant
seeds
1-q_{dorm}
dormant
seeds
seeds
1-g_{dorm}
g_{dorm}

Figure 4.2. Rainfall within the annual cycle of *Streptanthus bracteatus* (September to August) in Austin, Texas, from 1963 through 1996. The dotted line is the 33-year mean and the solid lines divide the data into three zones that contain 11 points each. The filled circles represent the three seasons of this study.

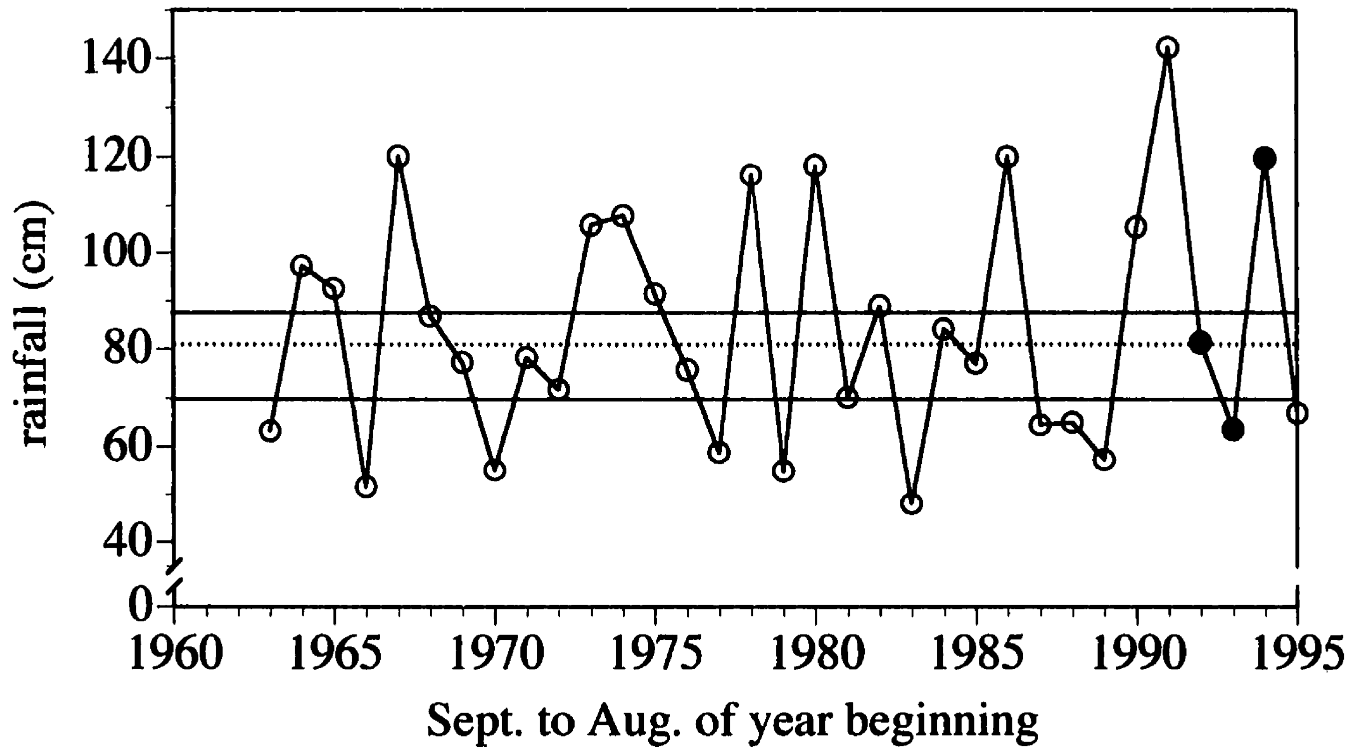


Figure 4.3. Diagram of the structure of the population projection model.

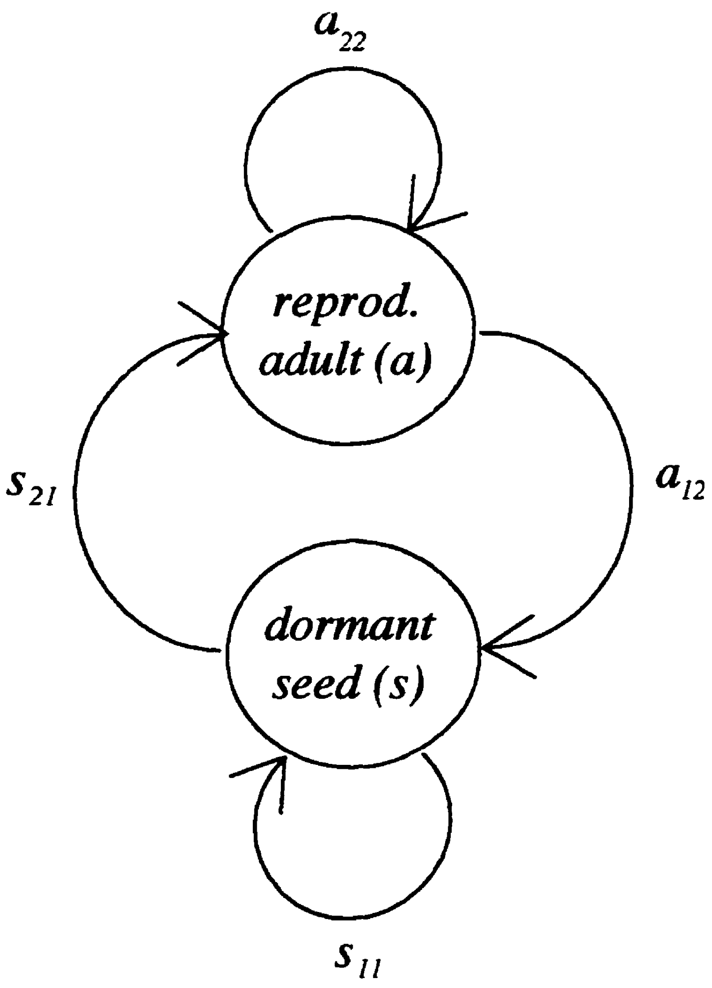


Figure 4.4. The fates of seeds of *Streptanthus bracteatus* sown in ten replicate plots of 100 seeds each for each harvest interval. Values are means of plot frequencies.

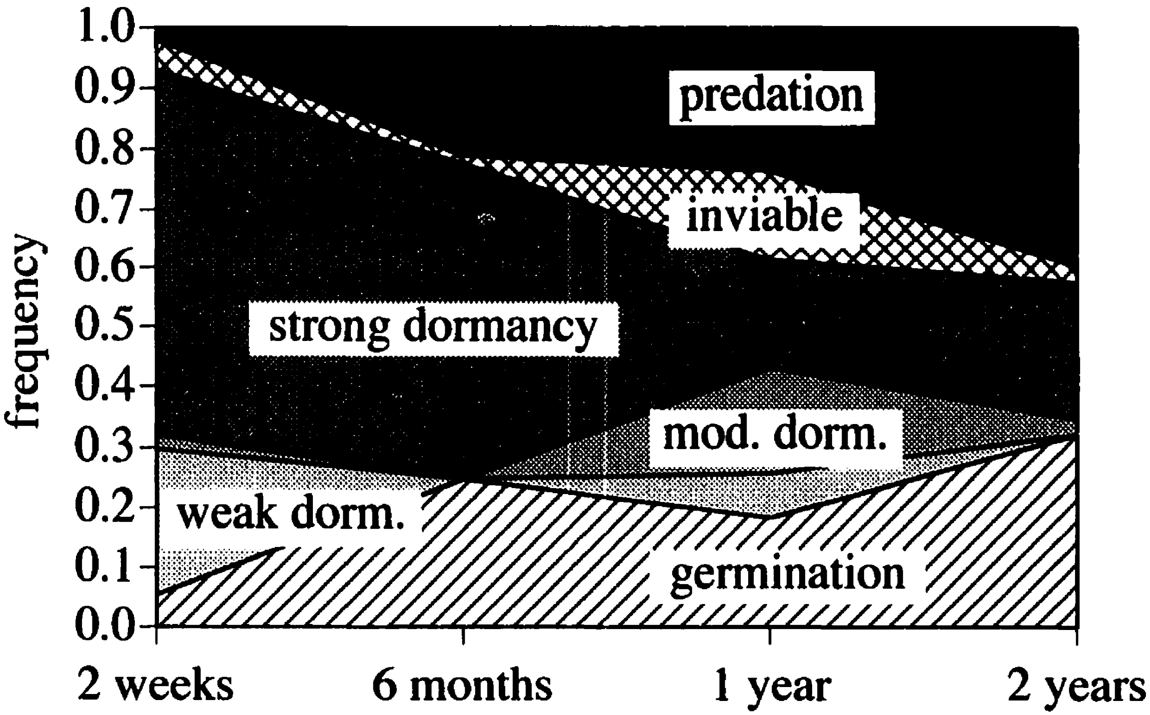
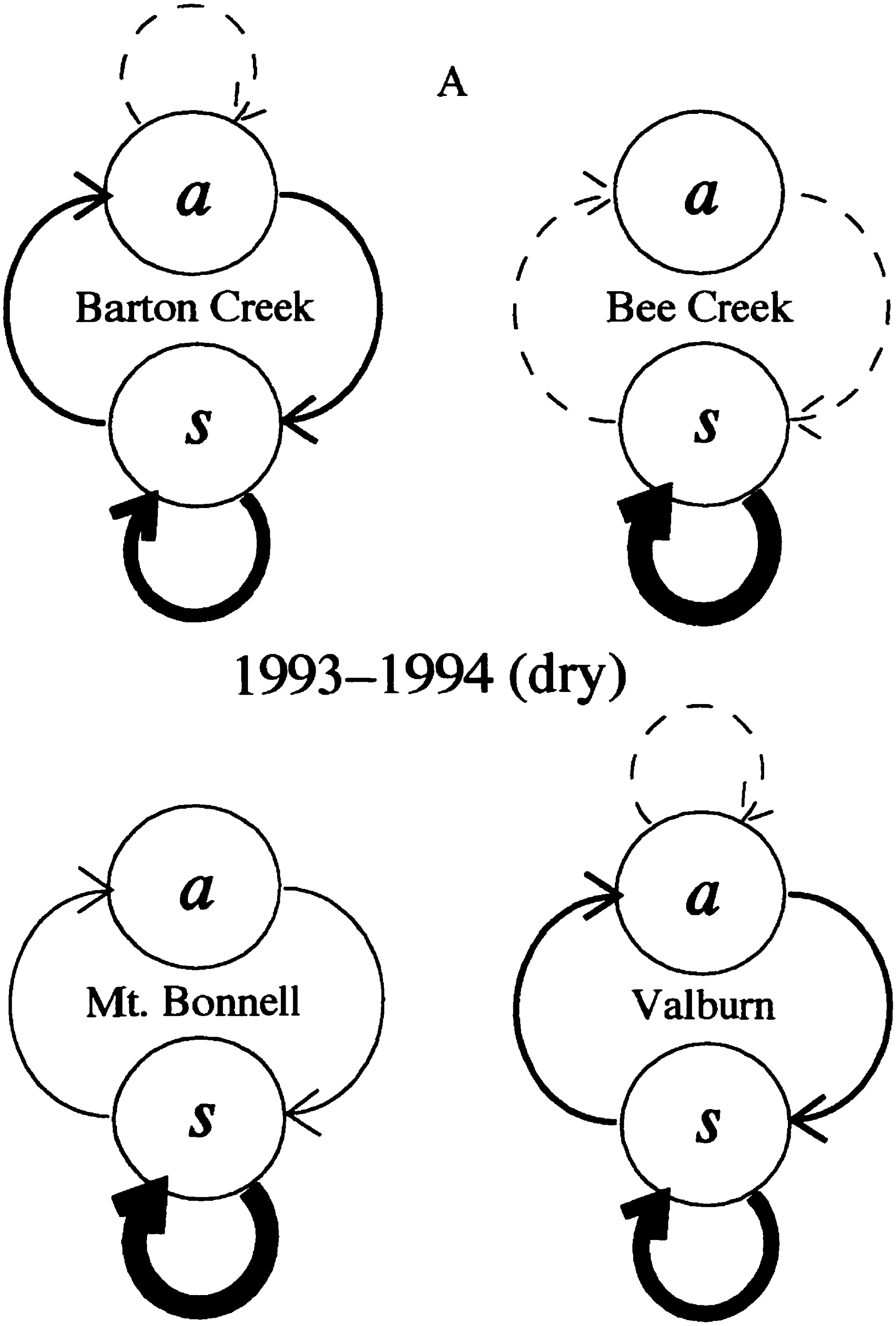
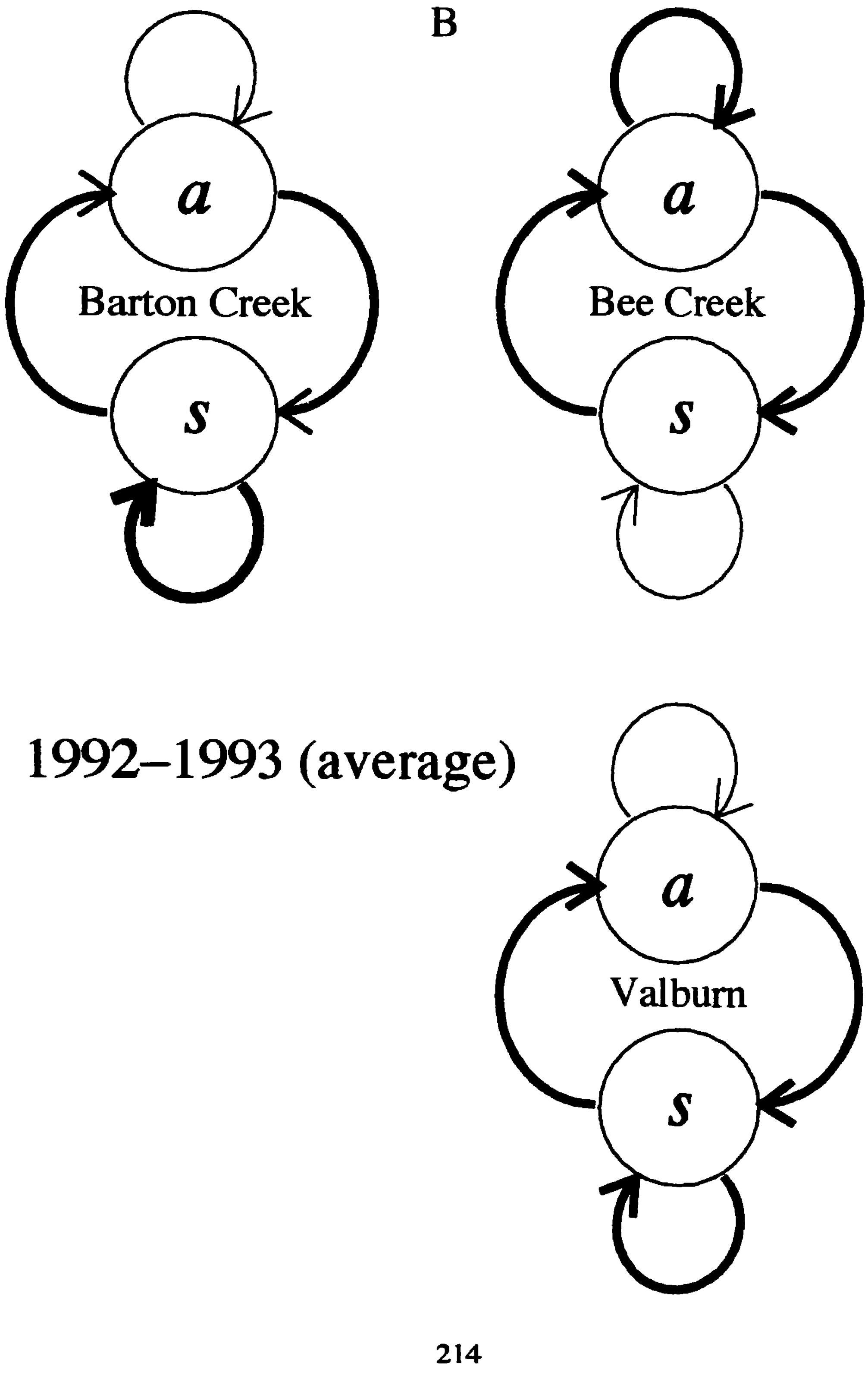


Figure 4.5. Elasticity diagrams for unmanipulated populations of *Streptanthus bracteatus* at four sites in the (A) dry year, (B) average year, and (C) wet year. The width of the arrows is proportional to the magnitude of the elasticity. Dotted lines indicate values from 0.002 to 0.05. Transitions without lines indicate values < 0.002.


A
a
Barton Creek
s
a
Bee Creek
s
1993–1994 (dry)
a
Mt. Bonnell
s
a
Valburn
s


B
a
s
Barton Creek
a
s
Bee Creek
1992–1993 (average)
a
s
Valburn

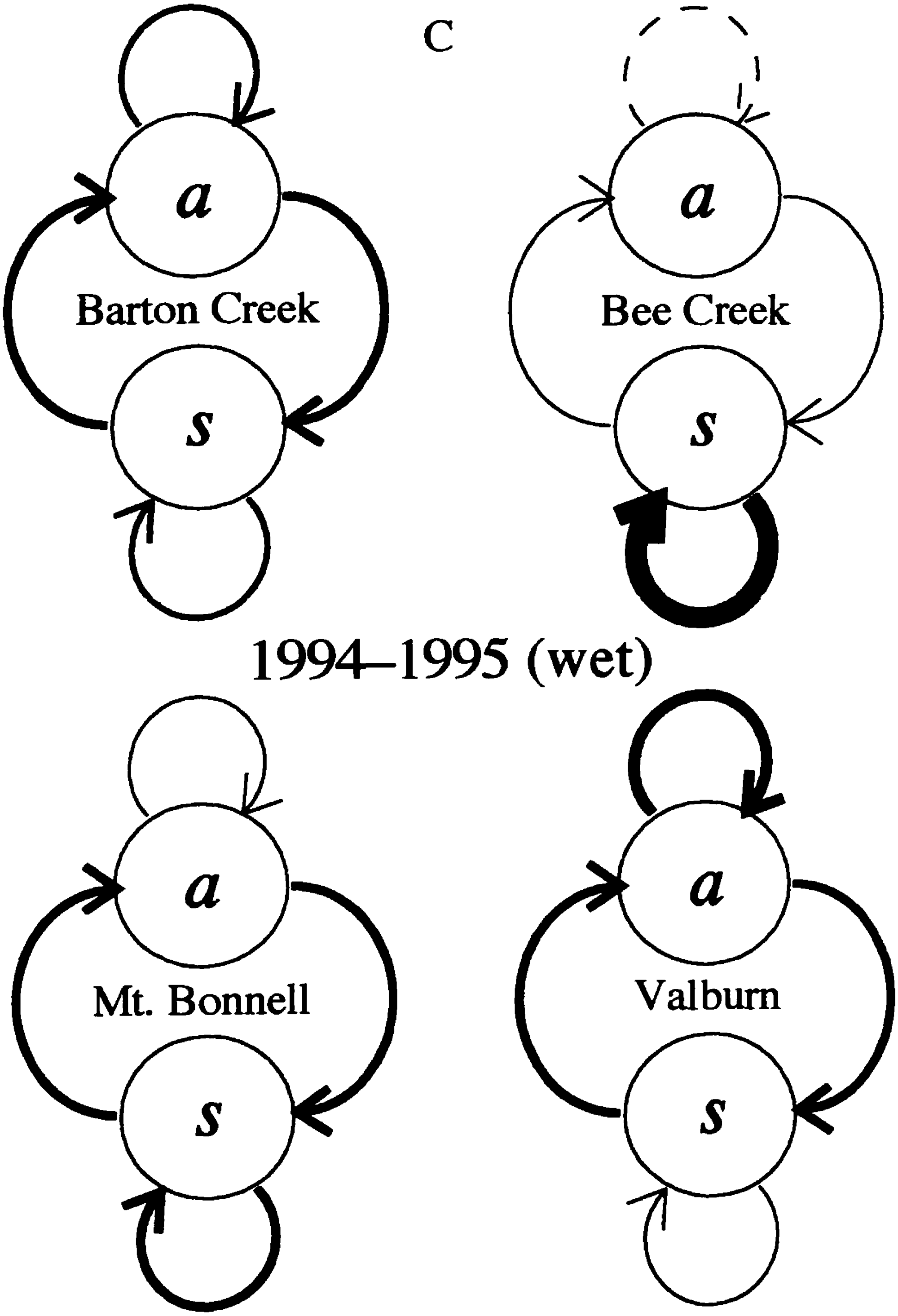
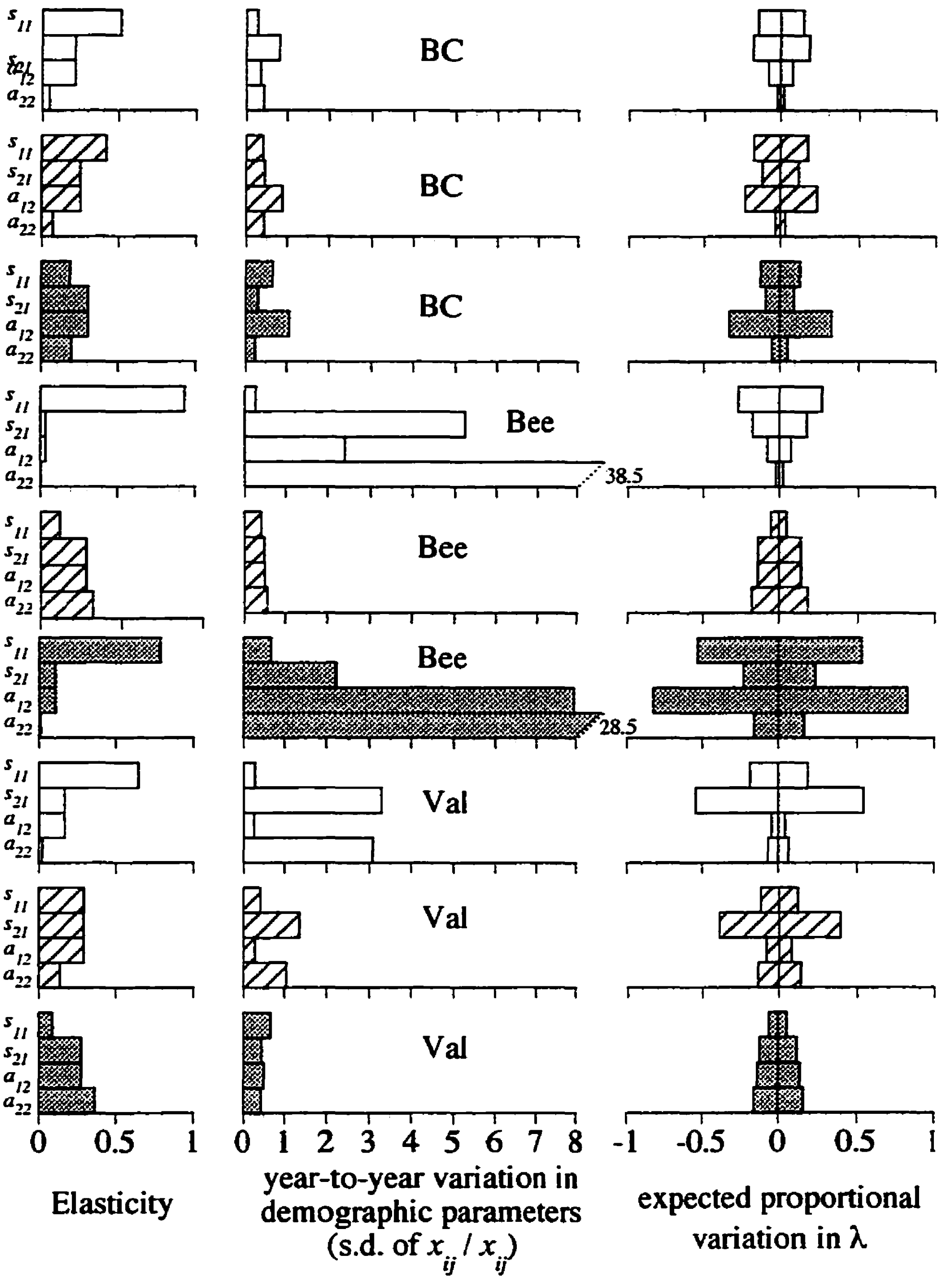

C
a
Barton Creek
s
a
Bee Creek
s
1994–1995 (wet)
a
Mt. Bonnell
s
a
Valburn
s

Figure 4.6. The 'importance' of projection matrix elements to the population growth rate, λ. Shown are three years at three populations: Barton Creek ('BC'), Bee Creek ('Bee'), and Valburn ('Val'). Histograms in the left column are elasticities, histograms in the center column are the variation in matrix elements, and histograms in the right column are the product of these two values. Rows correspond to each site and to the dry year (open bars), average year (hatched bars), or wet year (shaded bars).


s_{11}
s_{21}
a_{12}
a_{22}
BC
BC
BC
Bee
38.5
Bee
Bee
28.5
Val
Val
Val
0
0.5
1
0 1 2 3 4 5 6 7 8
-1
-0.5
0
0.5
1
Elasticity
year-to-year variation in demographic parameters (s.d. of x_{ij} / x_{ij})
expected proportional variation in λ

Appendix 1: The Status and Distribution of the Bracted Twistflower (*Streptanthus bracteatus*; BRASSICACEAE), a Rare Central Texas Endemic[2]

INTRODUCTION

A critical step in the preservation of biological diversity is the identification of species that merit conservation priority and action. However, for many taxa, this task can be difficult or nearly impossible due to a lack of even the most basic biological information such as population size or life-history traits. For plants the situation is particularly severe. Plants are the largest group of federally-listed endangered or threatened species (58% as of 31 October 1996). Moreover, 32% of flowering plants in the United States are thought to be in danger of extinction (Stein and Chipley 1996). However, for most plants, autecological data are very incomplete (Stein and Chipley 1996; Dobson et al. 1997). As a result, decisions about conservation priorities and management are often made with high degrees of uncertainty.

The genus *Streptanthus* (Brassicaceae) is one group of plants in particular need of biological data for conservation. It is composed of approximately 35 species of annual plants, most of which are found in the Southwest, especially California. Taxa also range into the intermountain west, northern Mexico, and as far east as southwestern Arkansas and northwestern Louisiana (Al-Shehbaz 1985). *Streptanthus* has an usually large proportion of highly restricted taxa. For example, approximately one-third of California's *Streptanthus* species and varieties are

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[2] This appendix was submitted to the *Southwestern Naturalist*

endemics or near-endemics and are considered rare, threatened, or endangered throughout their range (Hickman 1993; Skinner and Pavlik 1994). In Texas, six of seven species have highly restricted ranges (Rollins 1970; Correll and Johnston 1979; Al-Shehbaz 1985).

Here I report on the status and distribution of one of these taxa, *Streptanthus bracteatus* Gray, the bracted twistflower, an endemic of central Texas. This species has been included in a recent habitat conservation plan and has been identified as a species in great need of further study (Dieringer 1991; City of Austin 1996). It was listed as a federal Category 2 Candidate for listing as an endangered species (USFWS 1985). Its federal status was recently revoked when that category was eliminated (USFWS 1996). I report population sizes and basic life-history data from four years of monitoring at sites throughout the range of this species. I also present observational information on habitat characteristics and discuss factors that may be limiting its current distribution and abundance.

METHODS

To assess population size and qualitative habitat characteristics, I surveyed all known populations of *Streptanthus bracteatus* to which access was possible at least once from the period of spring 1993 to spring 1996. Populations were defined as plant groups at least one kilometer from all other groups. Within single populations there were sometimes several sub-populations separated by roadways or narrow residential developments. Because these sub-populations were often found on different properties and experienced different degrees of disturbance, I counted and report each separately. For each site I also noted qualitative habitat characteristics such as species associates, canopy cover, and soil surface features. Since there are few populations known, a general description of this species' local habitat may be premature. Instead, I describe specific habitat characteristics and species associates within each county. When new populations were discovered I surveyed them as soon as access became possible. Repeated censuses were not possible at some sites because of population extirpation by housing developments. At these sites, I harvested all seeds on the final census and sent a random sample to the National Seed Storage Laboratory in Ft. Collins, CO, for long-term storage and preservation.

I obtained information about population size and location data before 1993 from two sources. I determined historic locations of populations from herbarium records at the University of Texas and Missouri Botanic Garden. I gathered population size data from records at the Texas Parks and Wildlife Department Natural Heritage Program.

In order to establish the occurrence of major life-history events such as germination, flower production, seed set, and death, I conducted more detailed surveys at four sites within Travis County. I established permanent plots in April 1993 and followed individuals of *S. bracteatus* throughout their lifetime during the 1993–1994 and 1994–1995 seasons. When plants occurred in relatively small areas, I arranged plots in a grid; otherwise I centered individual plots on plant clusters. I began these detailed censuses on 5 November 1993 and 10 October 1994 and continued them monthly through July or early August. In April and May, during the peak of the growing season, I performed censuses bi-monthly. At each census I mapped all new recruits, marked them with a plastic tag adjacent to the plant, and put a colored wire around the base of the stem. For each adult plant (defined as having a stem) and at each detailed census, I measured stem basal diameter to the nearest 0.1 mm with dial calipers. I used this measure to provide another indication of site quality. I chose stem basal diameter because it is a non-destructive measure that is highly correlated with main stem length, or height (Pearson correlation coefficient = 0.86, $p < 0.001$, N = 348). Moreover, this measure remained largely unchanged throughout the season despite the often large fluctuations in above-ground biomass due to stem herbivory and regrowth (D. Zippin, *unpublished data*). For each plant, I noted life-history traits such as flowering, fruit production, and seed set. At some of these four sites in some years populations size surveys were not made for the entire site (i.e. inside and outside permanent plots). In these cases, I estimated population size based on the proportion of plants inside permanent plots (range = 39%–84%) during years in which censuses inside and outside of the plots were performed.

RESULTS

Extant populations of *Streptanthus bracteatus* are known from four counties along the eastern and southern margins of the Edwards Plateau in central Texas: Uvalde, Medina, Bexar, and Travis (Figure A1). Historic collection records indicate that populations were once known at Commanche Springs and New Braunfels (Comal Co.), Bandera Pass and Medina Lake (Bandera Co.), and Leakey

(Real Co.). At least three populations in Travis County have been extirpated or heavily disturbed within the last decade due to urbanization of the Austin area. Most of the extant populations occur in Travis County. Access was not possible to only one sub–population in Travis County < 0.5 km from the Lakewood site. The site is on private land and as of 1996 was still undeveloped. Most remaining populations in Travis Country are on public lands.

Populations of this species are very small. During the study period they ranged from less than ten to as many as 590 individuals (Table A1). At most sites, population size fluctuated dramatically between years. Within sites, numbers of plants sometimes varied over two orders of magnitude (Table A1; Figure A2). By contrast, at some sites (e.g., Lakeview, Garner State Park), population size was consistently less than 100.

The life cycle of this species is that of a true winter annual. In 1993 and 1994, germination began as early as October and continued until early April (Figure A3). However, the majority of recruits (79% and 90% in 1993 and 1994, respectively) emerge during October and November. A morphological character of winter plants which helps distinguish this species from similar-looking species such as *Arabis petiolaris* or rosette-forming Asteraceae is a deep purple color on the leaf underside. A typical plant overwinters as a rosette of leaves and produces a single stem in March about 0.5m in height (up to 1.5m). Large plants or plants that are repeatedly eaten by herbivores may produce more than a dozen stems during the growing season. Plants in Travis County begin to produce showy lavender flowers in late April; flowering peaks in early May (Figure A3). Populations farther west appear to complete their life cycle at least 2 wk earlier; their peak flowering time is late April or the first week in May.

Adult plant size varies substantially among sites (Figure A4). Stem basal diameter declined slightly as the season progressed. Values were lowest at the final census when all plants were dead and stem tissue was dry. Plant sizes were greater in 1995 at almost every site. Despite this variation, Bee Creek, Scenic Loop, and Mesa had among the largest mean plant sizes in both years. Mt. Bonnell had the smallest plants (by far in 1995) and Valburn and Barton Creek had intermediate-sized plants.

I found *S. bracteatus* almost exclusively over limestone of the Glen Rose, Walnut, and Edwards formations (USDA 1974, 1976, 1977). However at Barton Creek, the site is mostly underlain by Quaternary alluvium. Soils at all sites were of the Tarrant, Brackett, Speck, or Rockland–Real series. These are clays or clay loams that are generally very shallow (< 25 cm), rocky, and moderately basic (pH > 7.5). Elevations of known sites ranged from 177 to 439m. Plants were found on all types of topographic relief from flat areas to steep slopes. At Barton Creek, some plants were even growing in small pockets of leaf litter trapped on vertical cliff faces.

Travis County

Populations within Travis County are found growing in a wide range of vegetation, from under dense overstories to open, shrubby clearings. Dominant trees are always *J. ashei* and *Q. fusiformis*, while shrub associates varied but often included *Berberis trifoliolata, Diospyros texana, Sophora secundiflora,* and *Bernardia myricaefolia.* Consistently abundant herbs include *Carex planostachys* and *Salvia roemeriana.* The Barton Creek site differs from other known populations because most plants there grow in a large riparian corridor. Canopy and shrub dominants at this site include, in addition to those listed above, *Ulmus crassifolia* and *Aesculus pavia* var. *pavia.* Herbaceous cover approaches 100% at this site.

Medina County

All known populations in Medina County are found near Medina Lake in road right-of-ways in which the overstory has been cleared and a diverse shrub assemblage 1–2m high has developed. Shrub cover ranges from 25% to 75%. Common and conspicuous associates include *Acacia roemeriana, B. trifoliolata, Dasylirion texanum, Diospyros texana, Quercus sinuata* var. *breviloba, Q. fusiformis, Mimosa borealis,* and *Rhus virens.* At least 30% of the plants in these populations are growing deep within dense shrub clusters of a variety of species. Surveys of adjacent woodland habitat within visual range of right-of-ways failed to detect any more plants. It is not known how much, if at all, these populations extend into adjacent woodlands.

Bexar County

In 1995 a single small population of *S. bracteatus* was discovered in Eisenhower County Park. Plants there are found under a moderately shaded (50-

75% cover) canopy of *J. ashei* and *Q. fusiformis*. Herbaceous cover is very sparse (<5%) and associated shrubs include *R. virens, B. trifoliolata, Celtis laevigata,* and *Acacia* sp. An extensive survey on 17 May 1995 in Eisenhower Park failed to find more plants.

Uvalde County

The only population known from Uvalde County is in Garner State Park. Canopy and shrub dominants include, respectively, *J. ashei* and *Q. fusiformis,* and *Garrya lindheimeri, B. trifoliolata,* and *S. secundiflora.* Herbaceous cover is 10-25% and is composed primarily of *Schizachyrium scoparium, C. planostachys, Argythamnia aphoroides*, and *S. roemeriana.* Extensive surveys of this site by myself and others (W. Carr, *personal communication*) during several springs did not locate other subpopulations. A 1987 survey revealed 133 plants (J. Poole, *personal communication*), although it is not known if the same areas were sampled.

DISCUSSION

In *S. bracteatus* small population size is combined with relatively large fluctuations in population size. As a result, almost all populations were very small in at least one year of this study. Both small population size and high variation in population size puts a population at higher risk of extinction from chance events (Menges 1991). A possible cause of the fluctuations in population size is variation in winter rainfall. Winter precipitation in central Texas commonly varies by an order of magnitude or more (33-year mean in Austin = 22 cm; s.d. = 13.7; range =

4.1 to 78.7 cm). In Austin during the 1995–1996 season, rainfall from December to March was less than 30% of normal. These conditions corresponded to an almost total absence of plants at some sites in March 1996, suggesting a positive correlation exists between winter precipitation and recruitment into the adult size classes.

A seed bank probably buffers *S. bracteatus* populations against extinction during years of low population size or high rates of herbivory. Although the length of time that *S. bracteatus* seeds survive in the soil is not known, this study has confirmed that *S. bracteatus* does form a persistent seed bank. At Mesa during 1993 and 1994, over 95% of the seeds were harvested, essentially simulating two consecutive seasons of poor performance. Despite this, recruitment into the subsequent season (1995) was greater than in either of the two previous seasons. Furthermore, at Bee Creek during the spring of 1994, only about 15 seeds were produced within permanent plots, but recruitment the following winter was the highest yet recorded. Seed rain from outside the plots could not have been the source of these recruits since at least 85% of the plants at Bee Creek were within the plots.

Streptanthus bracteatus is rare in two different ways (Rabinowitz 1981; Fiedler and Ahouse 1992): it has small (sometimes very small, < 100) populations and its populations themselves are infrequent and few in number. There are at least four possible explanations for this.

First, shrub-dominated sites with a thin or absent overstory may be most favorable for the species, as suggested by the large size of the plants in vegetation of this type in Medina County. Overstory competition, either above- or belowground, may be reduced in this habitat, leading to greater plant size. The increase in woody cover in the region during the last 150 years, primarily by *Juniperus ashei*, has resulted in the reduction of grass- and forb-dominated communities (Buechner 1994; Johnston 1963; Weniger 1988), which may have reduced the amount of habitat favorable for *S. bracteatus*. Some studies have found a link between increases in woody cover and the decline of other rare species (e.g., Brewer 1980; Menges 1990).

Second, herbivory by white-tailed deer (*Odocoileus virginianus*) may be responsible for the scarcity of *S. bracteatus* populations (McNeal 1989; Dieringer 1991; City of Austin 1996). White-tailed deer densities on the Edwards Plateau are among the highest in North America (Young and Richards 1994; Gill 1990). Moreover, deer in the suburban areas in which many *S. bracteatus* populations are found may have population densities much higher than those in more rural regions of central Texas due to hunting restrictions and the greater availability of food during winter. The effect of deer on annual forbs may be particularly strong. White-tailed deer on the Edwards Plateau prefer annual forbs in the spring and early summer (McMahan 1964; Bryant et al. 1981; McPherson and Rasmussen 1989), when *S. bracteatus* is completing its life-cycle and time and resources for a plant's recovery from herbivory are low.

Third, the species may have evolved recently, after the last glaciation. Many plant taxa are rare simply because of their young evolutionary age and limited colonization abilities (Fiedler and Ahouse 1992). A relatively distant origin would not preclude persistent rarity, but a relatively recent origin would suggest it. Studies of genetic variation in endemic *Streptanthus* species in California suggest that there are a variety of neoendemic taxa in the genus (Mayer et al. 1994). Until the evolutionary history of *S. bracteatus* is resolved, the potential exists for evolutionary history to at least partially explain its rarity.

Finally, the species could be a specialist on a habitat that is itself rare (Kruckeberg 1969; Menges 1990). Soil types and their associated plant communities in which I found *S. bracteatus* appear to be typical of the dissected canyons of central Texas: limestone overlain by shallow clay soils that support low-stature mixed woodlands composed mainly of *Juniperus ashei* and oaks, primarily *Quercus fusiformis* (Riskind and Diamond 1986). However, without a detailed analysis of the habitat of *S. bracteatus*, this hypothesis cannot be evaluated yet.

An important question for determining the conservation status of *S. bracteatus* is whether populations are growing, declining, or stable. Given the large fluctuations in population size observed during this study at most sites, quantitative measures of population growth rate over short time scales will not provide an accurate picture of population status. Moreover, a seed bank appears to play an important role in maintaining populations through periods of poor performance. Quantification of this stage is therefore critical to determining population status.

Because most of the potential range of *S. bracteatus* has not been surveyed or not surveyed under appropriate conditions, more populations may be discovered if additional surveys can be done. However, locating new or even existing populations can be difficult due to the cryptic morphology of this species during most of its life cycle and its brief (6-week) flowering period. Further surveys are needed in Medina and Bexar Counties, where the least amount of survey work has been performed, and in areas with historic records.

Given the uncertainties in our knowledge of this species, it is not possible at this time to determine the exact degree to which it is in danger of extinction. Habitat loss continues to pose the greatest threat: 30% of known populations have been lost to urban development since 1992. Because most of the remaining populations are on heavily-used public lands, impacts to this species from human disturbance may become increasingly important.

Table A1. Size of all known and accessible populations and subpopulations (indented) of *S. bracteatus* throughout its range. Censuses were in late April or early May unless otherwise noted. Bold face values are estimates based on the population size within permanent plots. Underlined values indicate the year the population was discovered. An "X" indicates when the population was eliminated by development. Values in the first two rows are the total precipitation from Sept.–Aug., ending on the year indicated, for Austin, TX (NOAA 1990–1996) and the percentage of the 30 yr mean value.

Site	1991*	1992	1993	1994	1995	1996
TRAVIS CO.						
RAINFALL (cm)	106	142	81	64	120	67
prop. of 30yr mean	126%	170%	97%	76%	143%	80%
Barton Creek[!]			**411**	373	**386**	**62**
Bee Creek			**72**	32	**165**	3
Cat Mountain			16		X	
Lakewood				86[§]	X	
Mesa			193[#§]	326[§]	432[§]	X
Enclave Cove			47[#§]	X		
Small			90[#§]	X		
Mt. Bonnell			**330**[†]	28	158	0
Valburn			**161**	116	590[§]	X
BEXAR CO.						
Eisenhower Park					40	
MEDINA CO.						
Lakeview	>100		29	28	66	
Scenic Loop N	>29		65	73	290	
Scenic Loop E					78	
UVALDE CO.						
Garner State Park	6		40	3	0	

[!] population area is within 10m of main trail along Barton Creek

* source: Texas Parks and Wildlife Department Natural Heritage Program

[†] census performed in late March

[#] census performed in June or July

[§] >95% of seeds harvested at final census of this year from entire site (Enclave, Mesa, Small, and Lakewood) or in permanent plots (Valburn)

Figure A1. Locations of extant (filled circles) and historical (open circles) populations of *S. bracteatus* in counties of the eastern and southern Edwards Plateau of Texas. Extirpated populations in Travis County are not shown due to the large map scale. The dotted line is the approximate boundary of the Edwards Plateau. The extent of the Edwards Plateau is shown by the shaded region in the inset map.

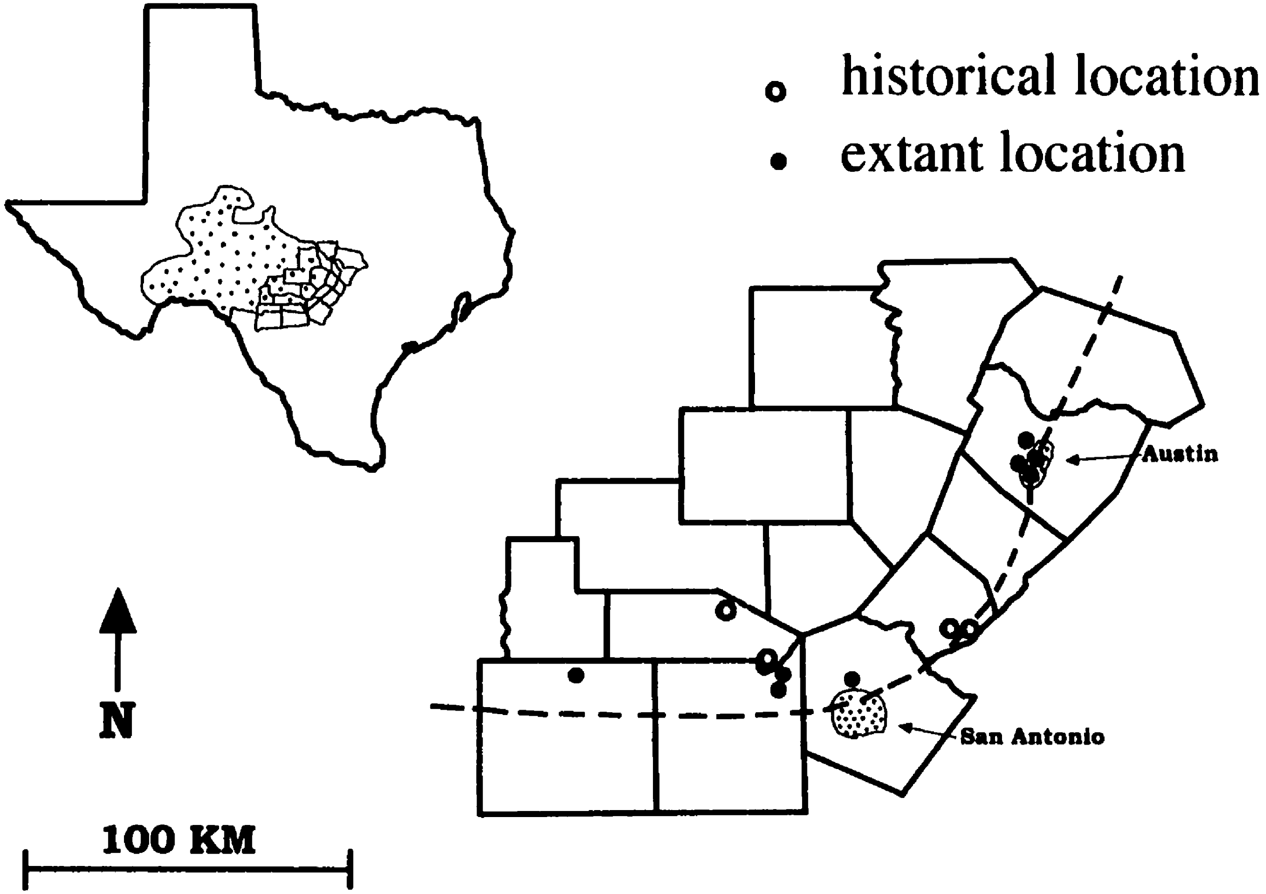

○ historical location
● extant location
Austin
San Antonio
N
100 KM

Figure A2. Numbers of plants within permanent plots in four years at four sites in Travis County, Texas. Data are from censuses in late April or early May except for 1996, when the censuses were performed in mid-March.

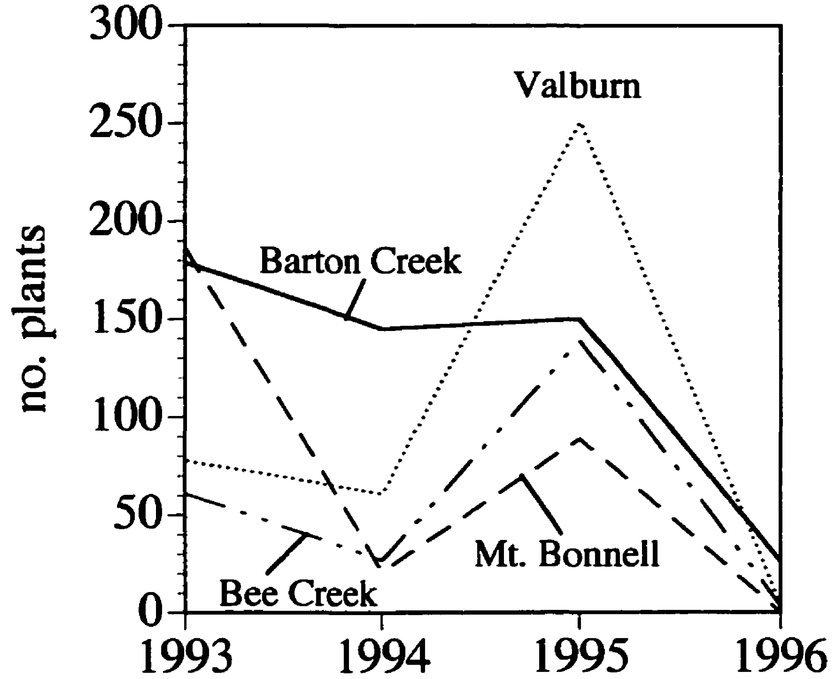
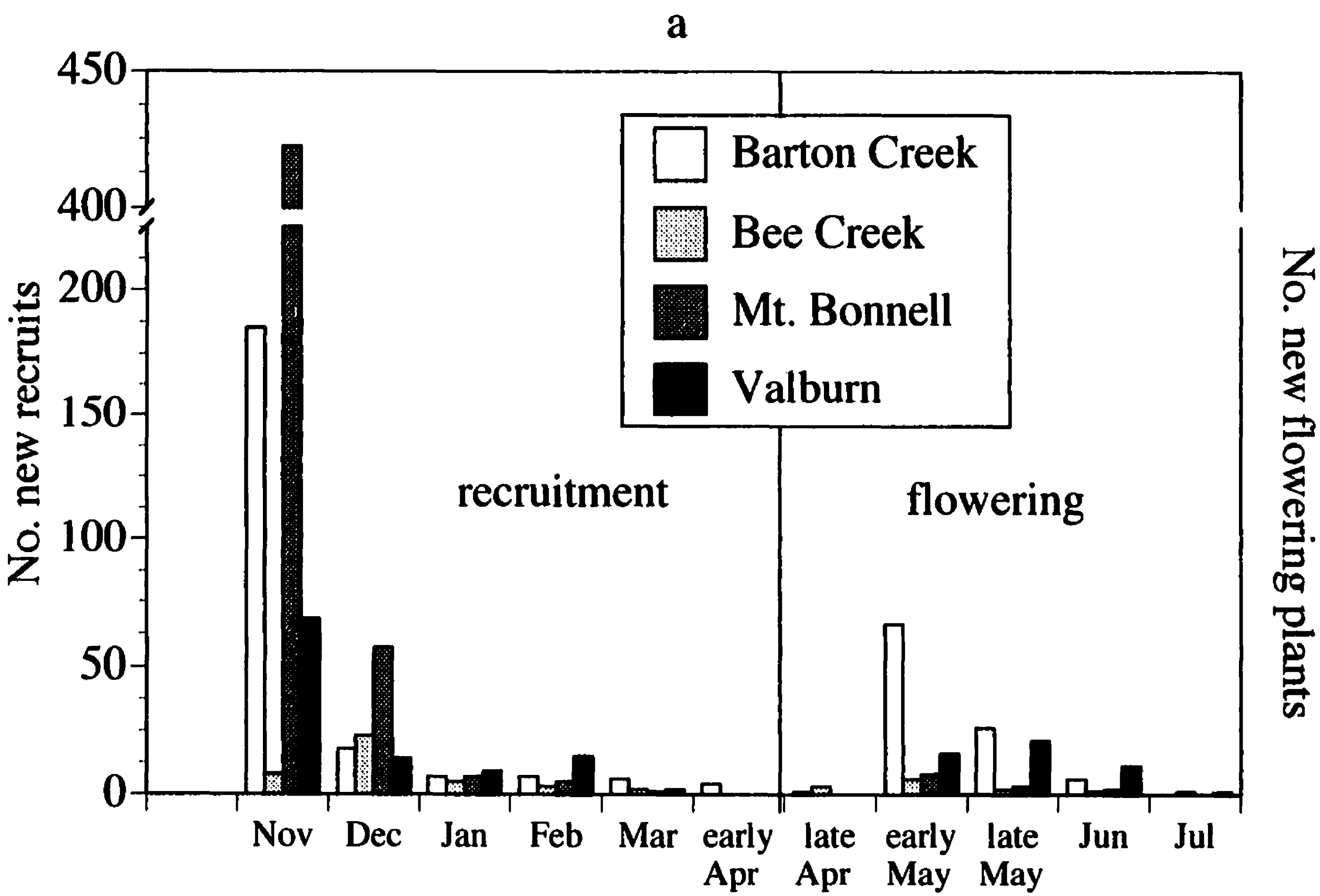


Figure A3. The timing of recruitment and flowering in *S. bracteatus* at four sites in (a) 1993–1994 and (b) 1994–1995. Values are either the number of new recruits during an interval (left of the vertical center line) or the number of plants flowering for the first time during the interval (right of the vertical center line). There was no overlap between recruitment and flowering.


a
450
400
200
150
100
50
0
No. new recruits
No. new flowering plants
Barton Creek
Bee Creek
Mt. Bonnell
Valburn
recruitment
flowering
Nov
Dec
Jan
Feb
Mar
early Apr
late Apr
early May
late May
Jun
Jul

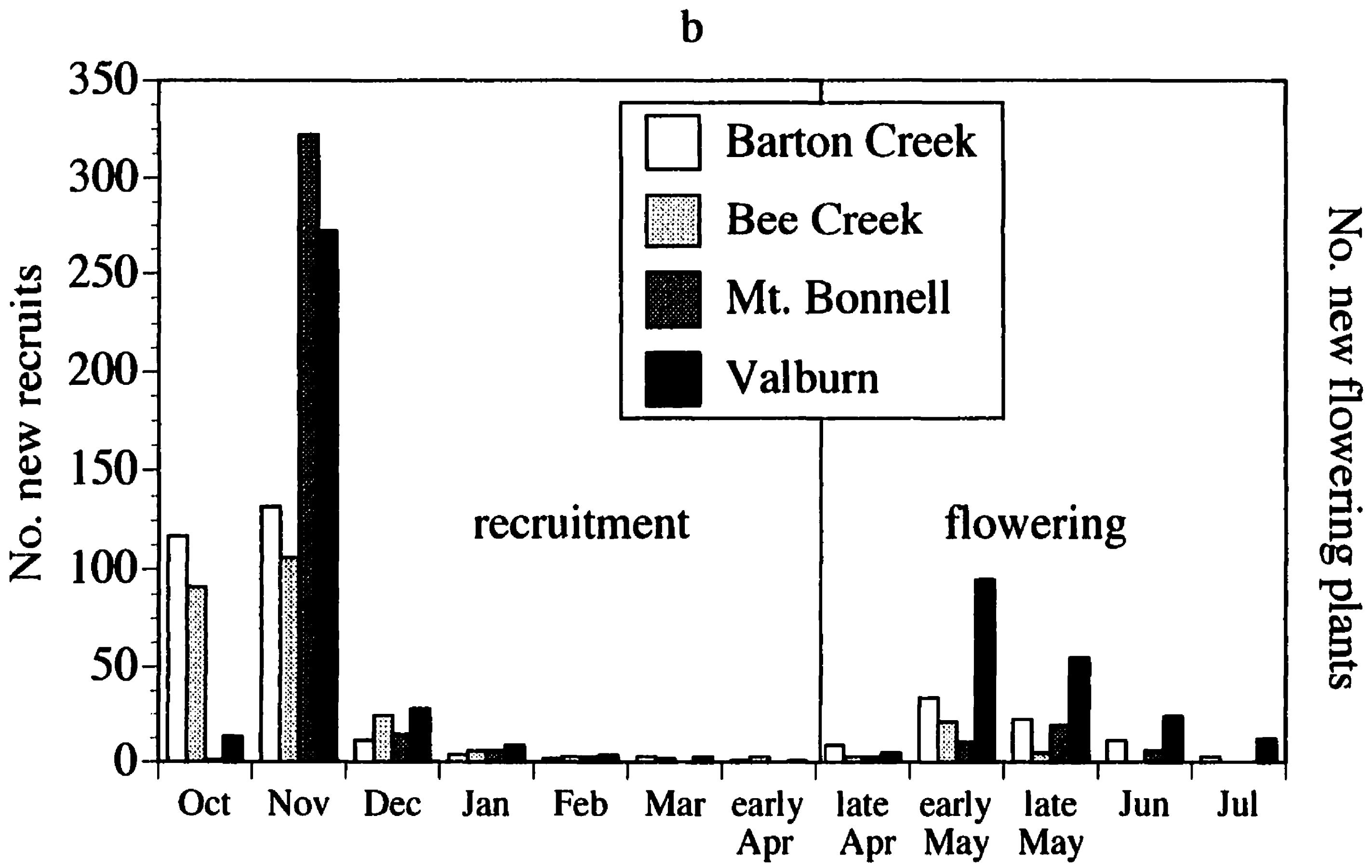
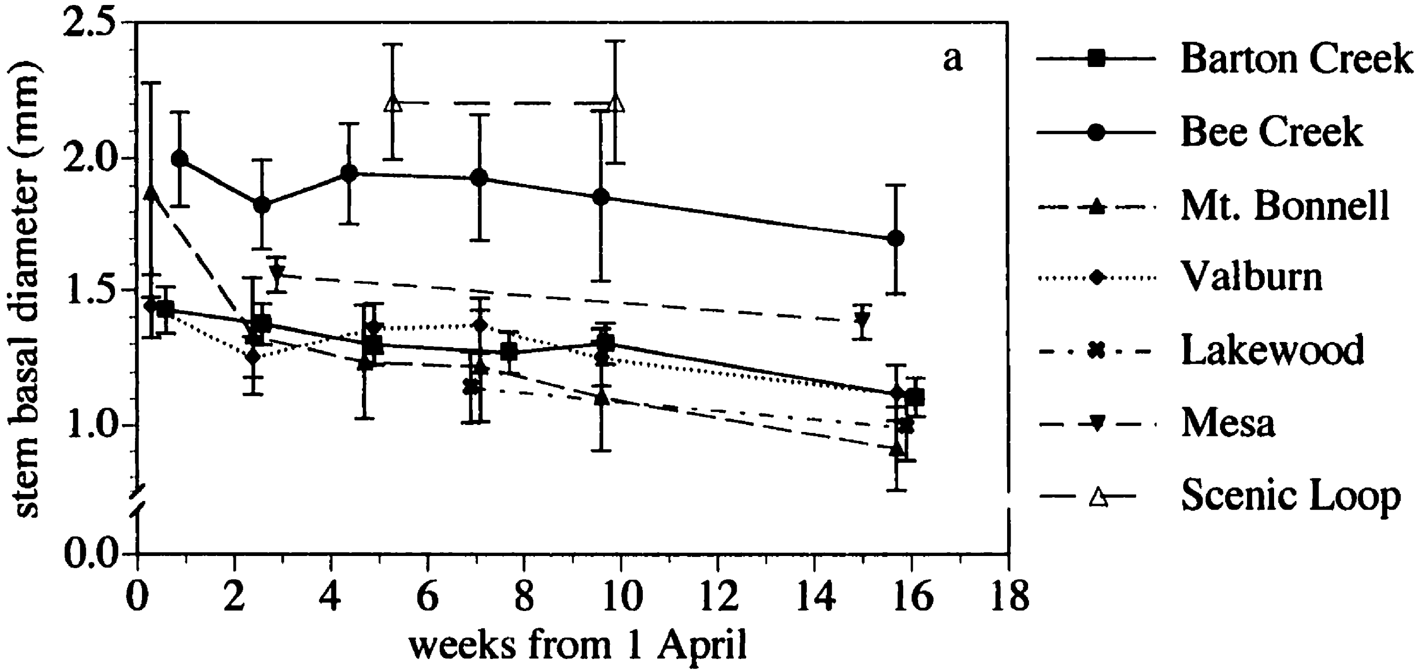
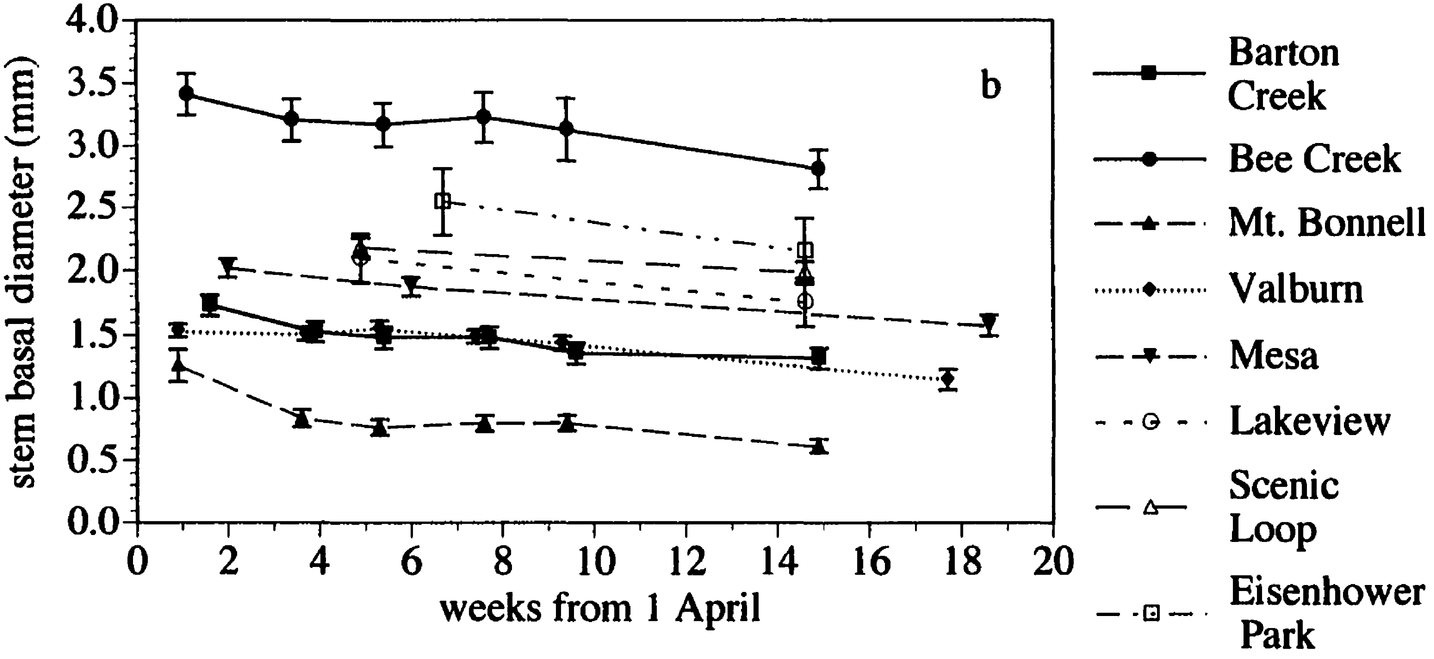

b
No. new recruits
No. new flowering plants
0
50
100
150
200
250
300
350
Barton Creek
Bee Creek
Mt. Bonnell
Valburn
recruitment
flowering
Oct
Nov
Dec
Jan
Feb
Mar
early Apr
late Apr
early May
late May
Jun
Jul

Figure A4. Size of adult *S. bracteatus* in (a) 1994 at seven sites and (b) 1995 at eight sites. Values are mean stem basal diameter ± standard error. Note that plants at some sites were only measured in one year. Sites in the western part of the range (closed symbols) are listed first; sites in the eastern part of the range (open symbols) are listed last in the legend.


a
stem basal diameter (mm)
2.5
2.0
1.5
1.0
0.0
0
2
4
6
8
10
12
14
16
18
weeks from 1 April
Barton Creek
Bee Creek
Mt. Bonnell
Valburn
Lakewood
Mesa
Scenic Loop


b
stem basal diameter (mm)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
2
4
6
8
10
12
14
16
18
20
weeks from 1 April
Barton Creek
Bee Creek
Mt. Bonnell
Valburn
Mesa
Lakeview
Scenic Loop
Eisenhower Park

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VITA

David Benjamin Zippin was born in San Francisco, California, on 20 August, 1967, the son of Patricia Jayne Zippin and Calvin Zippin. After completing his work at Redwood High School in 1985 in Larkspur, California, he entered the University of California in San Diego, California. He received the degree of Bachelor of Arts from the University of California at San Diego in December of 1989, graduating magne cum laude and Phi Beta Kappa. In the following year he was employed as an ecologist with a private consulting firm in San Diego, California. In August 1991 he entered the Graduate School of the University of Texas at Austin. During graduate school he published two papers, worked as an independent environmental consultant in Austin, Texas, and worked as an international environmental policy consultant to a non-profit organization in Vienna, Virginia.

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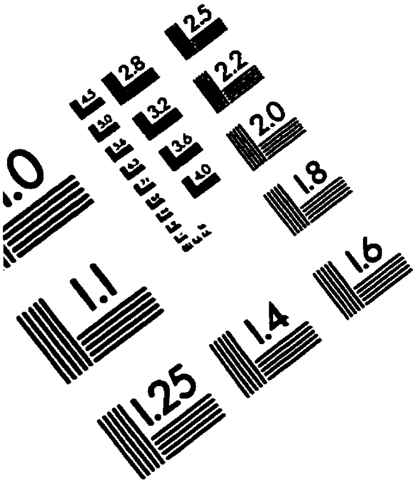
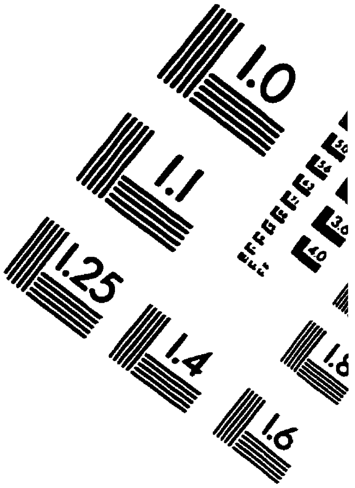

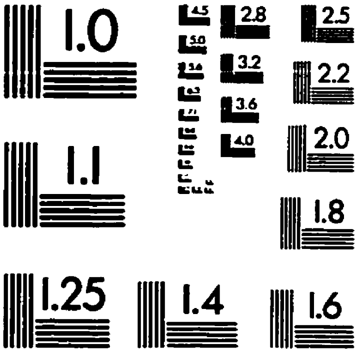

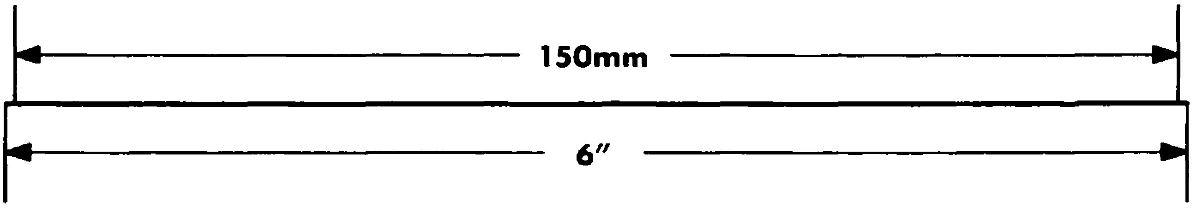

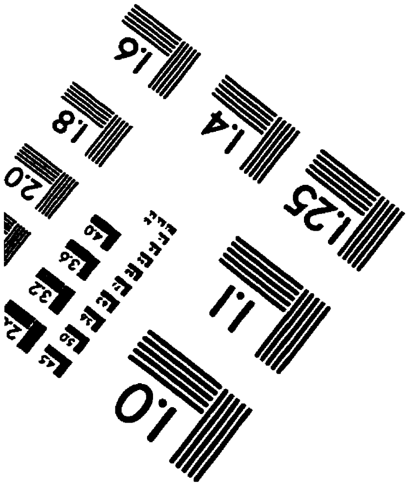

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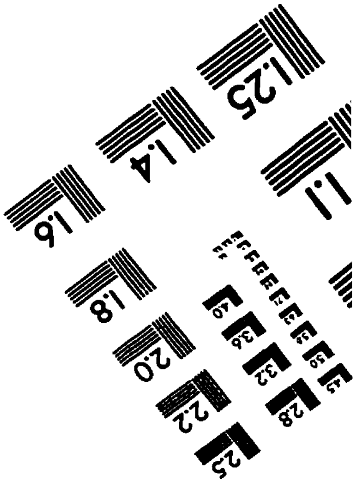

THE DEPARTMENT OF BOTANY
THE UNIVERSITY OF TEXAS AT AUSTIN

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Gena Janssen
Resource Protection Division
Texas Parks and Wildlife Department
3000 IH-35 South, Suite 100
Austin, TX 78704

18 March 96

Dear Gena,

Enclosed you will find the materials you will need for the *Steptanthus bracteatus* monitoring. I have included the following items:

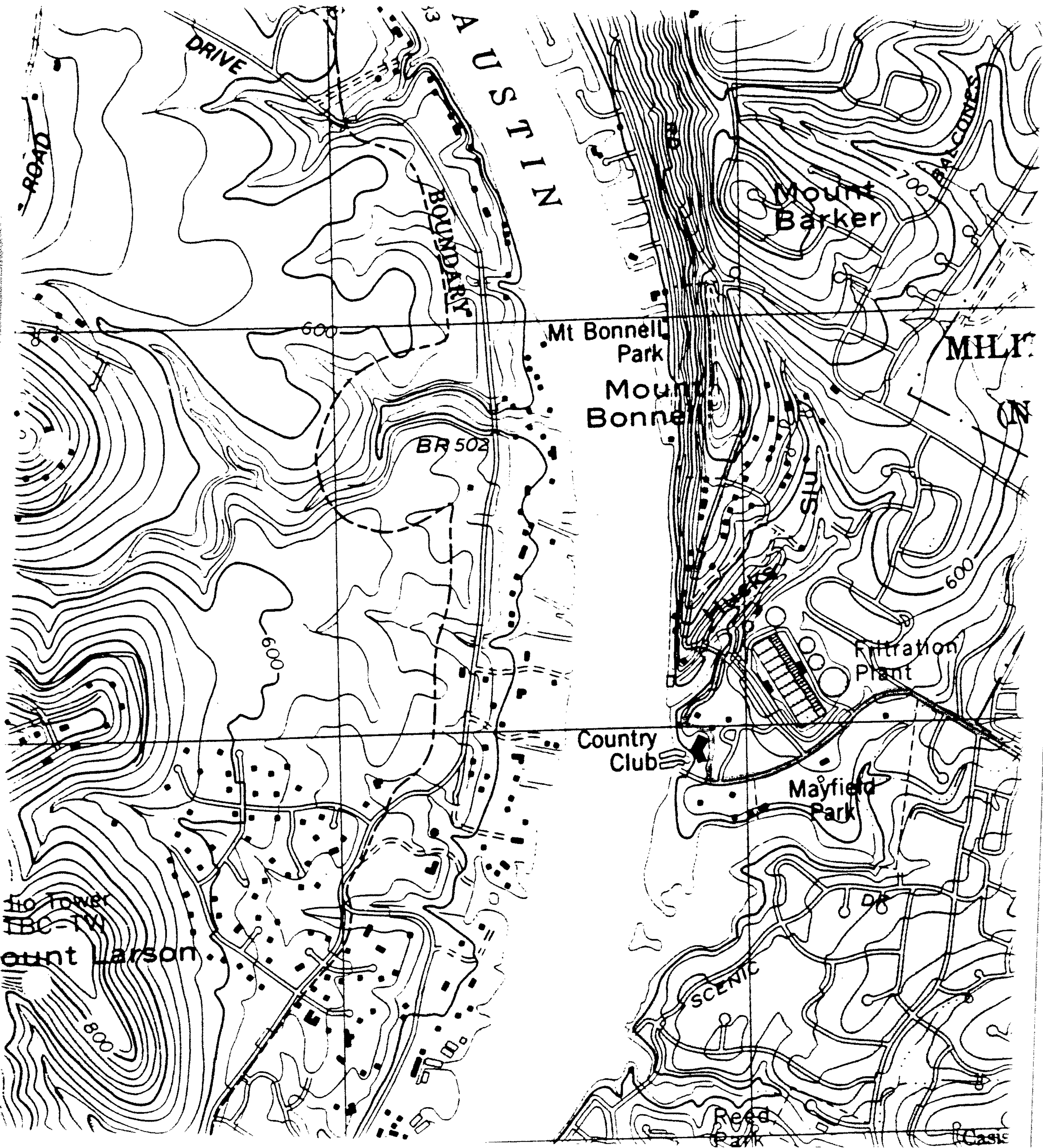
1. A list of my contacts since I began the project.
2. The maps (originals) that you and I started for the 1996 season (all 5 sites)
3. Maps from four Travis County sites of the 1994-1995 season
4. Maps of the 1993-1994 season from three Travis Co. (excluding Mt. Bonnell) sites, one Medina Co. site and Garner State Park.
5. Topo maps of the Mesa Dr. and Bluffs at Cat Mountain site. The former includes the previous development plan for the site. I have not seen the Bluffs site; the site is in an easement but it is unknown whether the plants still exist.
6. A letter dated Dec. 6, 1993 regarding the Barton Creek Greenbelt Management Plan. You might want to request a copy of this Plan.

Good luck with this and please give me a call (or email me!) if you have any questions.

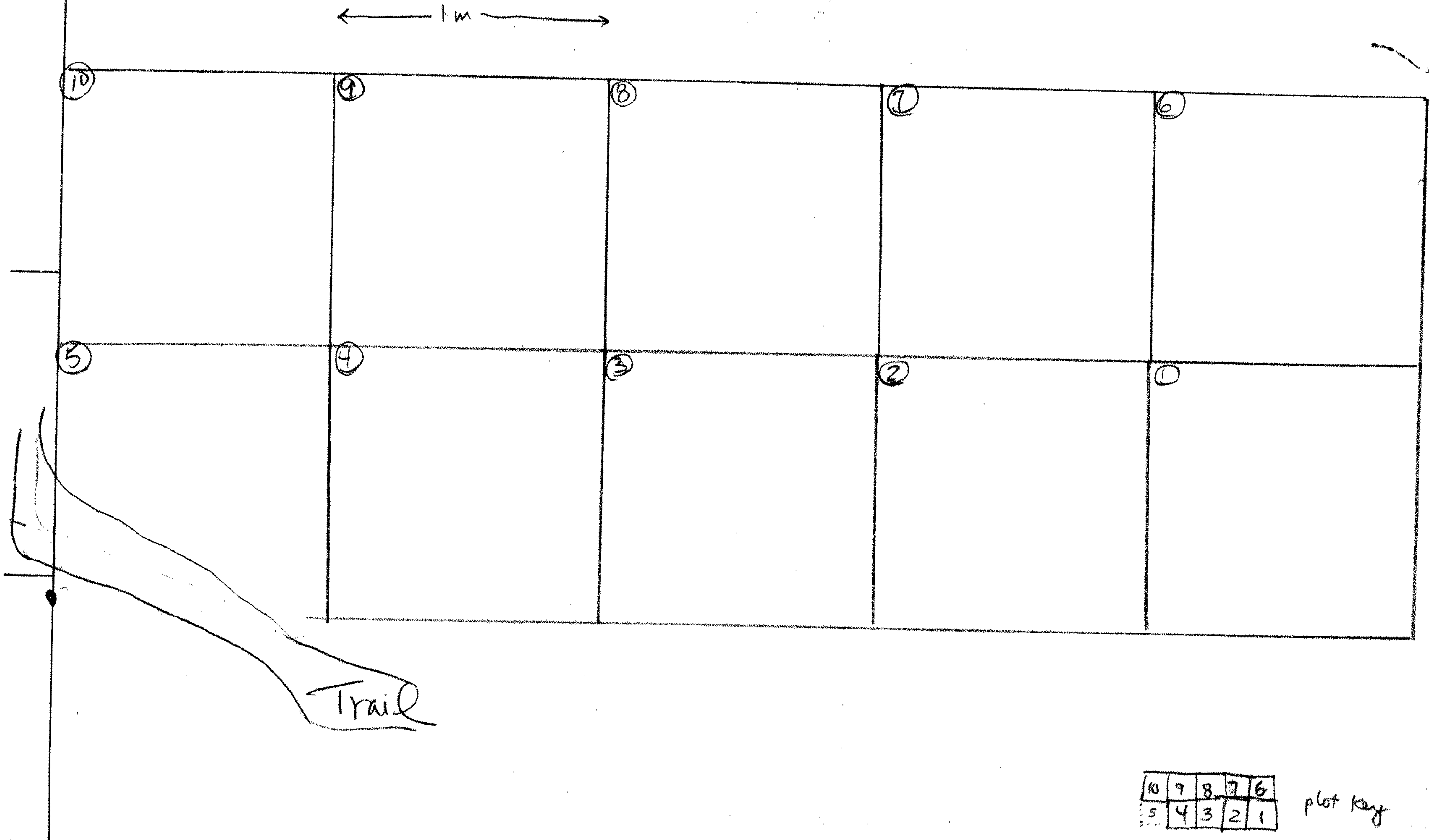
Regards,

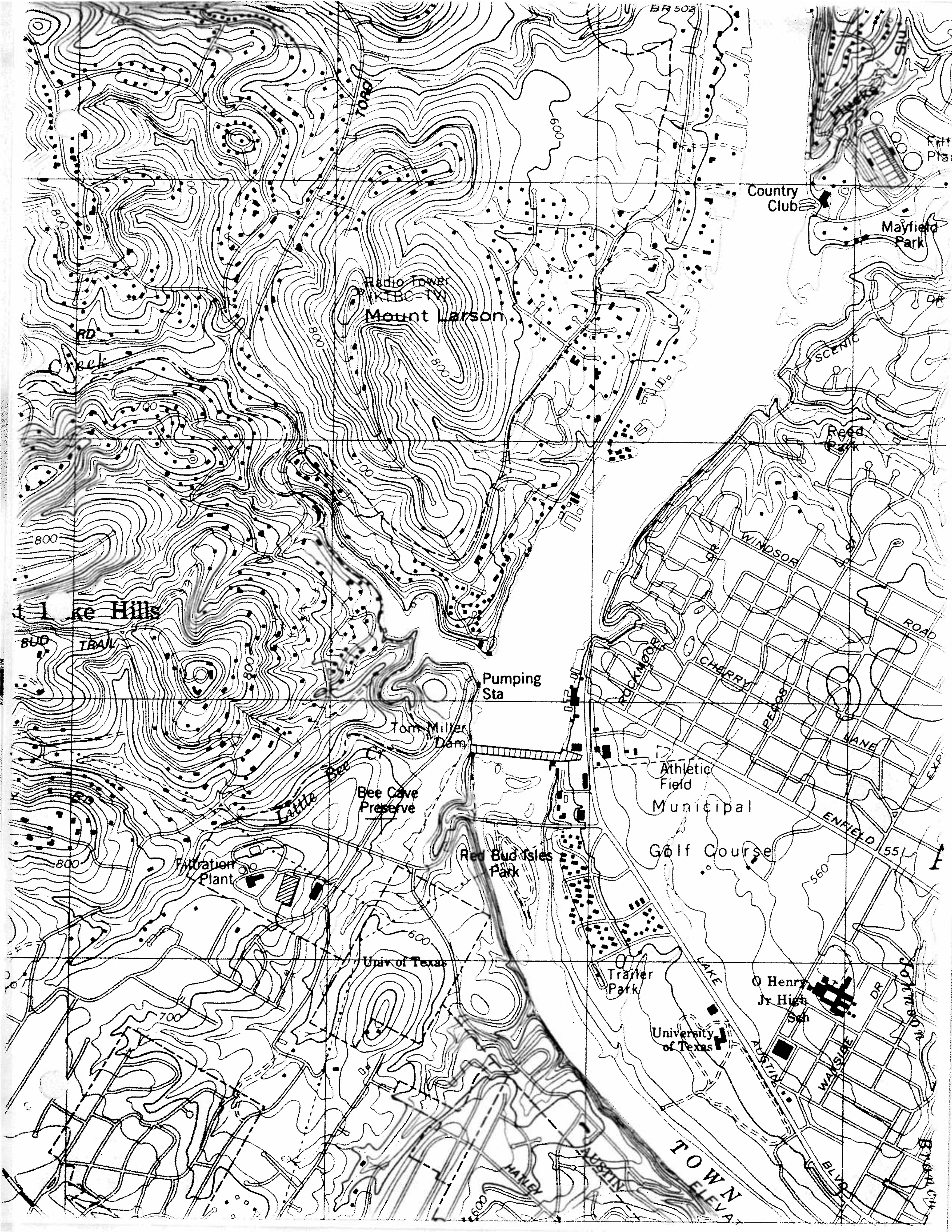
David Zippin
david.zippin@mail.utexas.edu

Streptanthus bracteatus



Mt. Bonnell Streptanthus bracteatus

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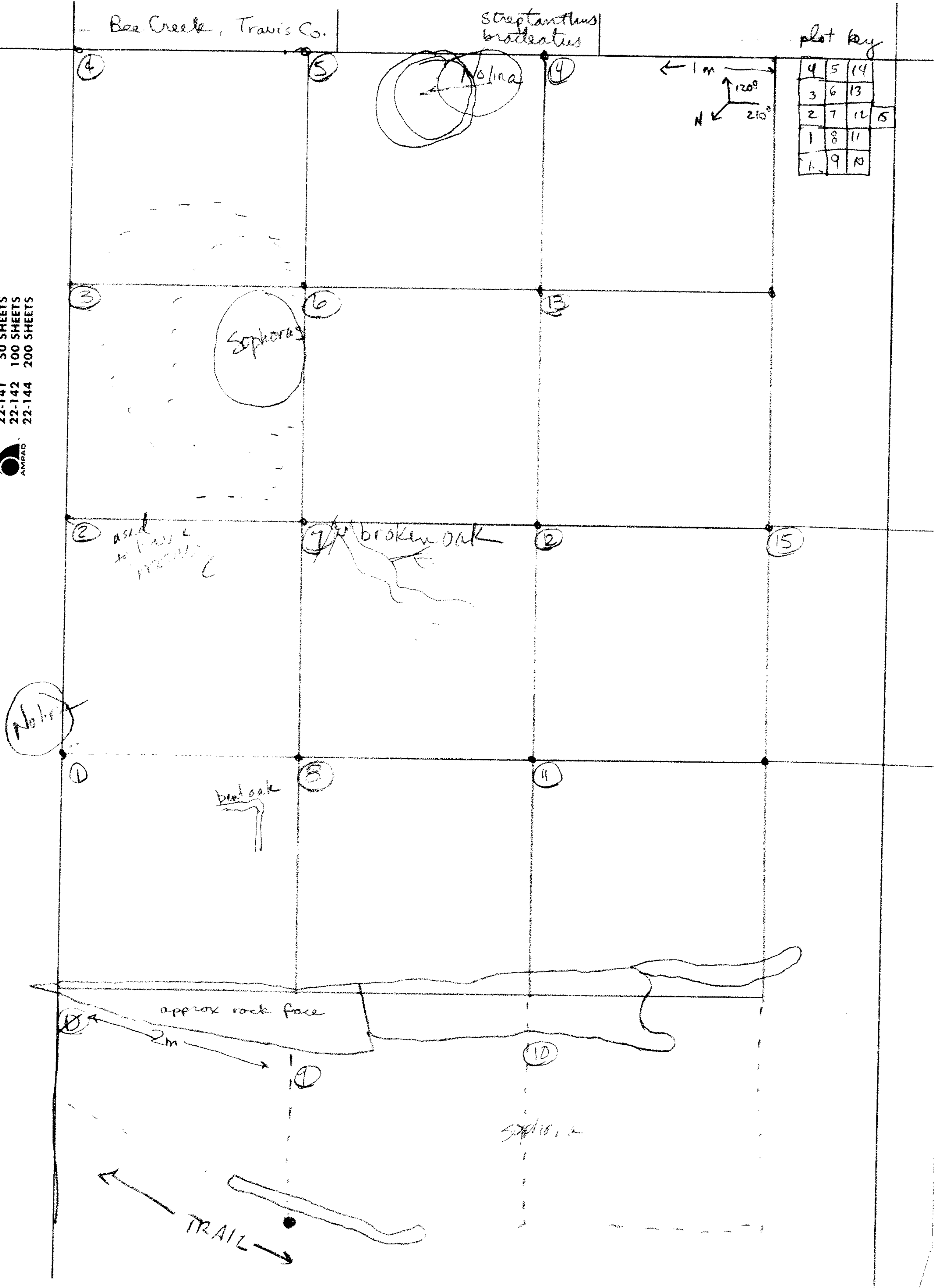
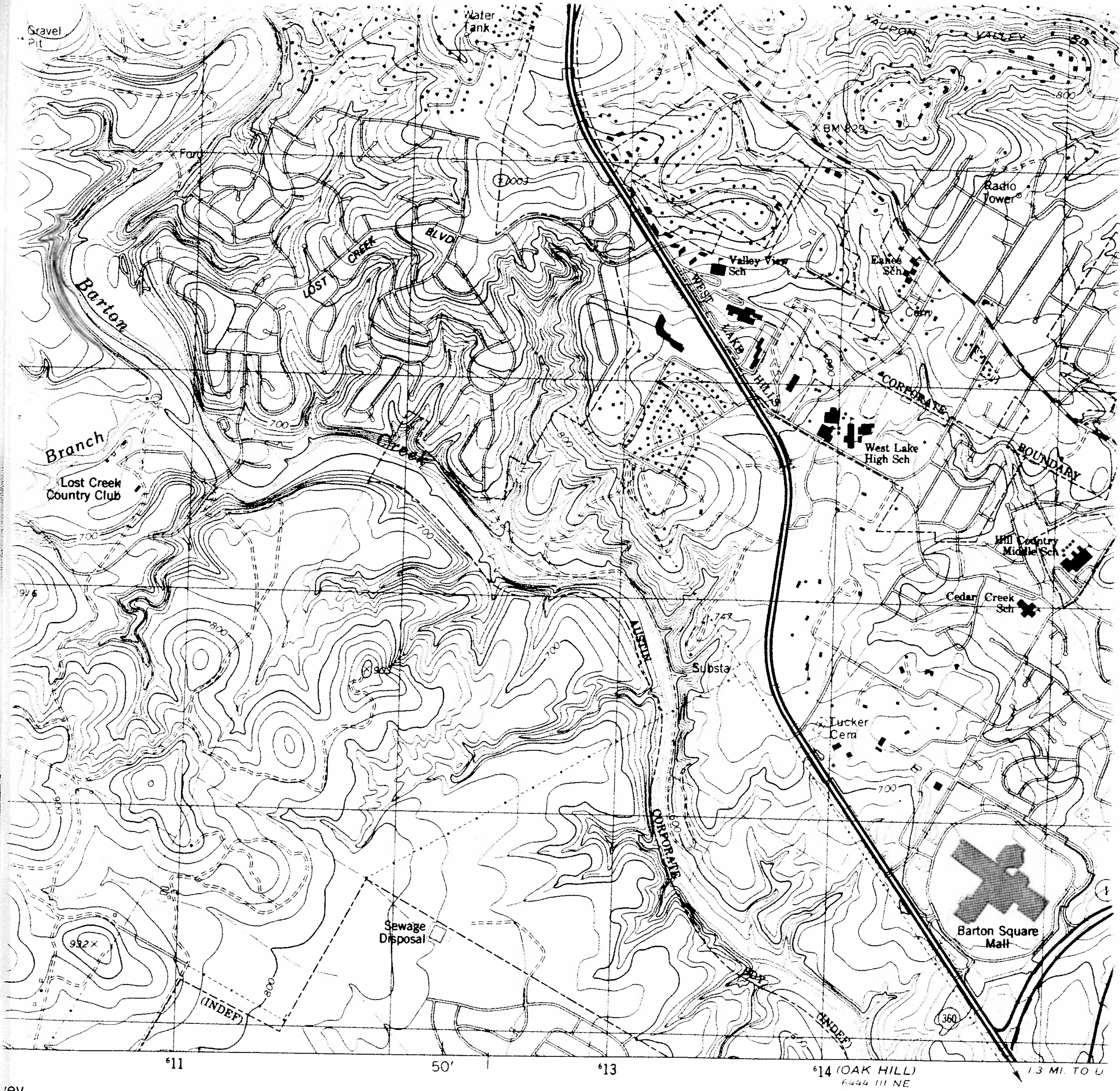
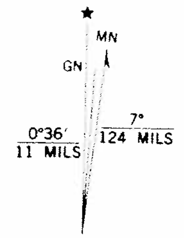
Trailer Park
O Henry Jr High Sch
University of Texas
LAKE
AUSTIN
BLVD
WAYSIDE
DR
TOWN
HANEY
AUSTIN


Bee Creek, Travis Co.
Streptanthus bracteatus
plot key
4 5 14
3 6 13
2 7 12 15
1 8 11
1 9 10
← 1 m →
120°
210°
N
4
5
4
Nolina
3
6
13
Sophoras
2
9
broken oak
12
15
Nolina
1
8
11
bent oak
approx rock face
1
2 m
9
10
Sophora
TRAIL



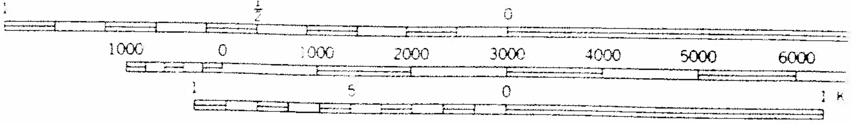
vey

hs



UTM GRID AND 1988 MAGNETIC NORTH
DECLINATION AT CENTER OF SHEET
DIAGRAM IS APPROXIMATE

SCALE 1:24 000

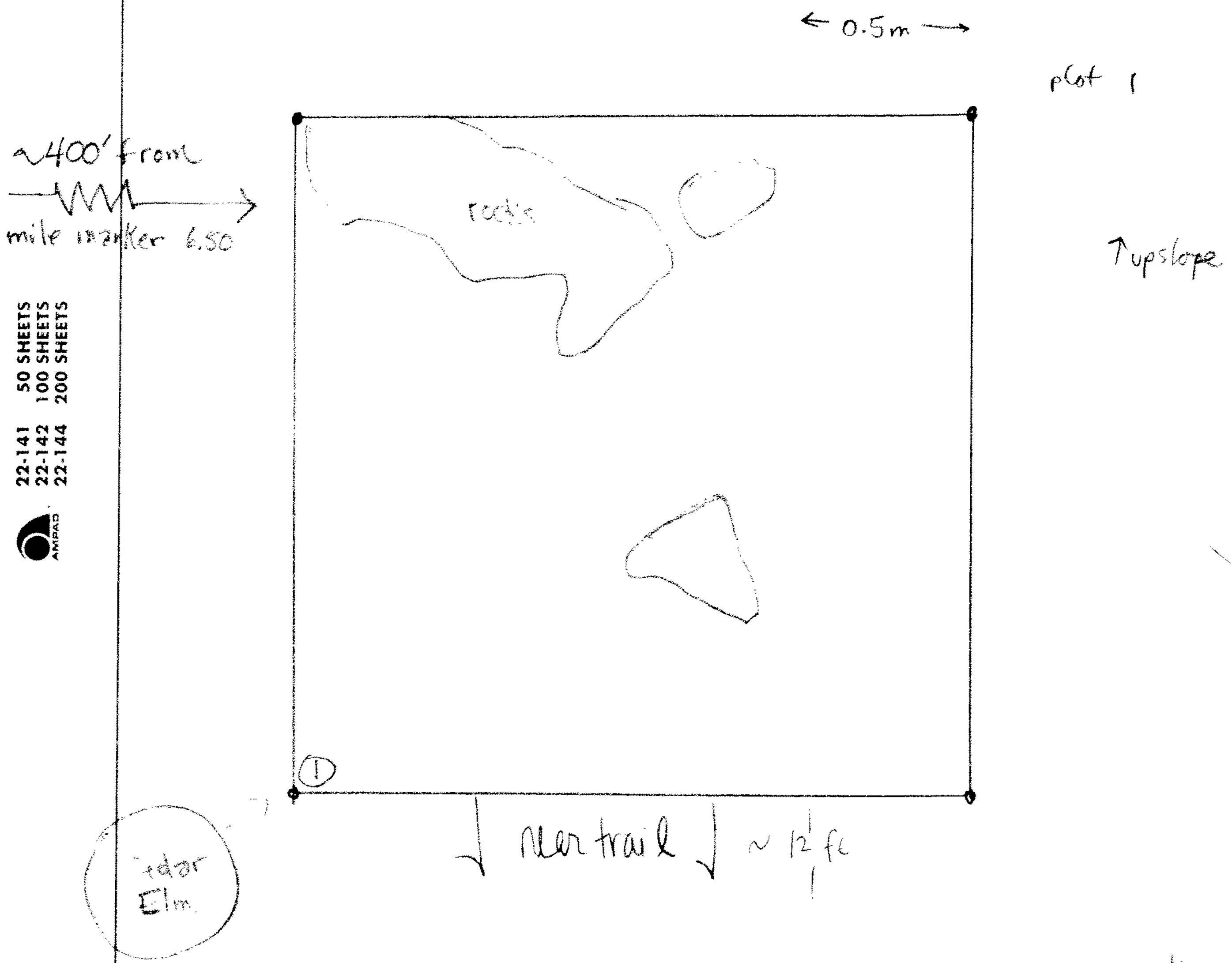


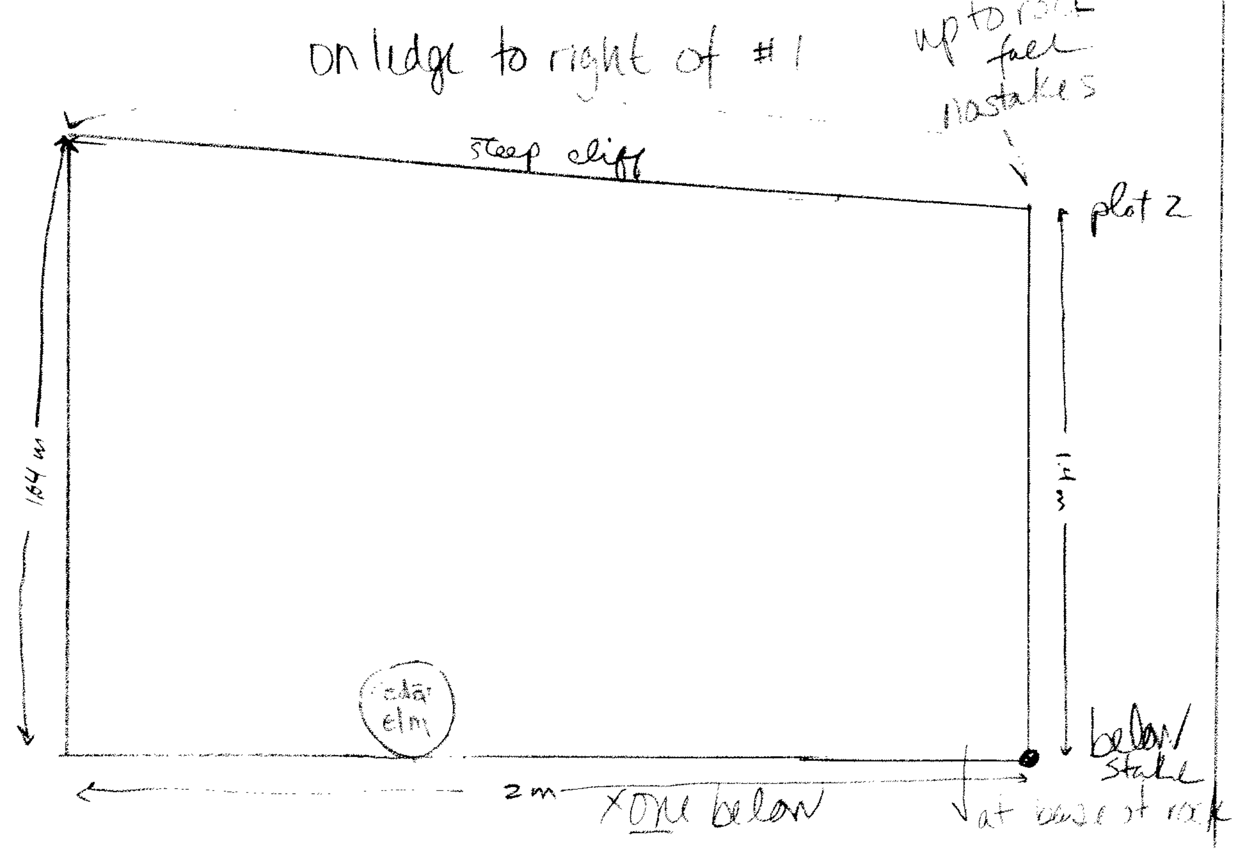
CONTOUR INTERVAL 20 FEET
NATIONAL GEODETIC VERTICAL DATUM OF 1929

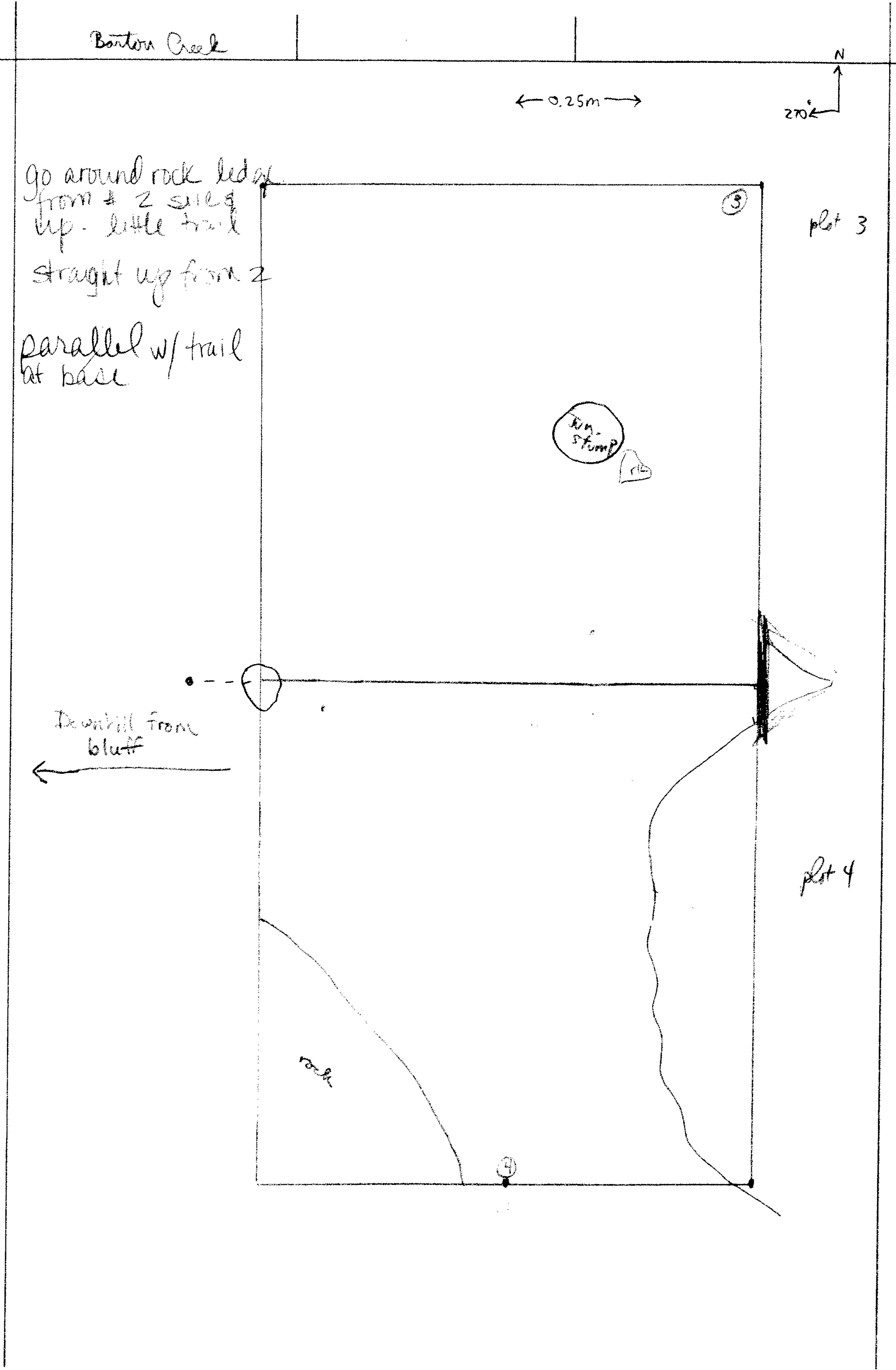
THIS MAP COMPLIES WITH NATIONAL MAP ACCURACY STANDARDS
FOR SALE BY U. S. GEOLOGICAL SURVEY, DENVER, COLORADO 80225, OR RESTON
A FOLDER DESCRIBING TOPOGRAPHIC MAPS AND SYMBOLS IS AVAILABLE ON R

Barton Creek | Streptanthus | bracteatus

Numbers go downstream







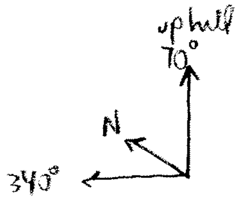
go around rock ledge from # 2 site & up - little trail

straight up from 2

parallel w/ trail at base

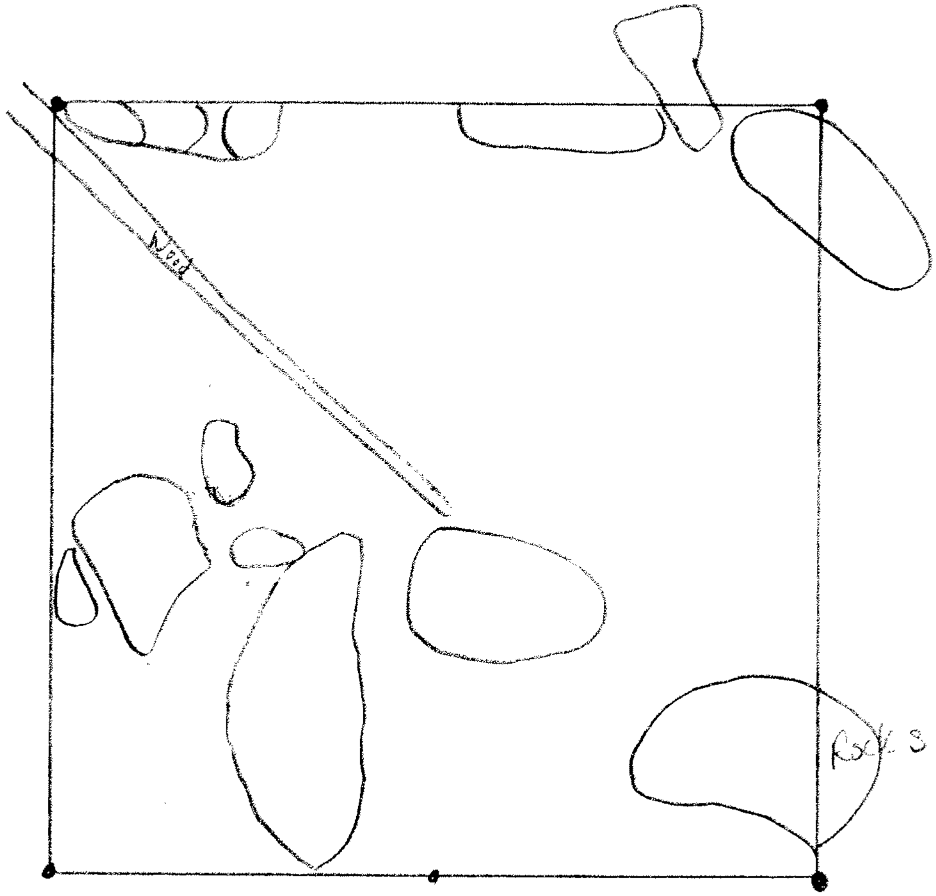
Barton Creek

to right & upslope from
3/4

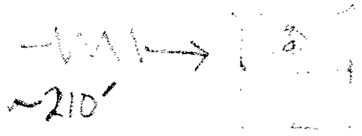


← 0.5m →

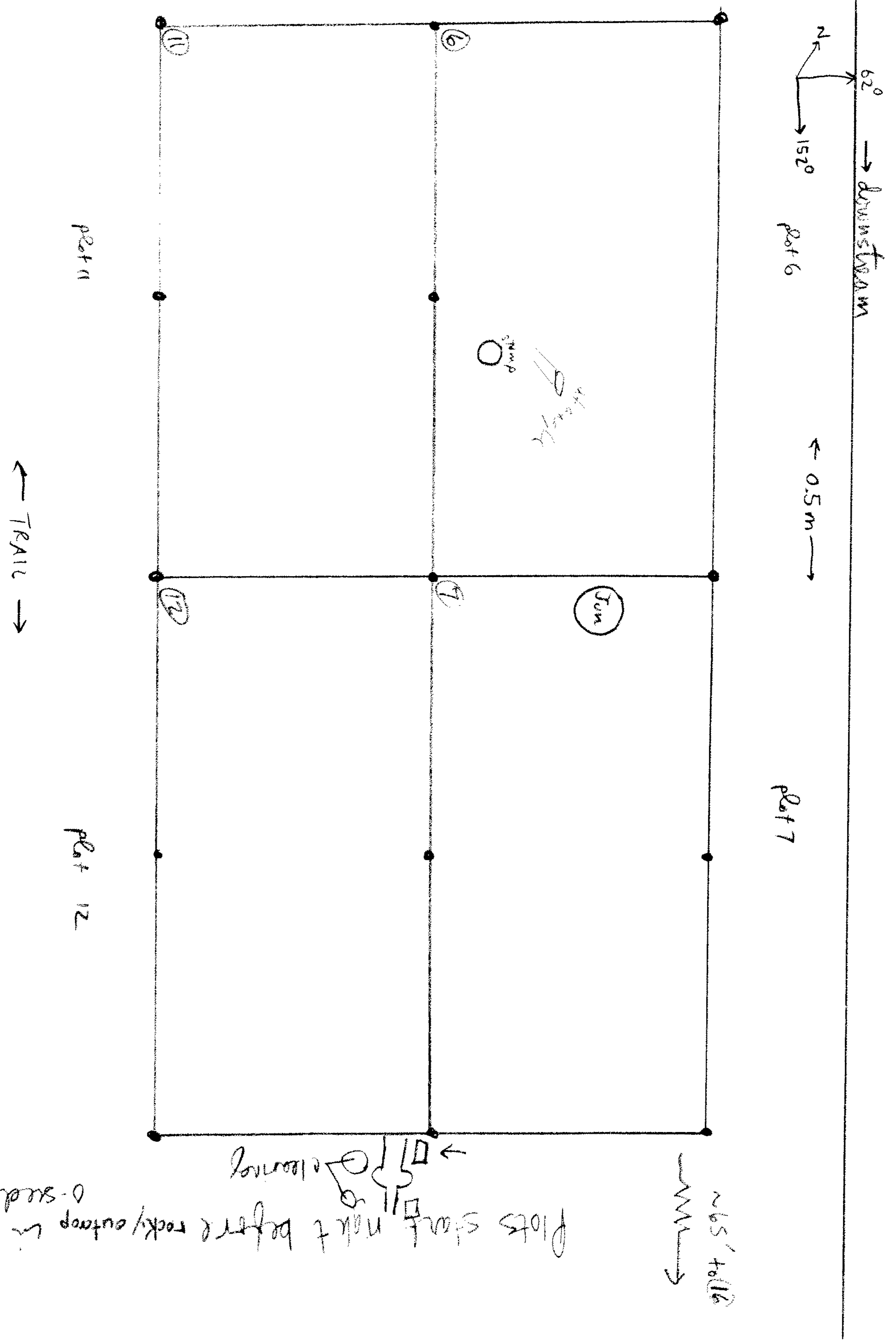
plot 5



go back down to trail & walk downstream
to 6

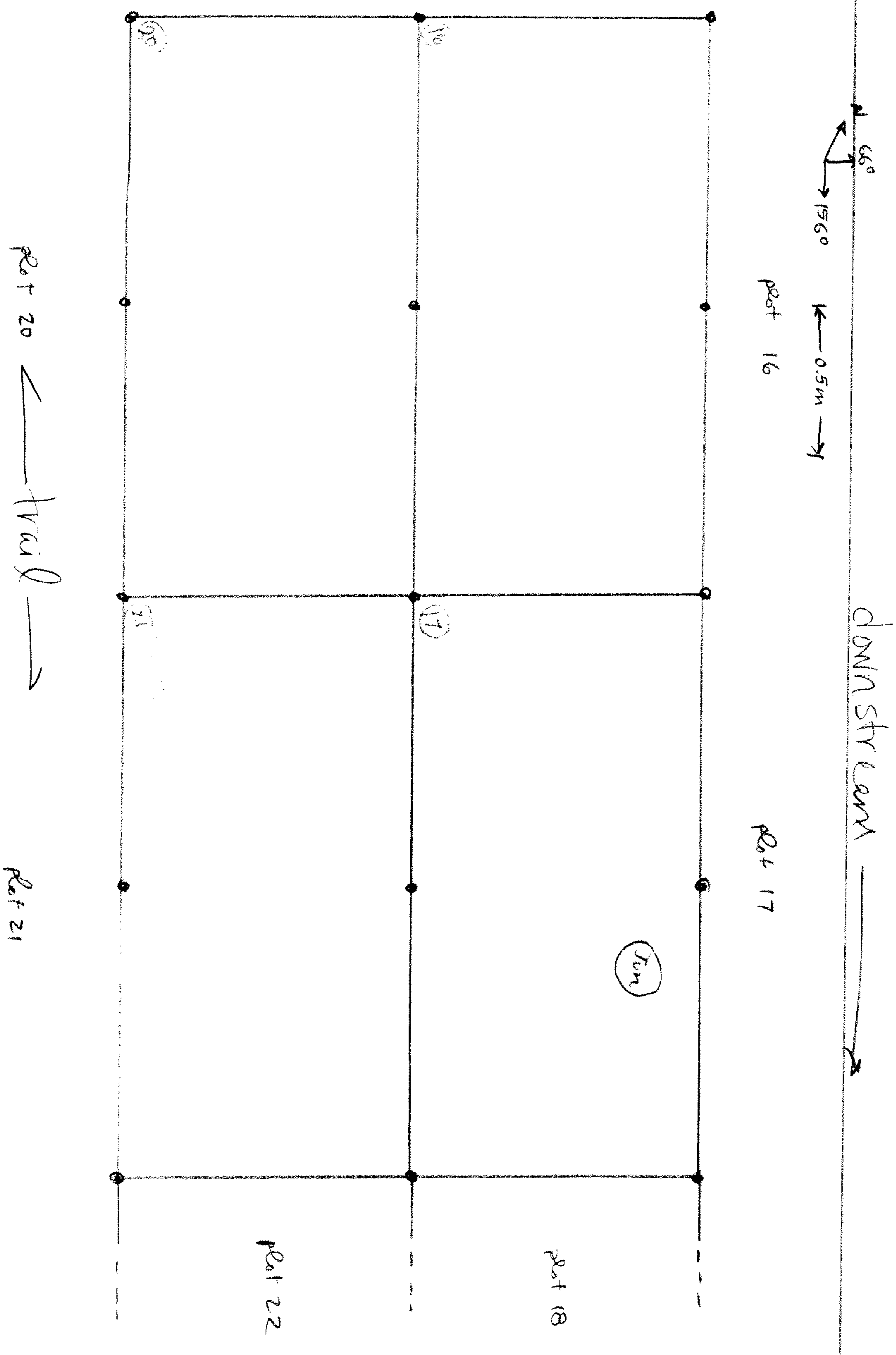


Barton Creek | | Streptanthus bracteatus

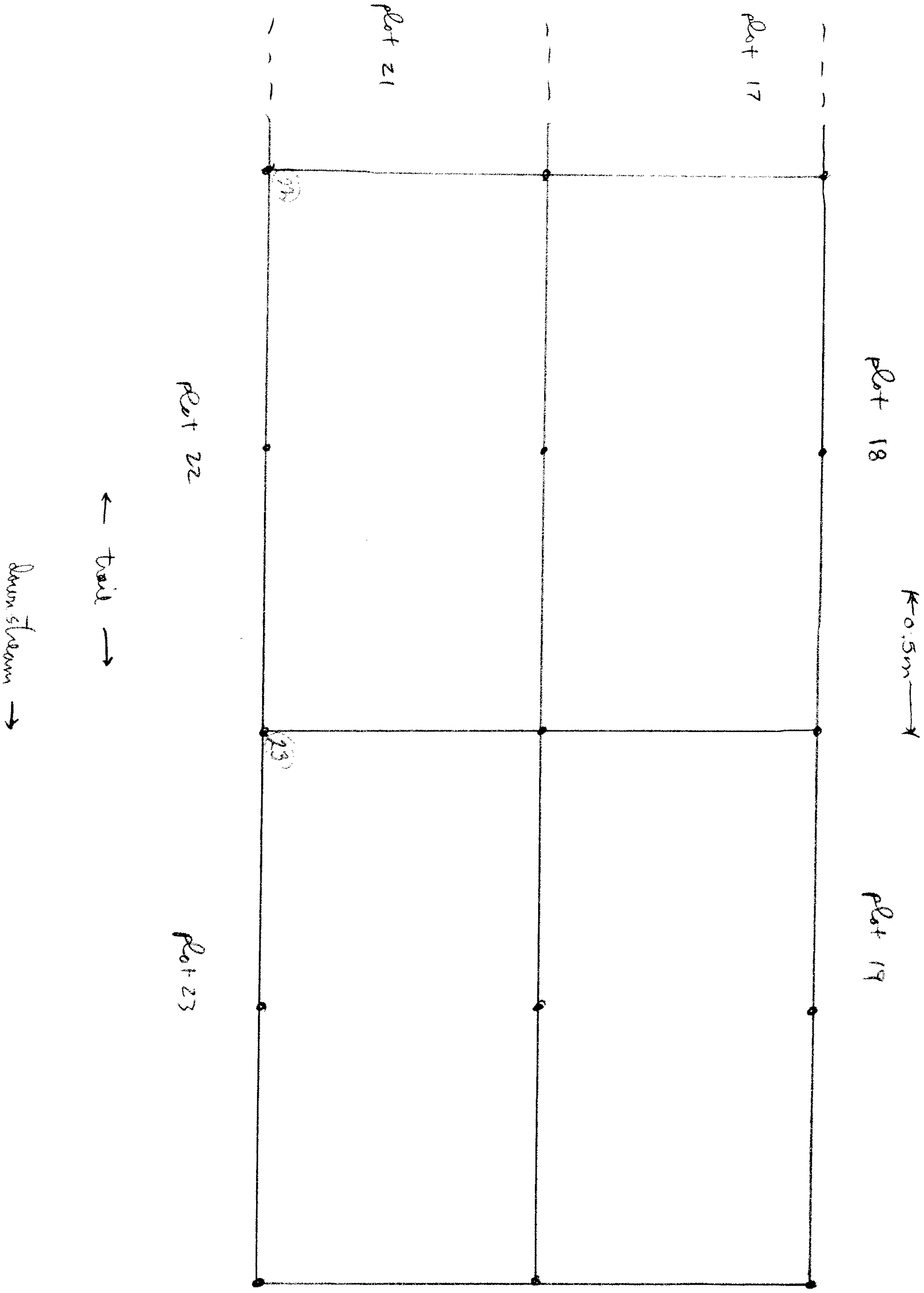


Plots start right before rocky outcrop in road
0-seedlings found

Barton Creek | | Streptanthus bracteatus

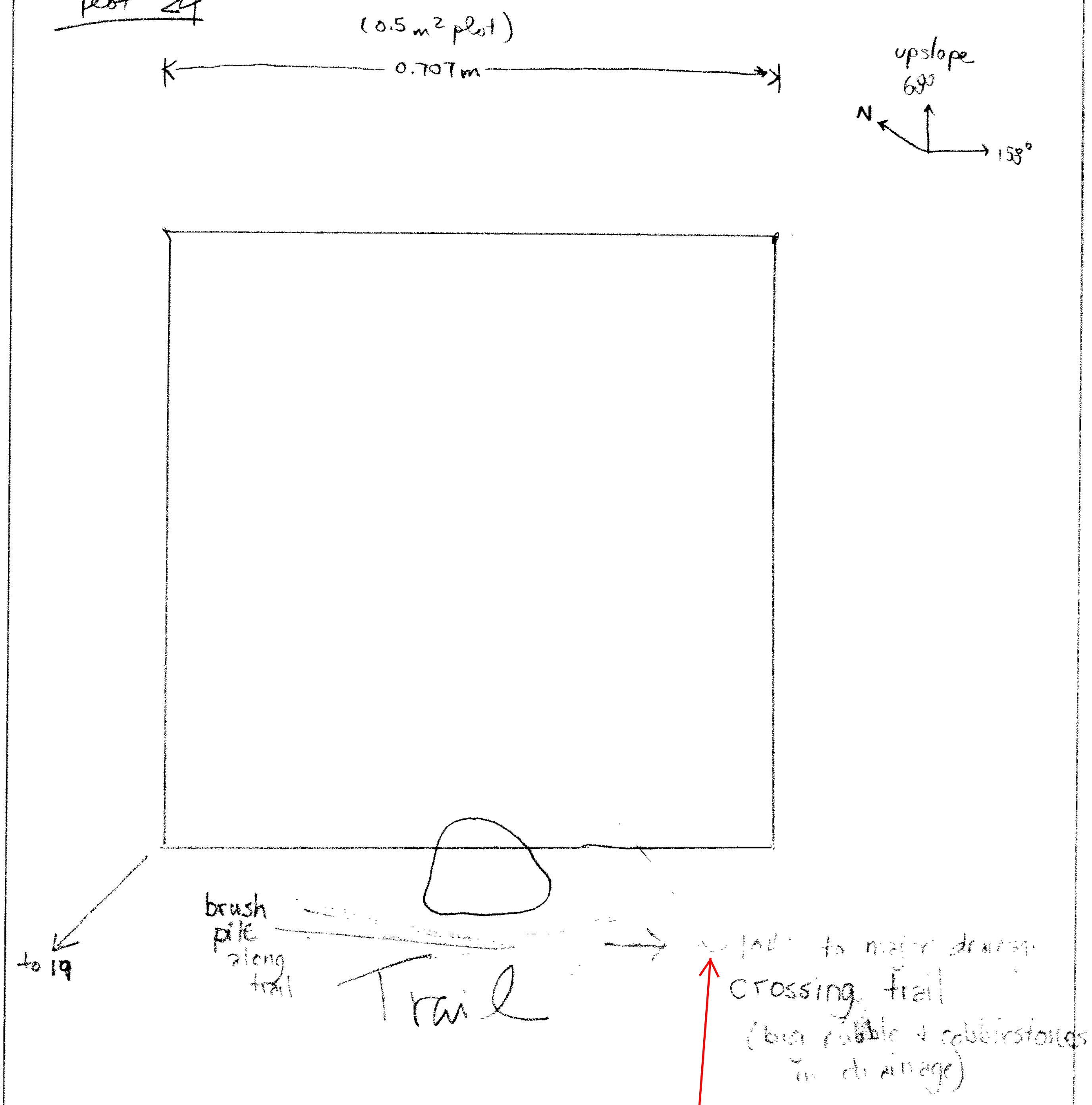


Barton Creek | Streptanthus bracteatus

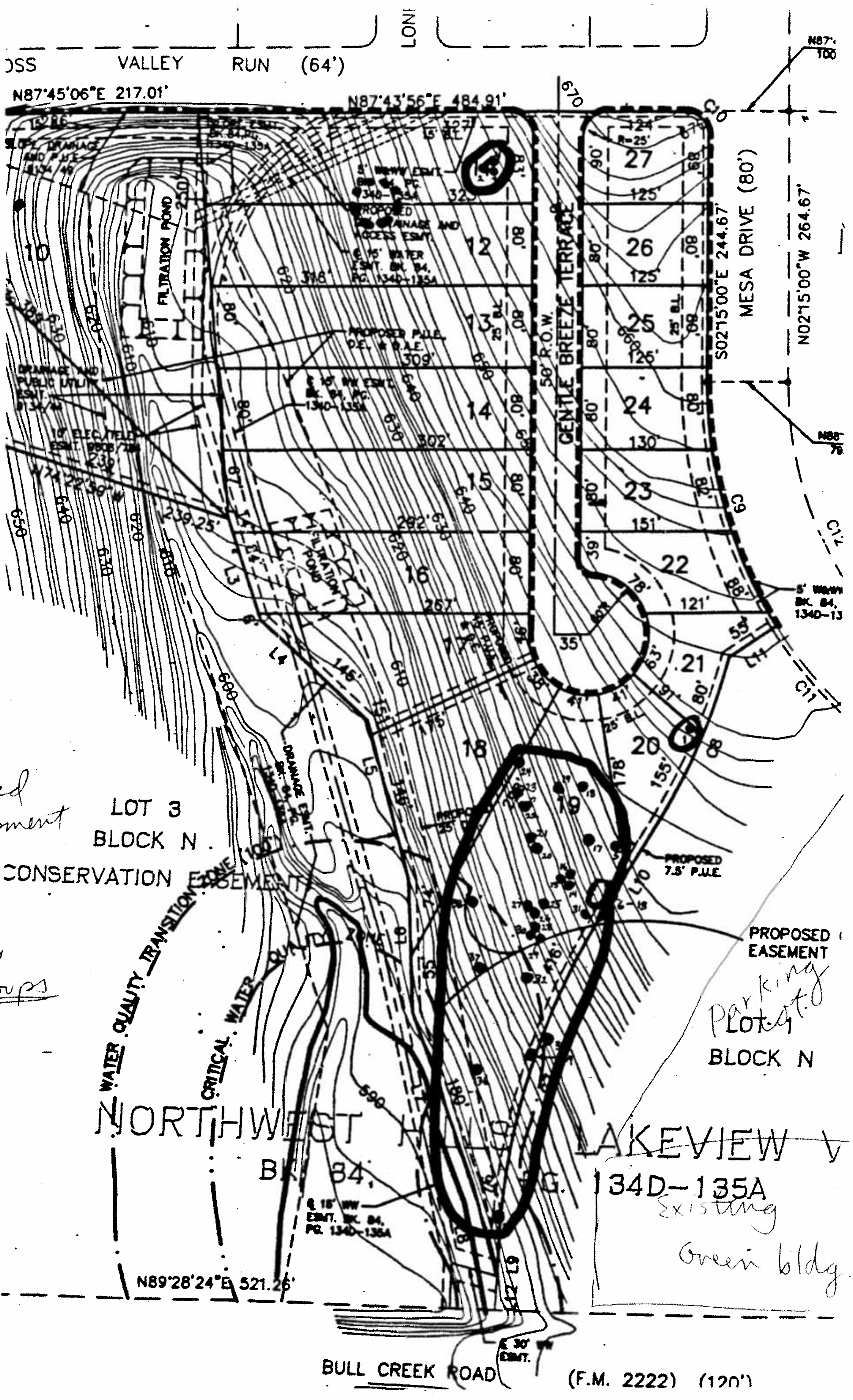


Barton Creek | Streptanthus bracteatus

plot 24



104 feet to major drainage crossing trail. (big rubble and cobblestones in drainage.



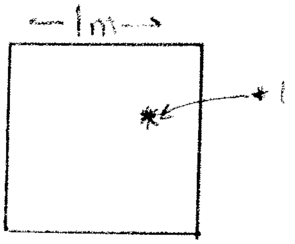
1992
Original proposed ~~date~~ development
- Mesa Dr. site
and locations
of plant groups
in 1993.

* seedling mapped | Mesa Drive | Mar 8, 1996

SITE # PLOT DIMENSIONS + seedling location

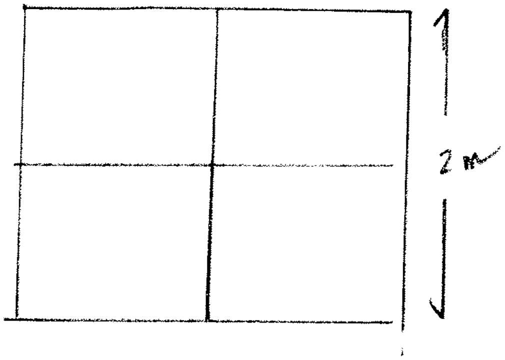
↑parking lot

(10)



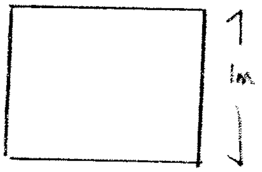
1-seedling

(9)



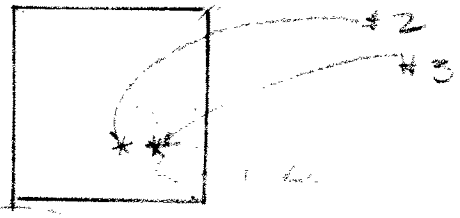
0-seedling

(12)



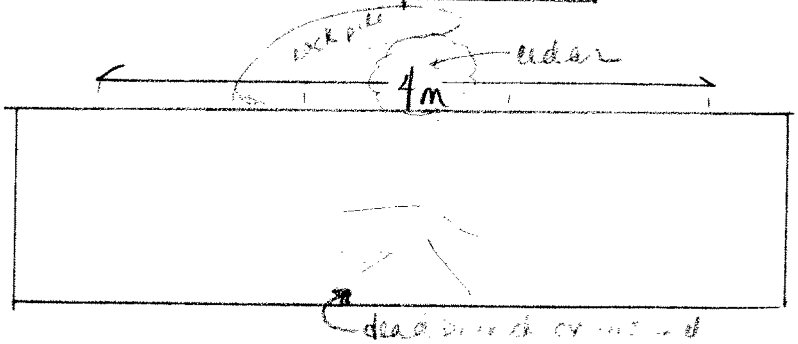
0-seedling

(11)



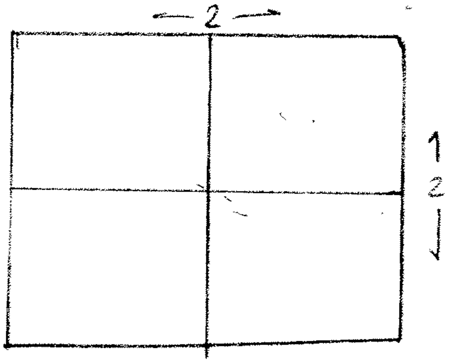
2-seedlings

(13)



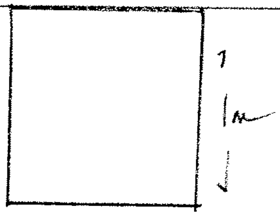
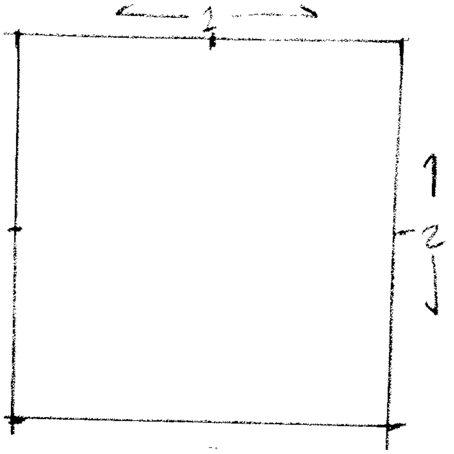
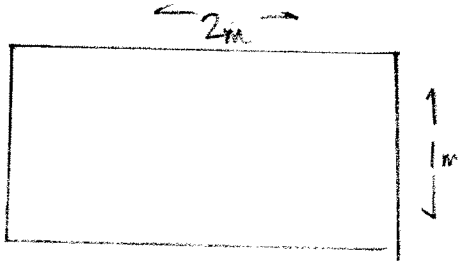
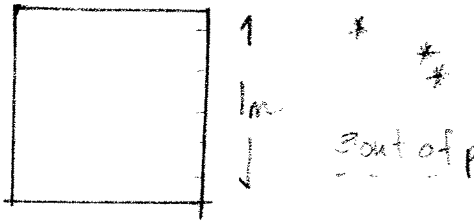
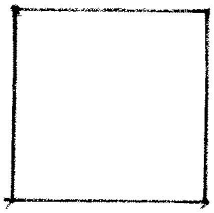
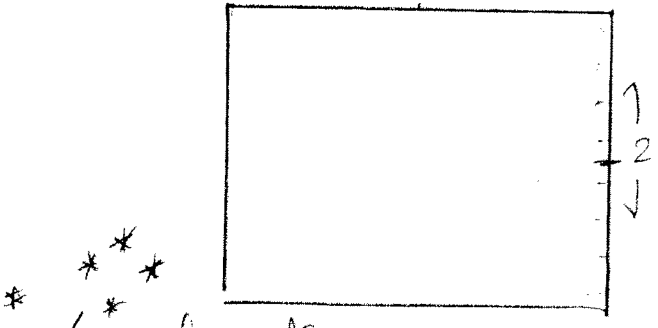
0-seedling

(14)



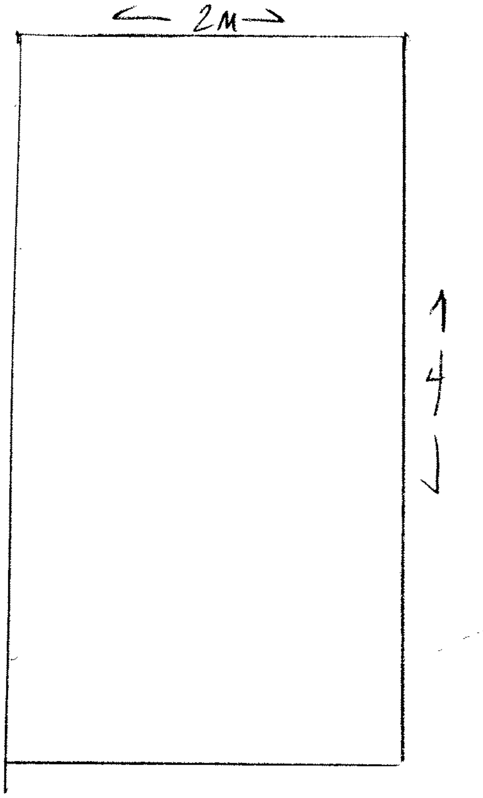
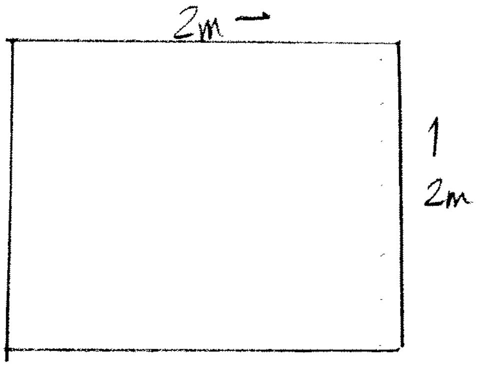
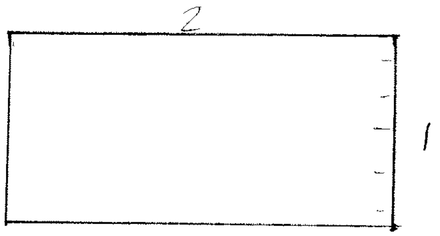
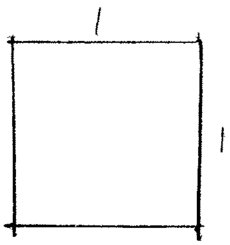
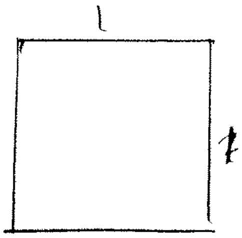
on edge of debris pile 0-seedling

USE DAVID'S ORIGINAL MAP OF AREA TO RELOCATE SITES. NOTE: TOP OF EACH PLOT WILL ALWAYS BE TOWARDS PARKING LOT.

SITE #	seedling locations Plot dimensions	Parking Lot 1
①		0-seedlings
②		0-seedlings
⑱		0-seedlings
⑰	 3 out of plot	0-seedlings
⑯		0-seedlings
⑮		0-seedlings

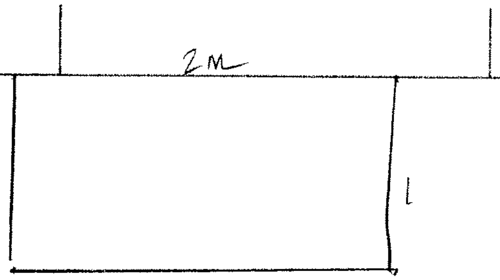
√ several towards debris pile

→ 24 counted outside of plots near pile

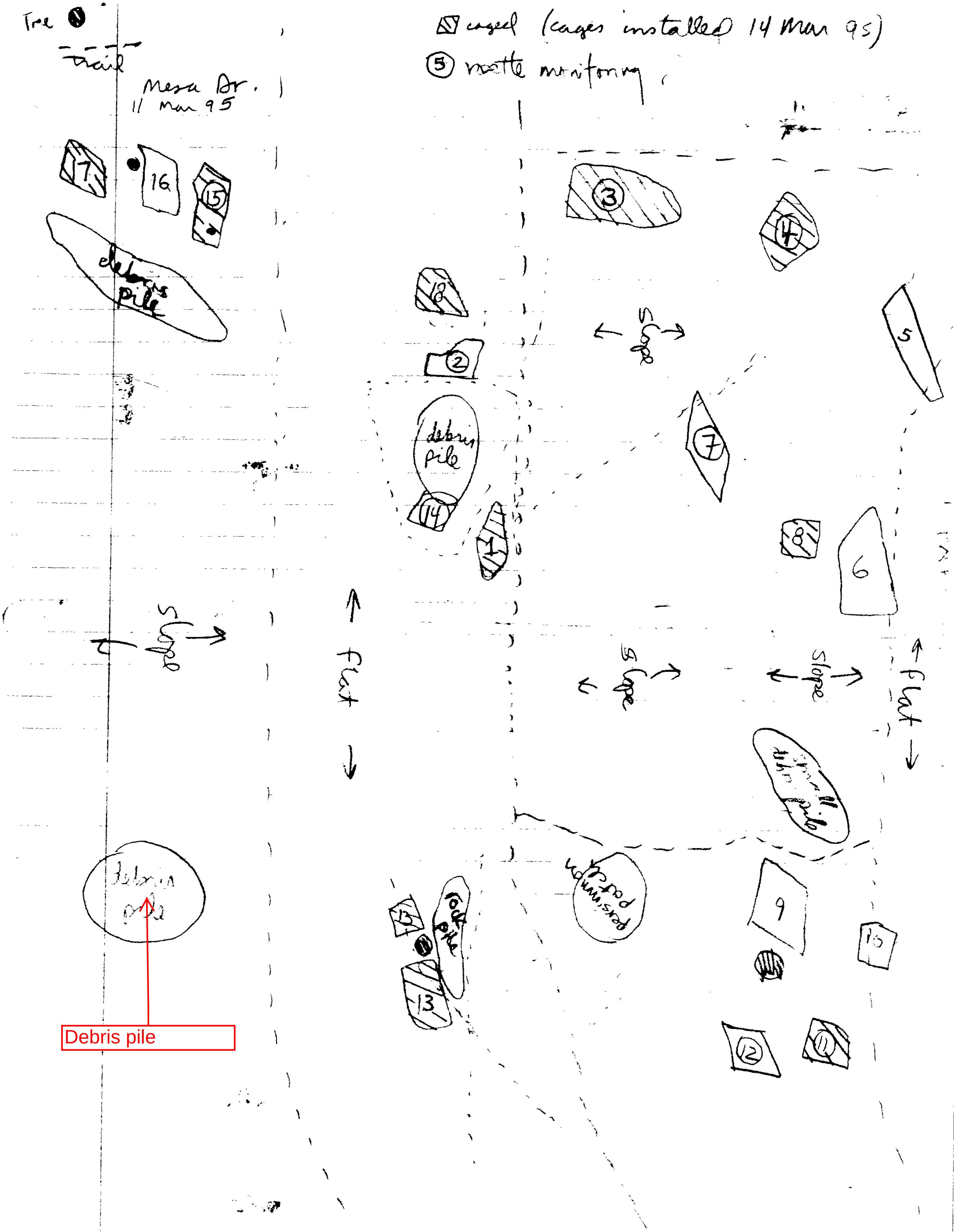
SITE #	Plot Dimensions	Parking Lot ↑
③		0-seedlings
④		0-seedlings
⑤		0-seedlings
⑦		0 seedlings
⑧		0-seedlings

Parking Lot 1

⑥



0-seedling


Mesa Dr.
11 Mar 95

Tree ●
- - - trail

▨ caged (cages installed 14 Mar 95)
⑤ rosette monitoring

Streptanthus bracteatus | Valburn Dr. | 1996

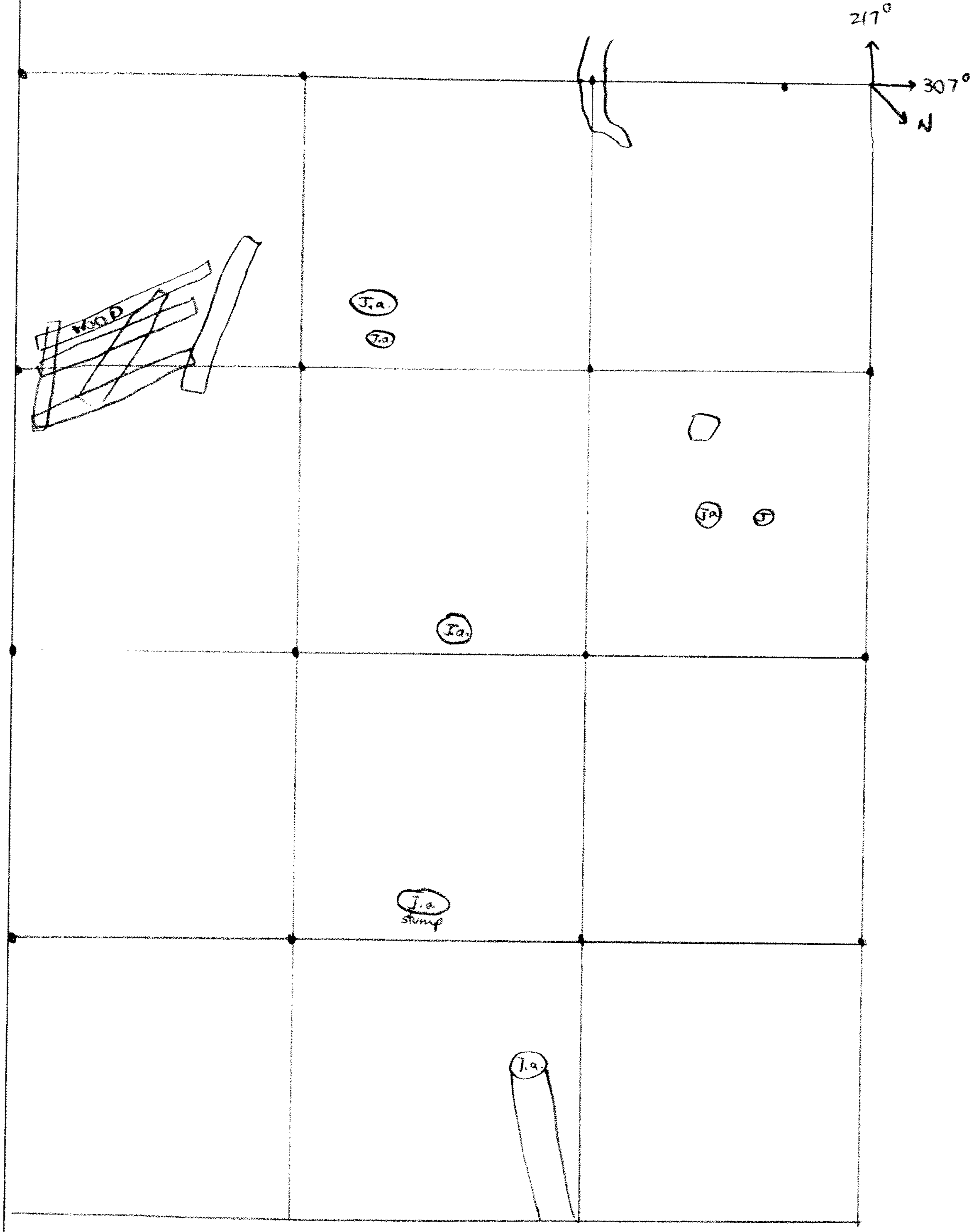
plot key

12	8	4
11	7	3
10	6	2
9	5	1

Survey date
1. 8 Mar 96

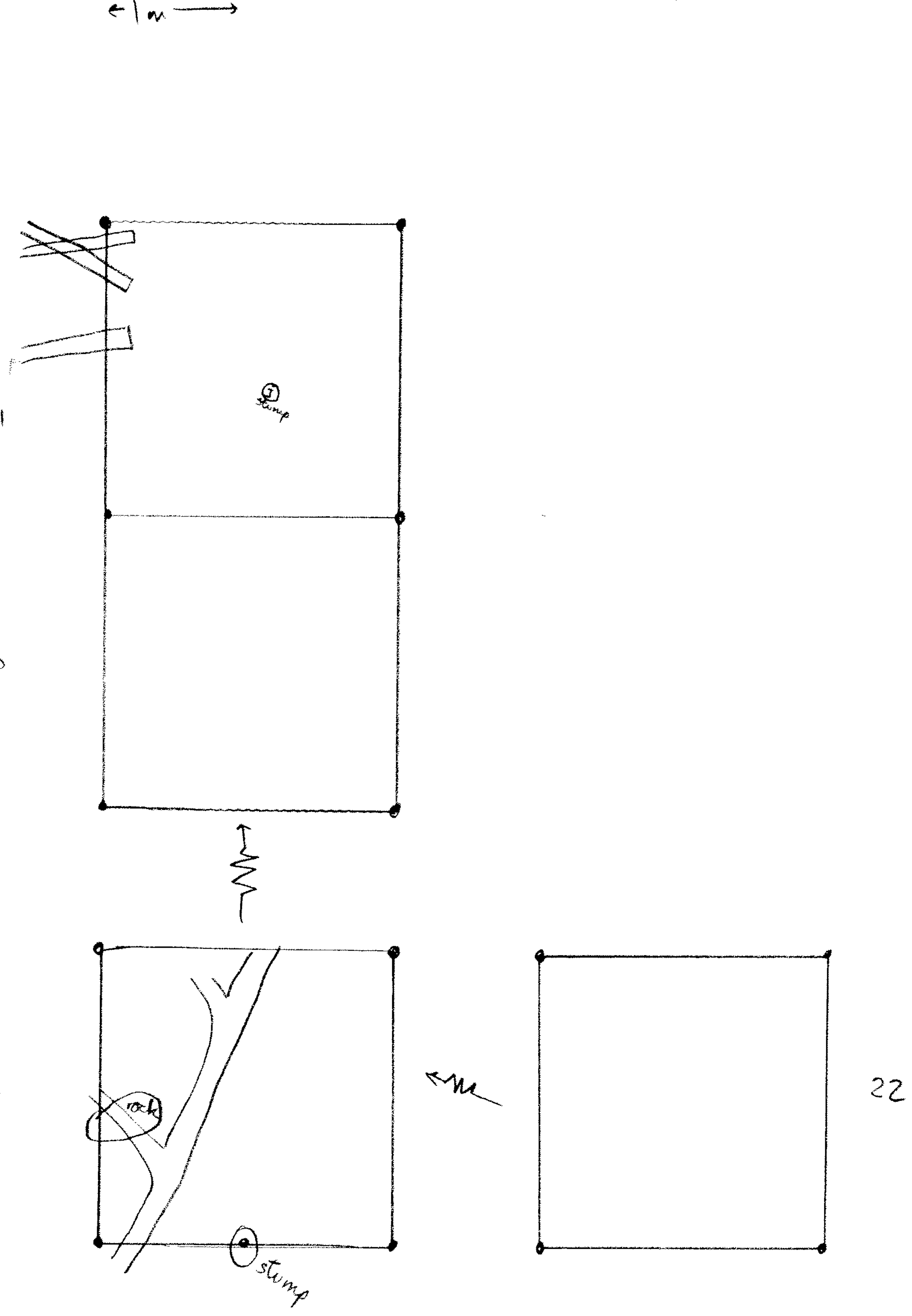
• = stake

← 1m →



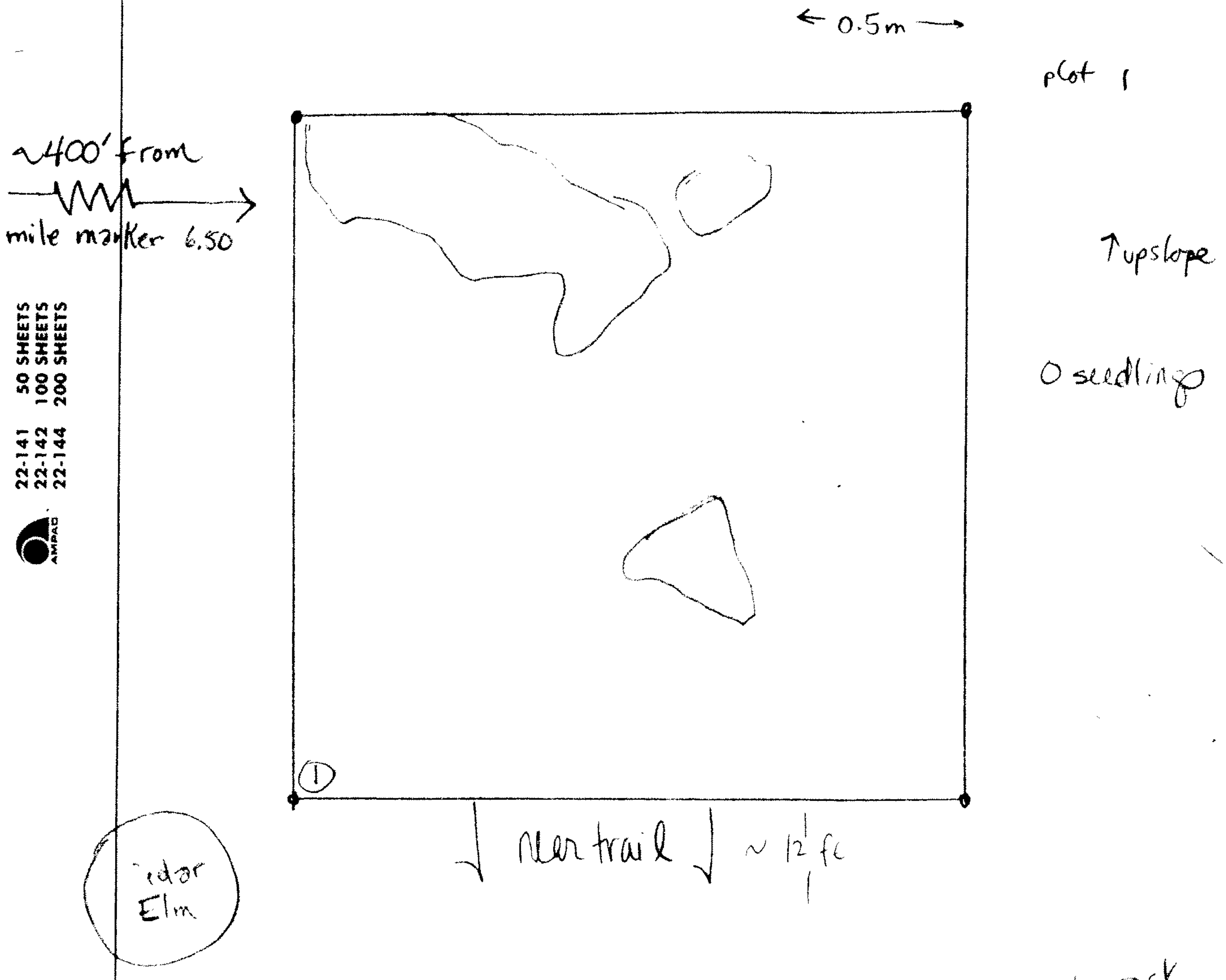
Vallburn Dr. | 1996 | (cont)

Streptanthus bracteatus



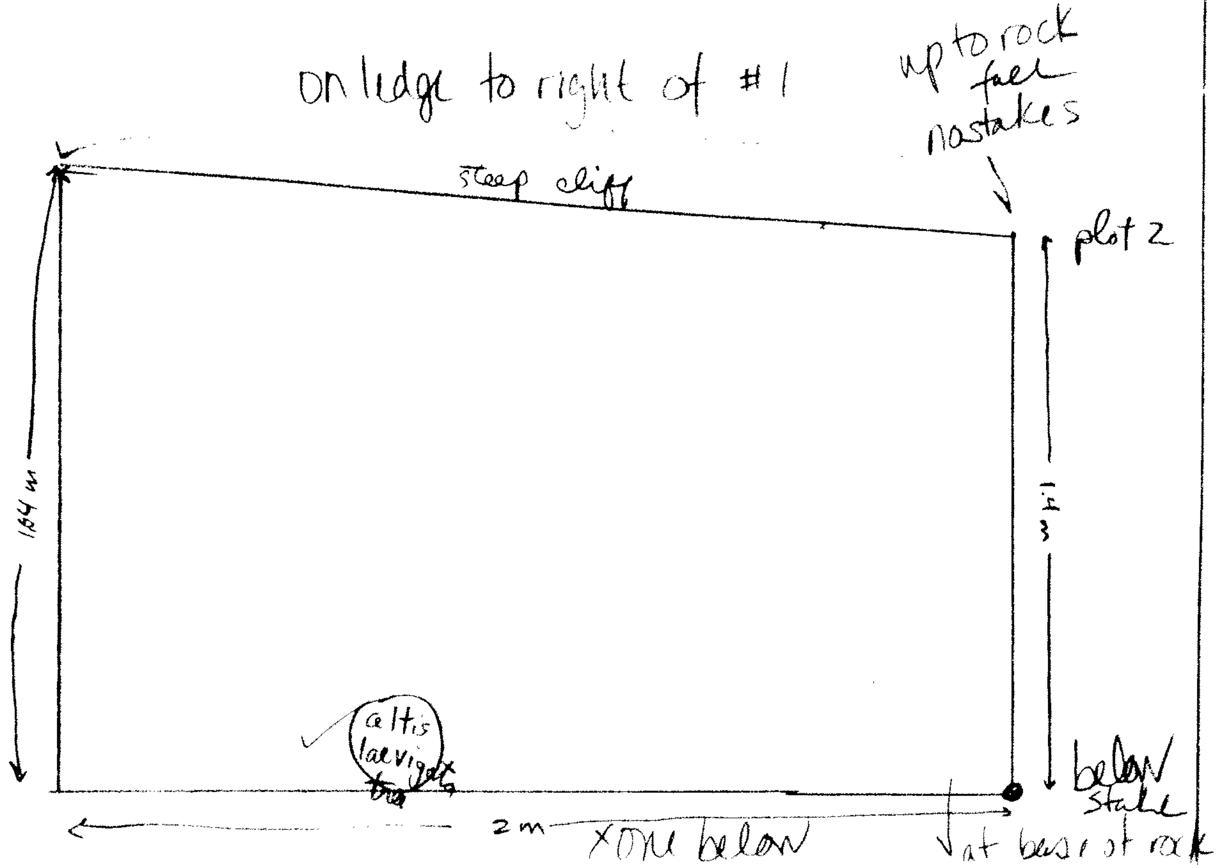
Barton Creek | 1996 Streptanthus | bracteatus

Numbers go downstream



0 seedlings

On ledge to right of #1

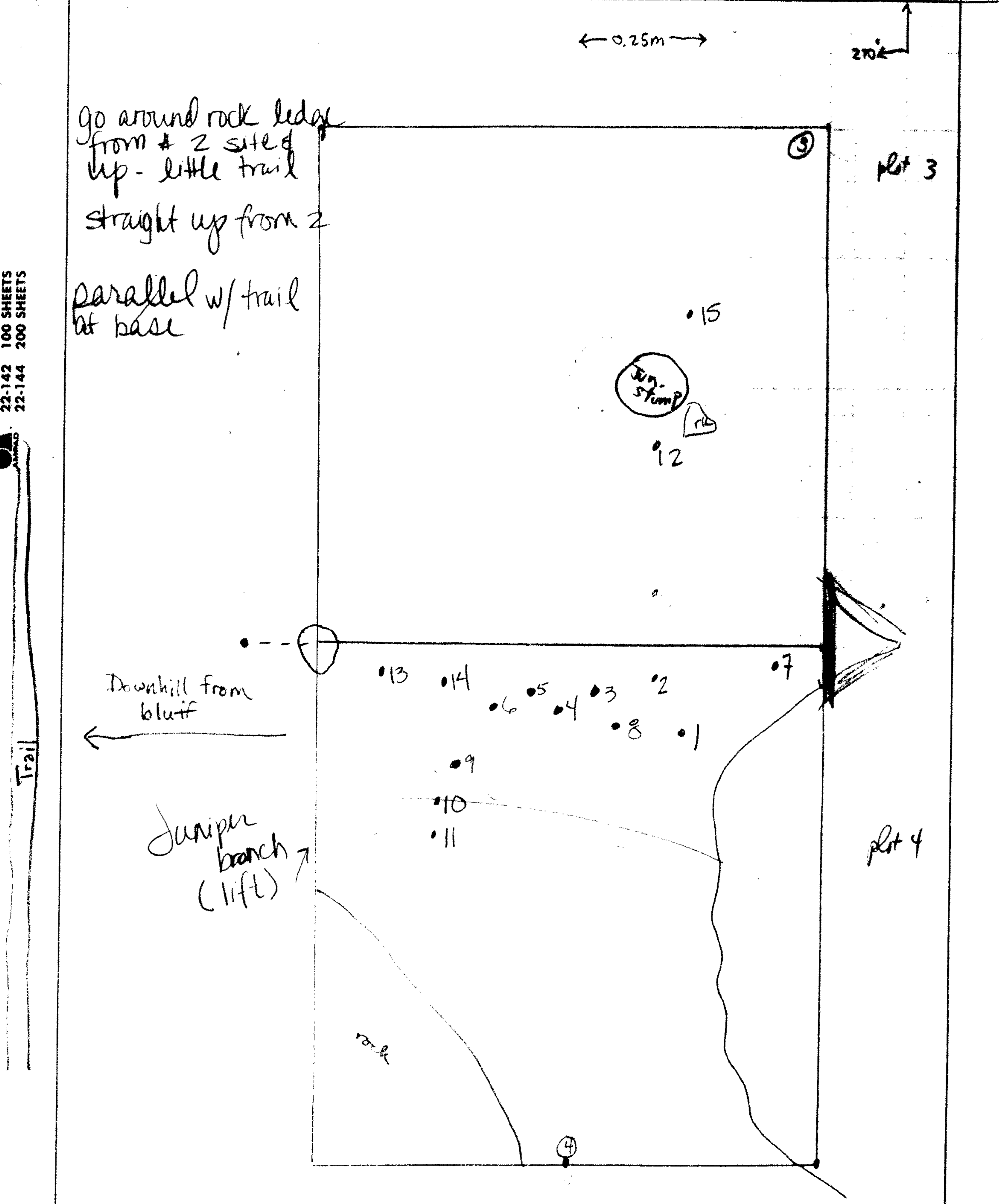


Barton Creek | 1996

go around rock ledge from # 2 site & up - little trail

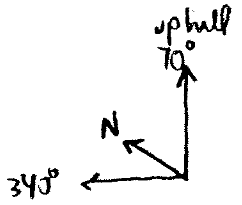
straight up from 2

parallel w/ trail at base



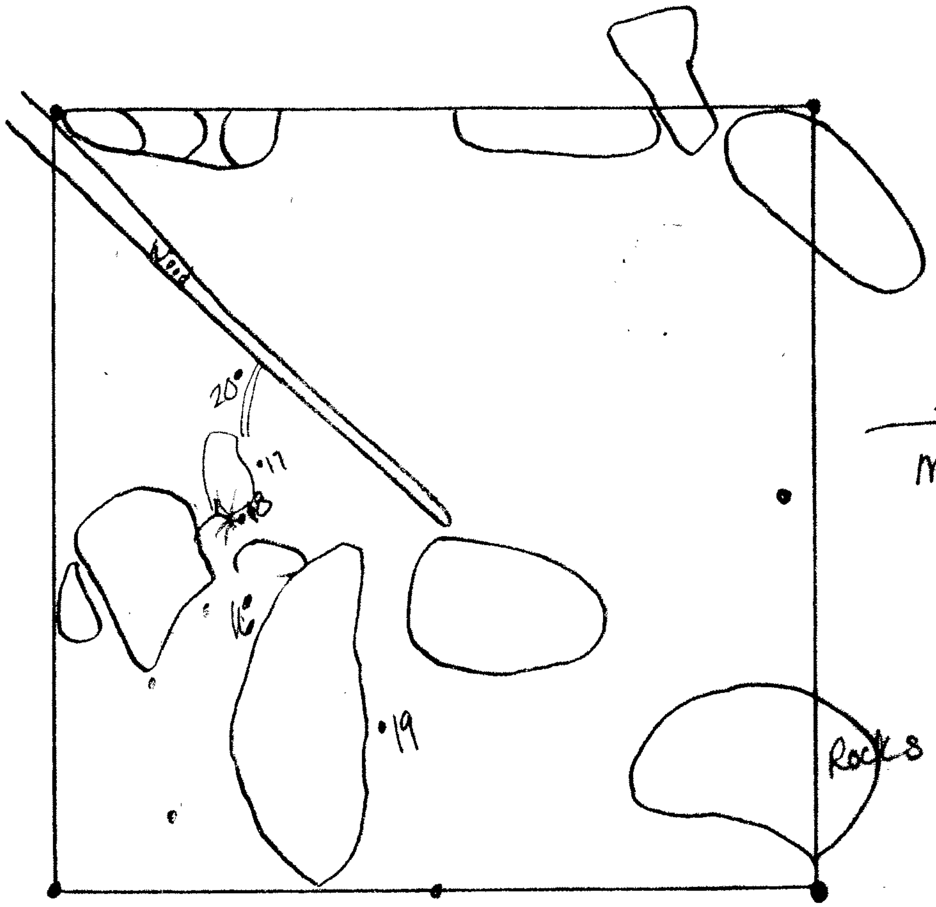
Barton Creek | 1996

to right of upslope from 3/4



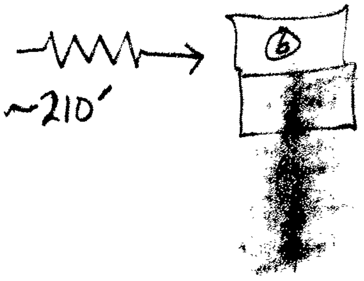
←0.5m→

plot 5

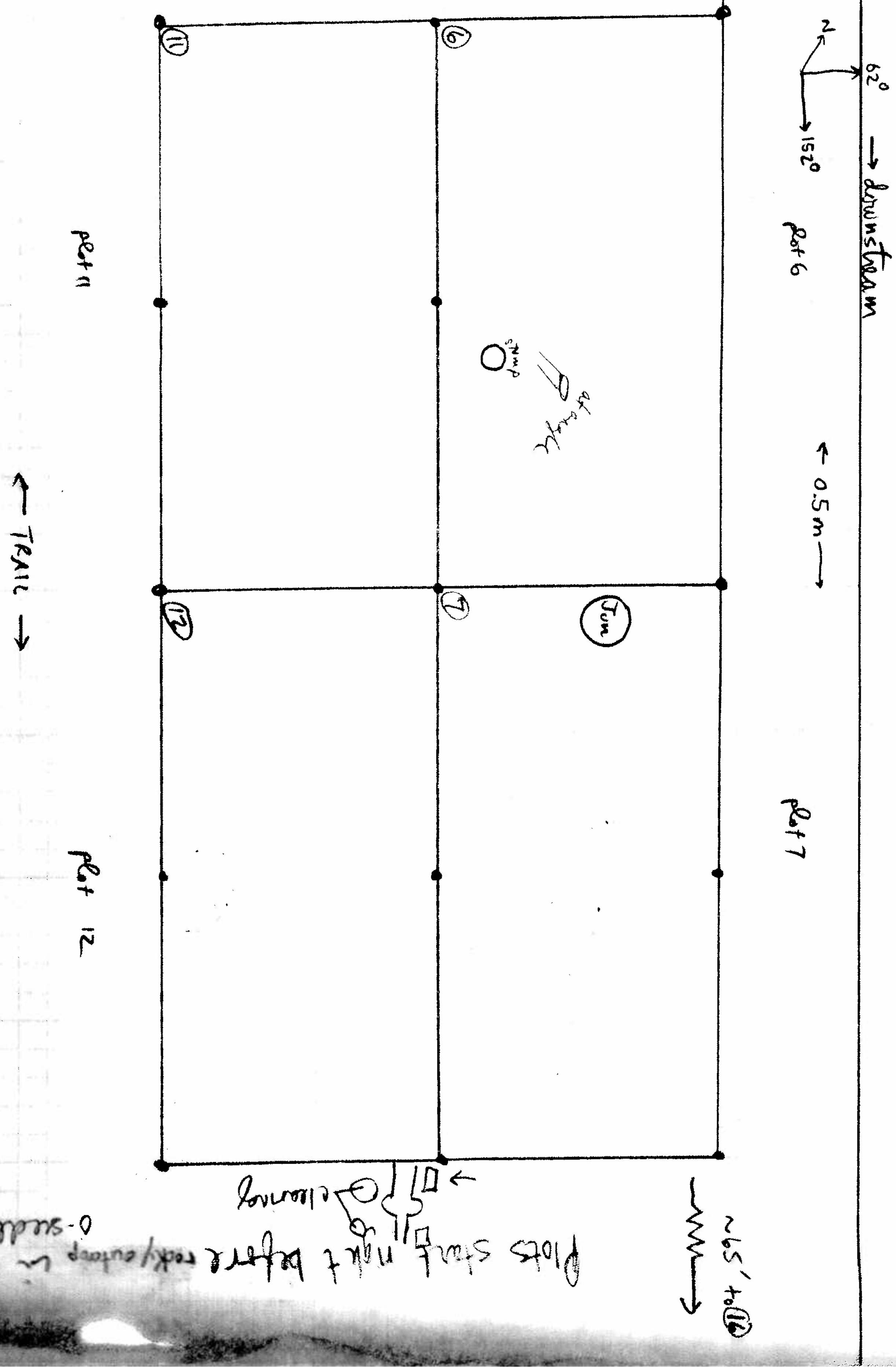


→ many additional plants

go back down to trail & walk downstream to 6



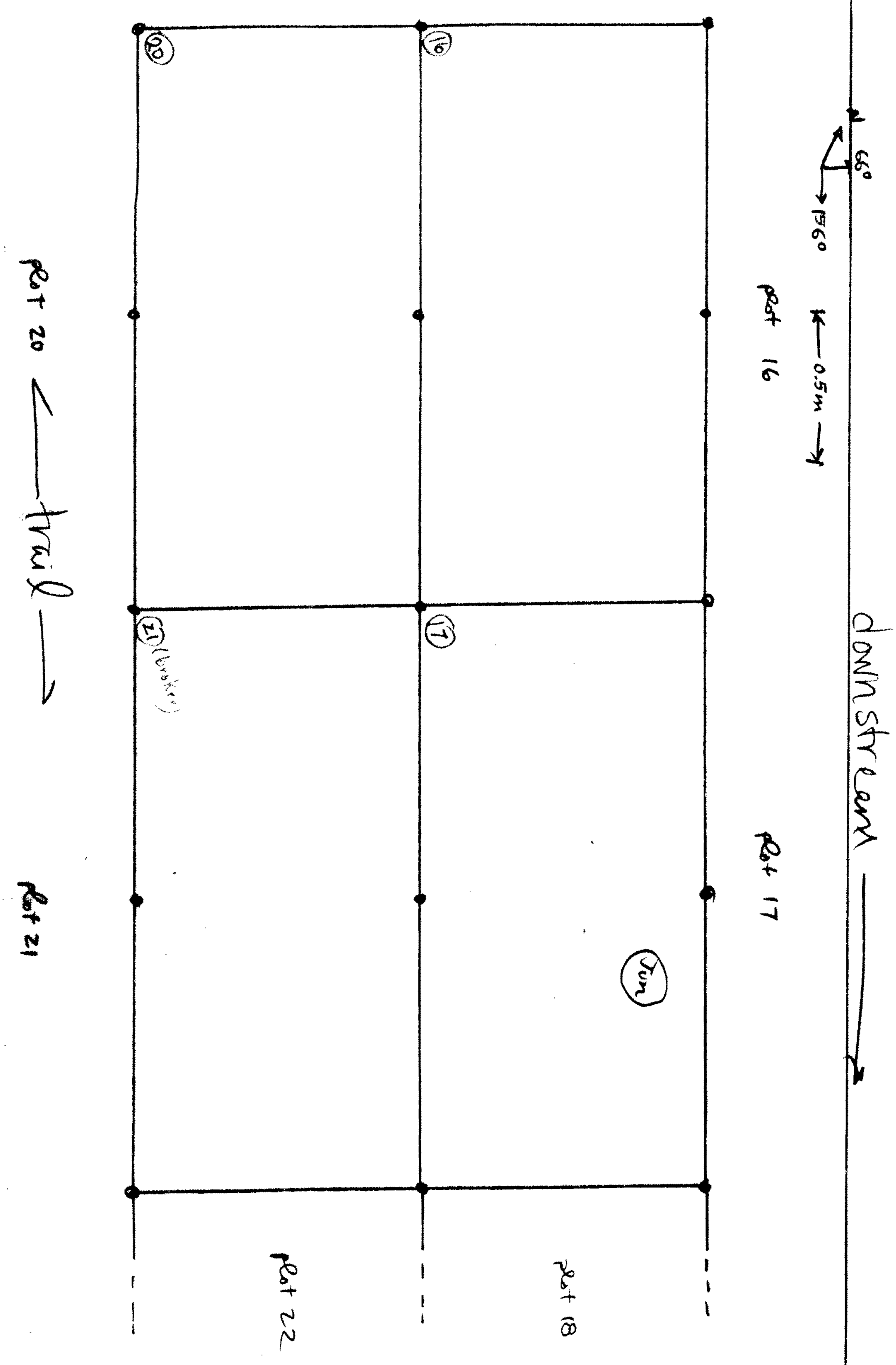
Barton Creek | 1996 | Streptanthus bracteatus



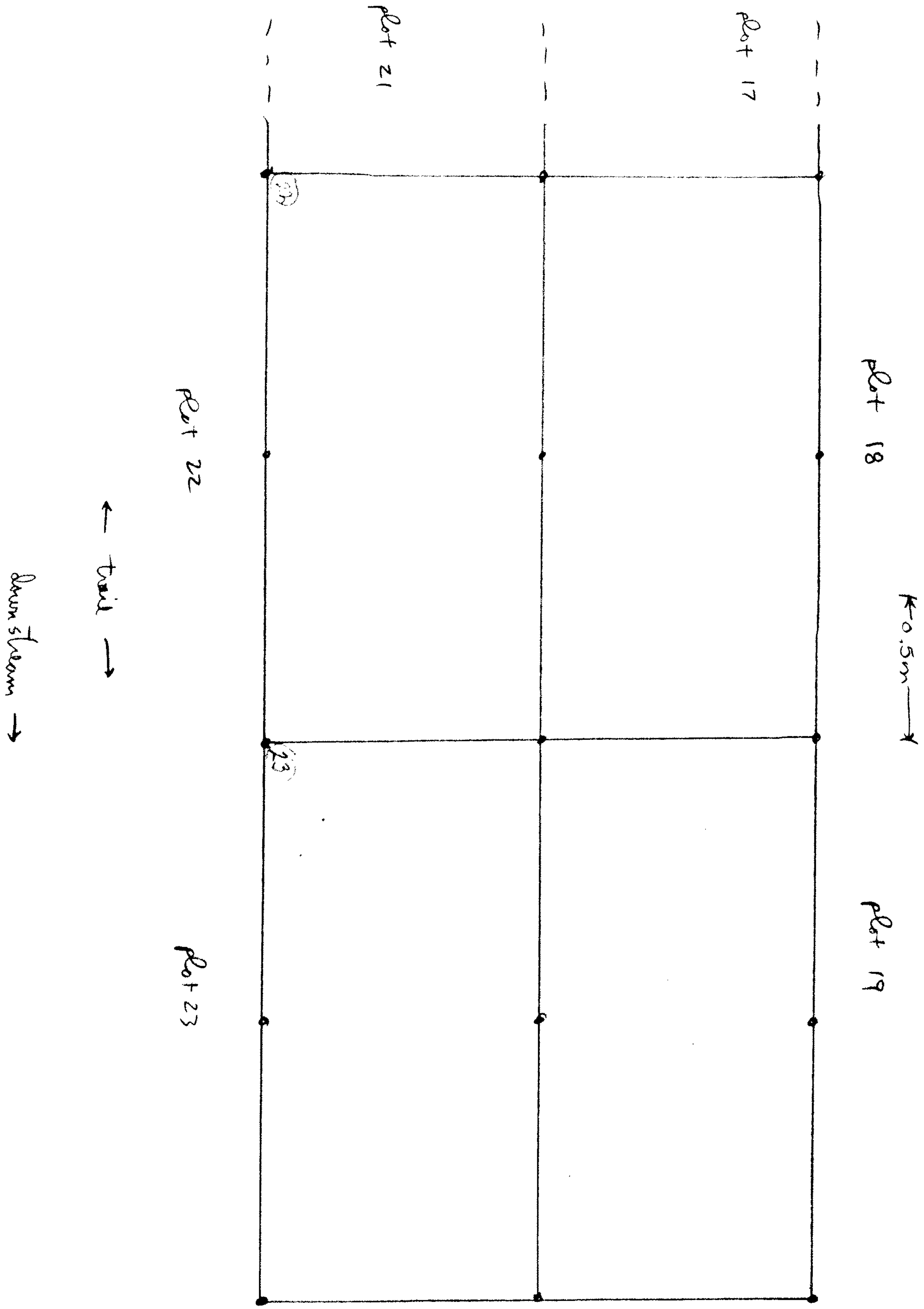
Plots start right before rocky/outcrop in road

0-seedlings found

Barton Creek	1996	Streptanthus bracteatus

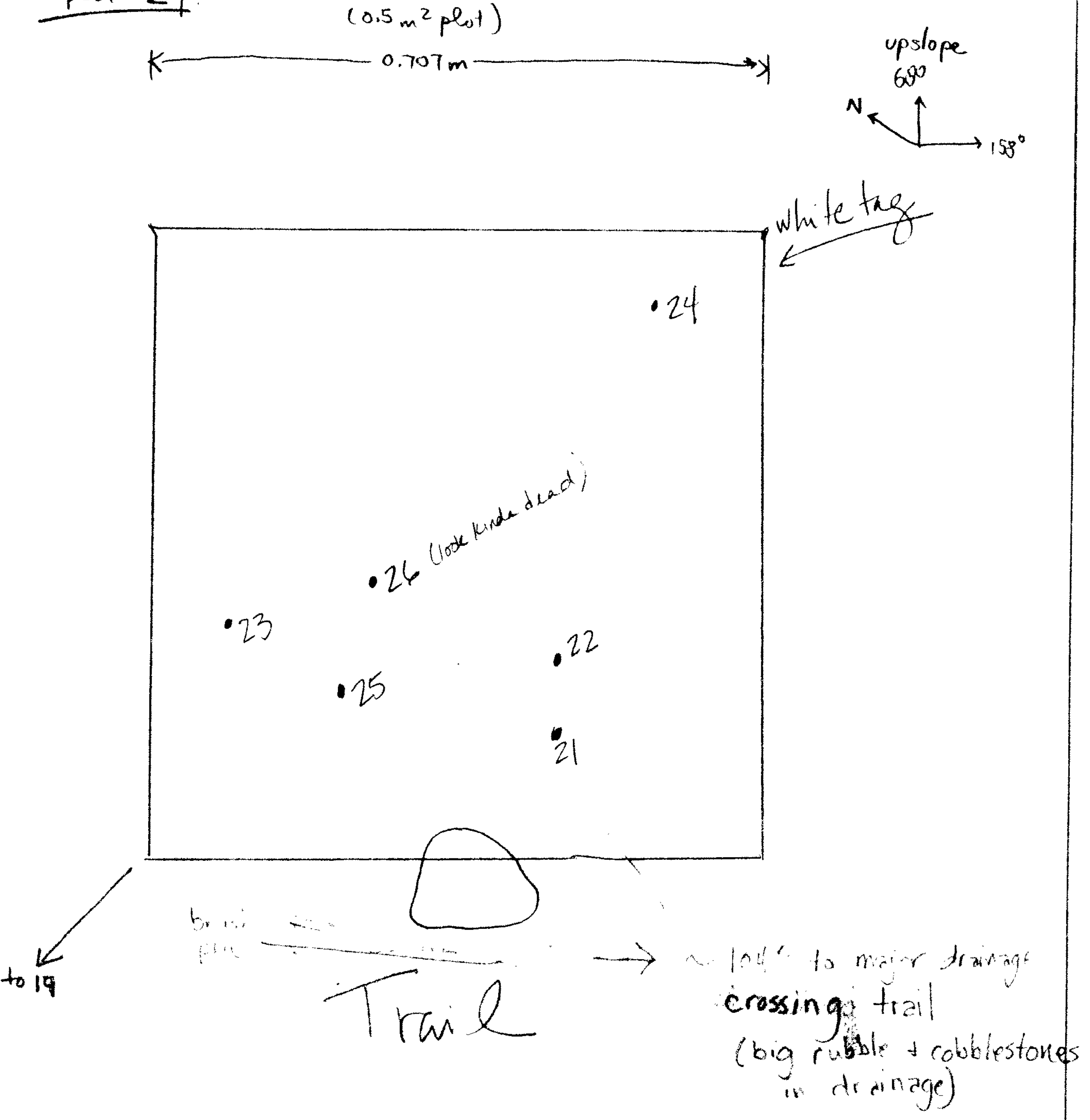


Barton Creek | 1996 | Streptanthus bracteatus



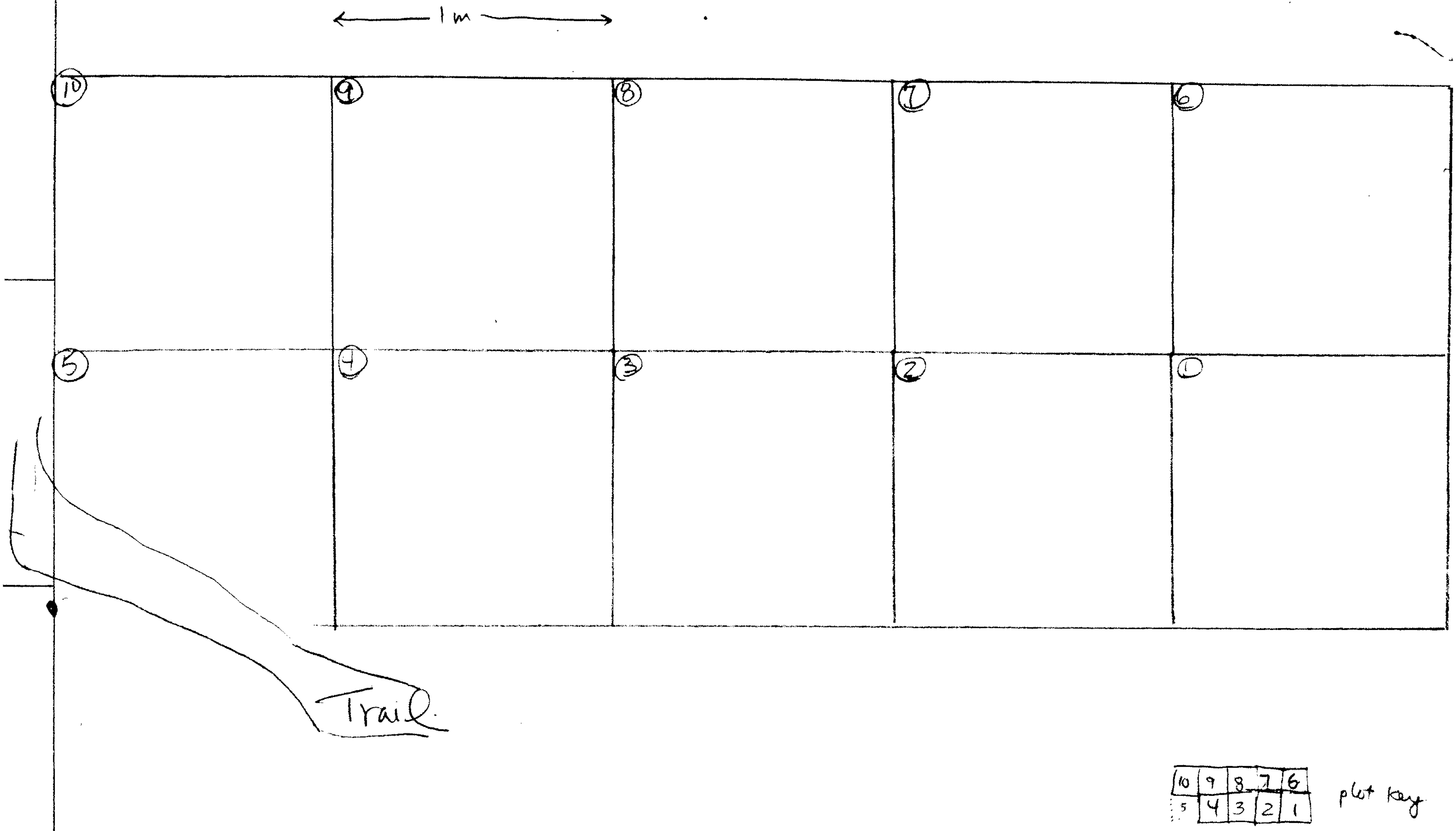
Barton Creek	1996	Streptanthus bracteatus

plot 24

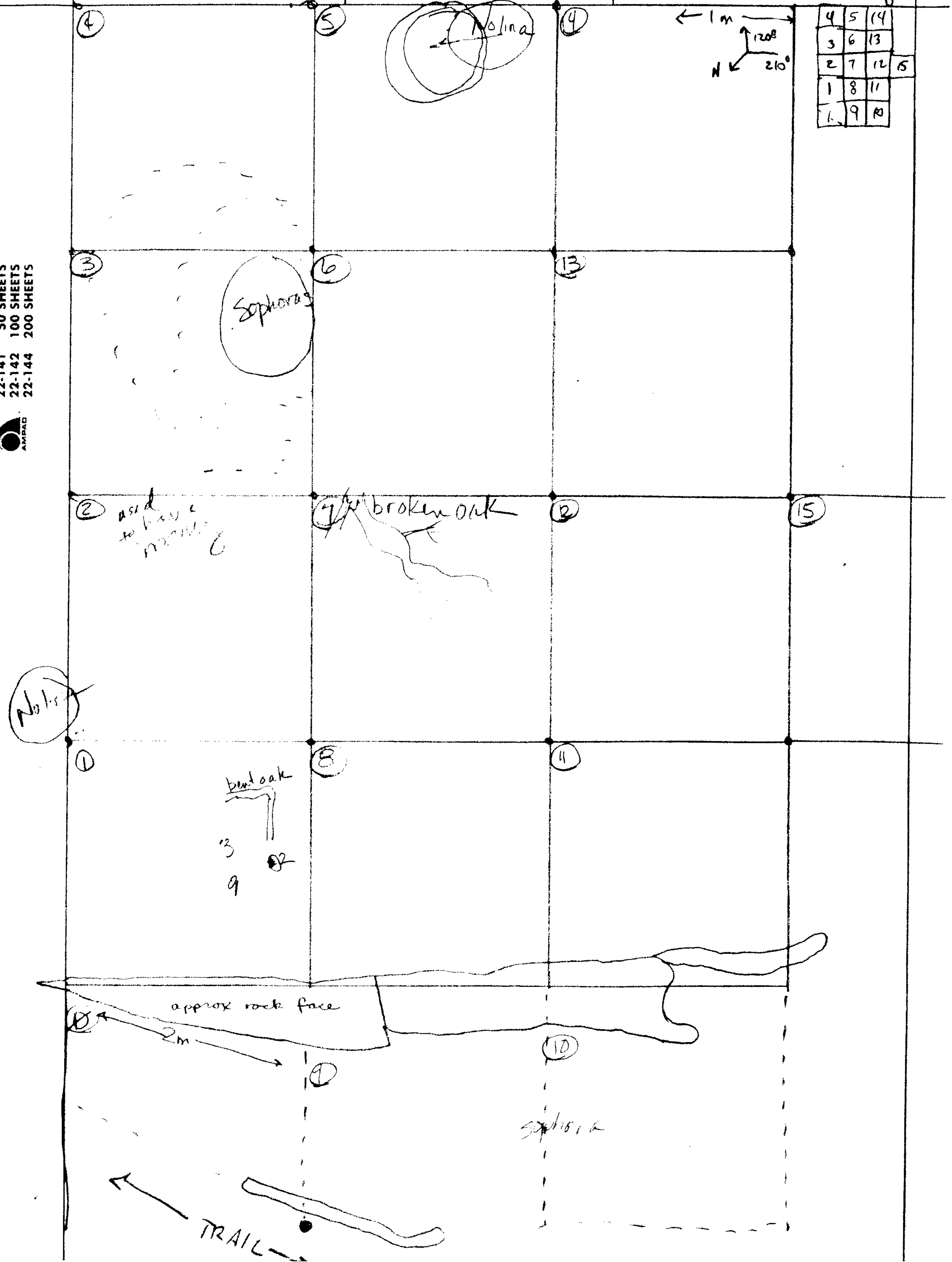


~104° to major drainage crossing trail (big rubble + cobblestones in drainage)

Mt. Bonnell Streptanthus bracteatus 1996 - none found



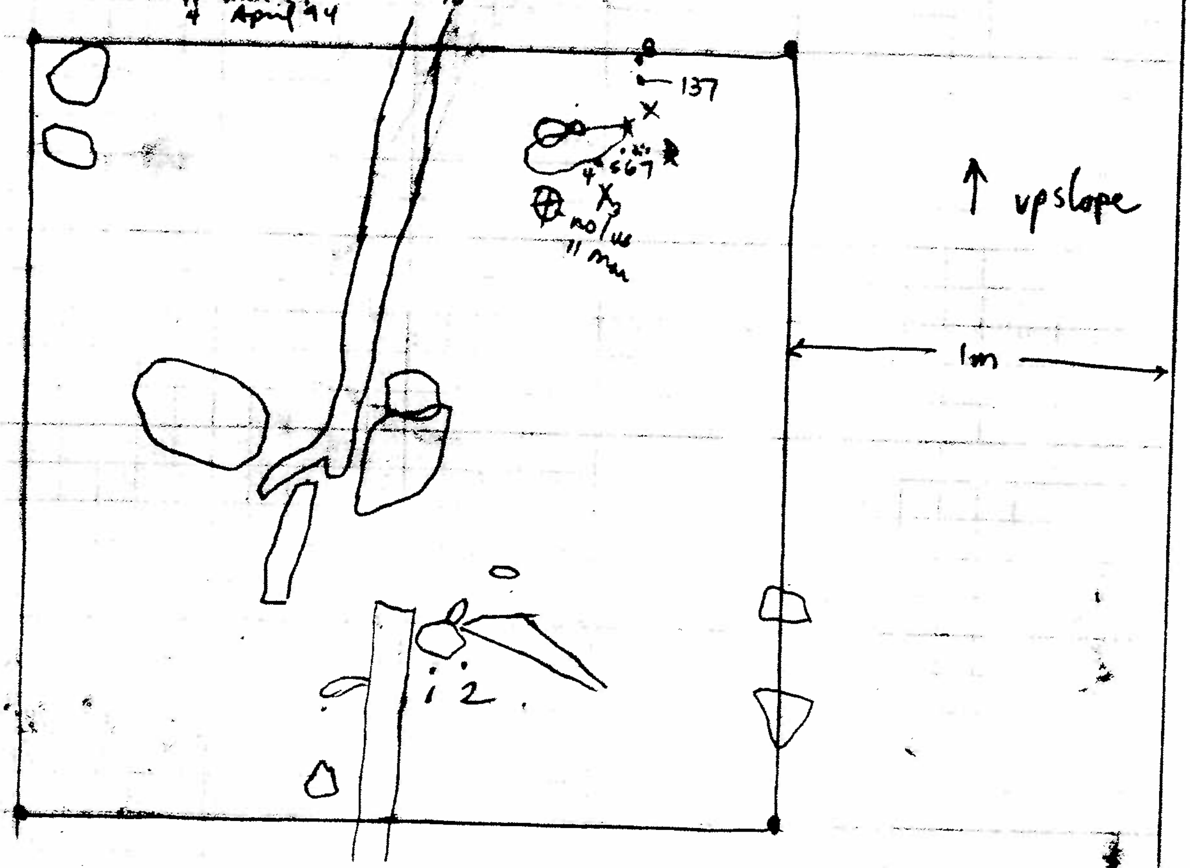
Bee Creek, Travis Co. 1996 Streptanthus bracteatus



Streptanthus bracteatus Census Maps 1993 - 1994 Barton Creek

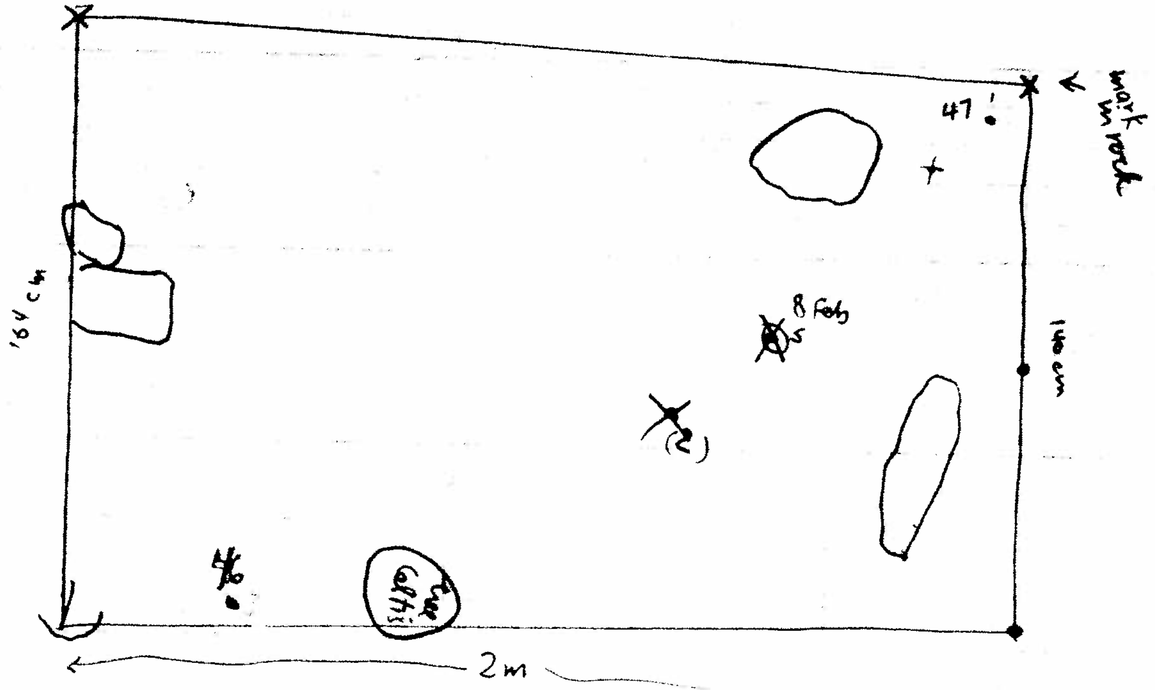
MAP 2A
plot 1

SURVEY DATE	#	color	season
22 NOV	13	w-bw	
29 Dec	4	–	
8 Feb 94	10	–	
11 Mar 94	10		
4 April 94			



MAP 2A
Plot 2

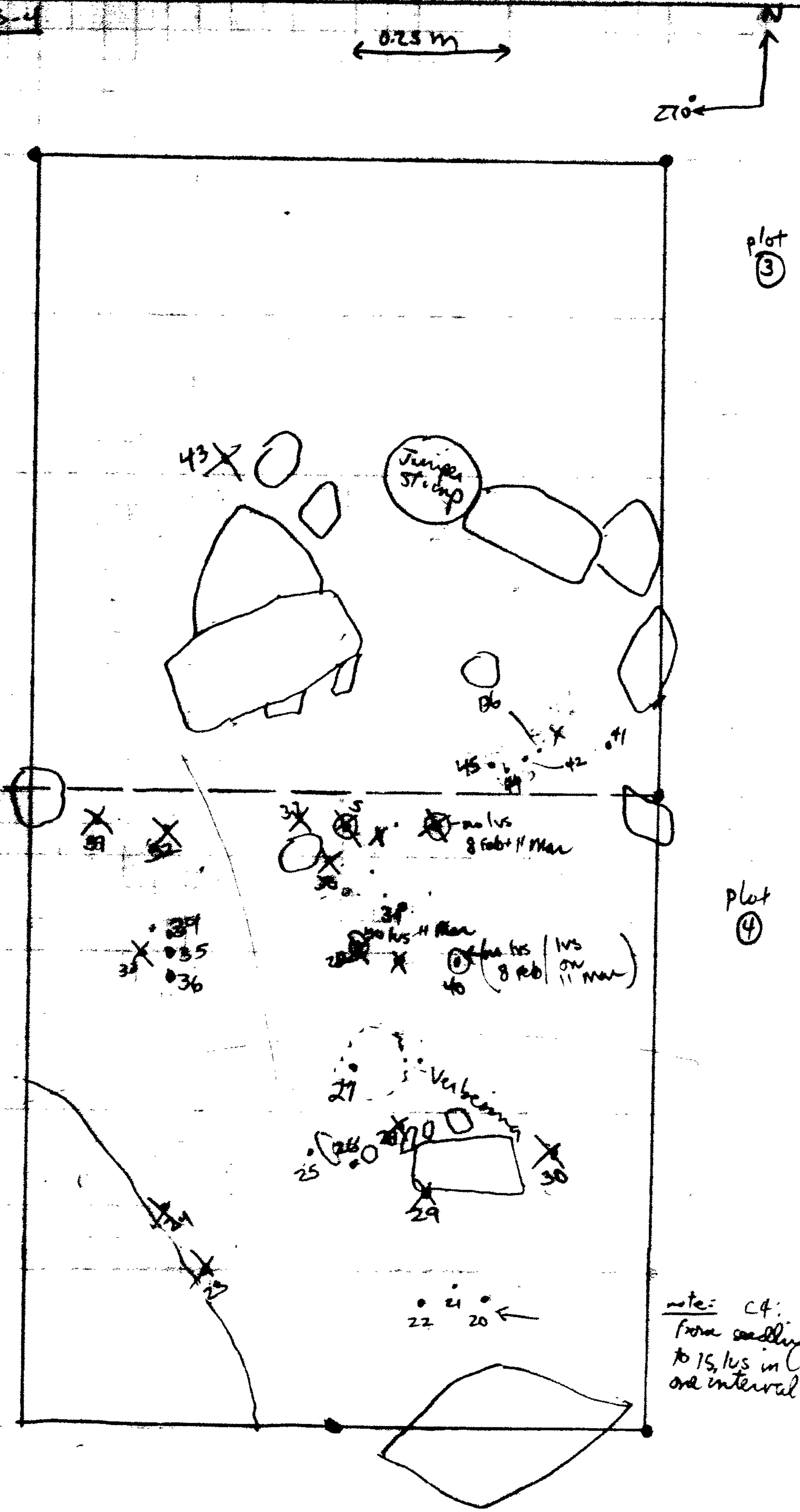
census date	#	color
22 NOV,	3	w-bw
29 Dec	2	–
8 Feb 94	4	blv-w



BARTON CREEK FLOODPLAIN

MAP 2B PLOT 3-4

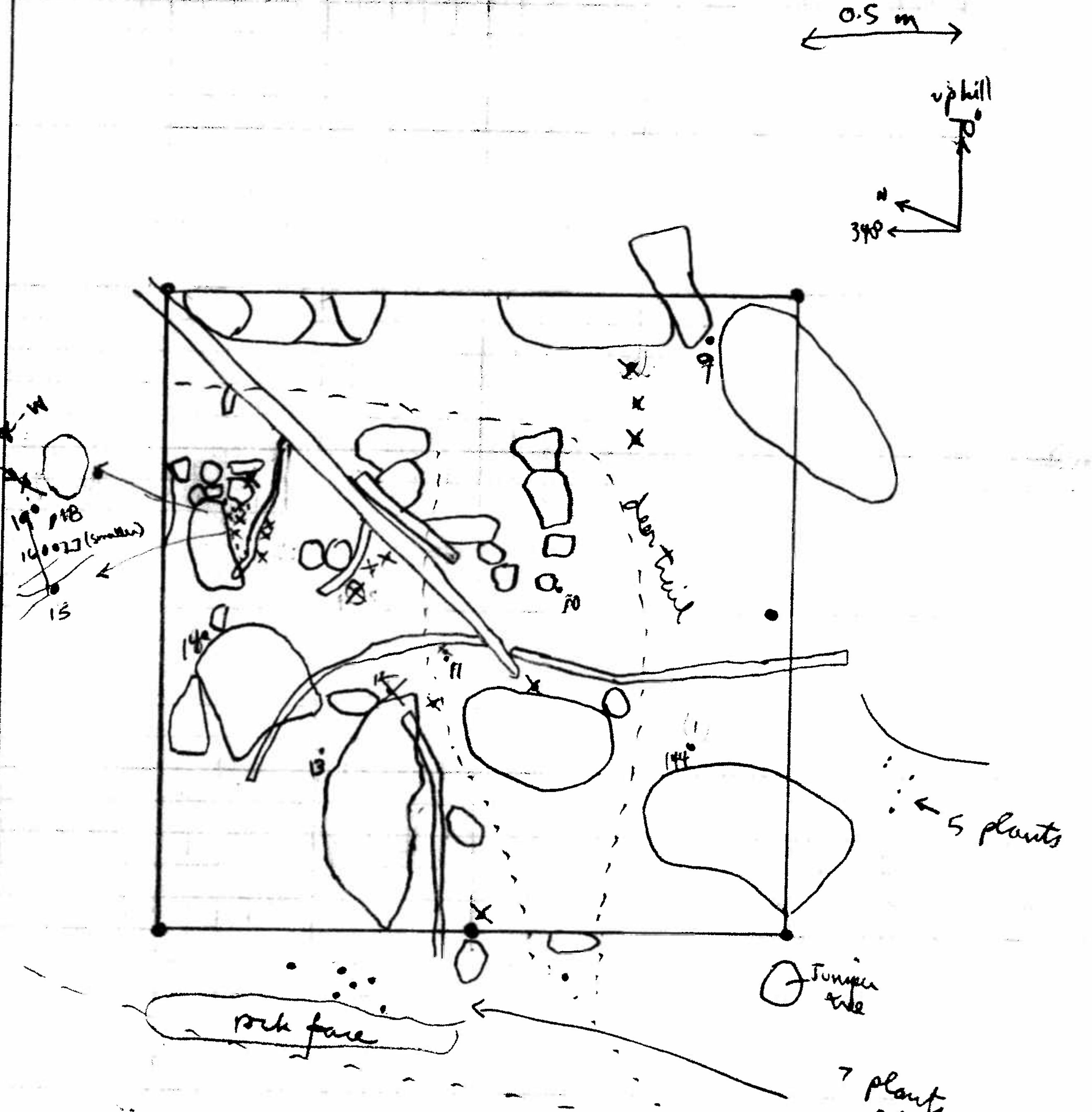
census date	#	color
22 Nov 93	6	W-g
29 Dec 93	6	–
8 Feb 94	5	–



note: C4: from seedling to 15 lvs in one interval ?!

census date	#	color
22 Nov 93	25	W-g
29 Dec 93	26	–
8 Feb 94	26	–

Barton Creek Flood | Map 2C | plt. 5

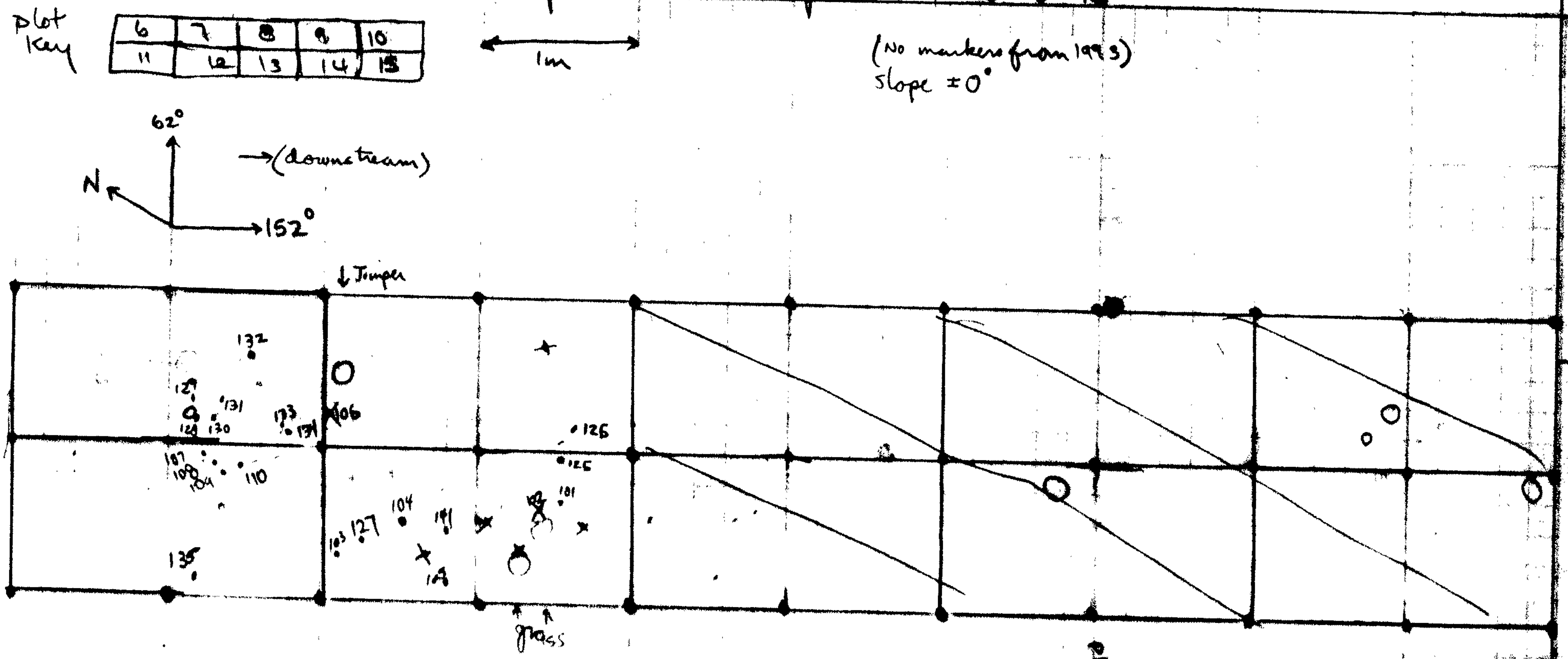


census date	#	wire color
22 NOV 93	28	w-green
29 Dec 93	18	O-W
8 Feb 94	15	blu-w
	14	
4 Apr 94	12	

4 april: *deer trail + tracks (- - - -)
clear within trail
Teroorm potential.

Barton Creek Floodplain Map 3A plots 6-15

(No markers from 1993)
slope ±0°

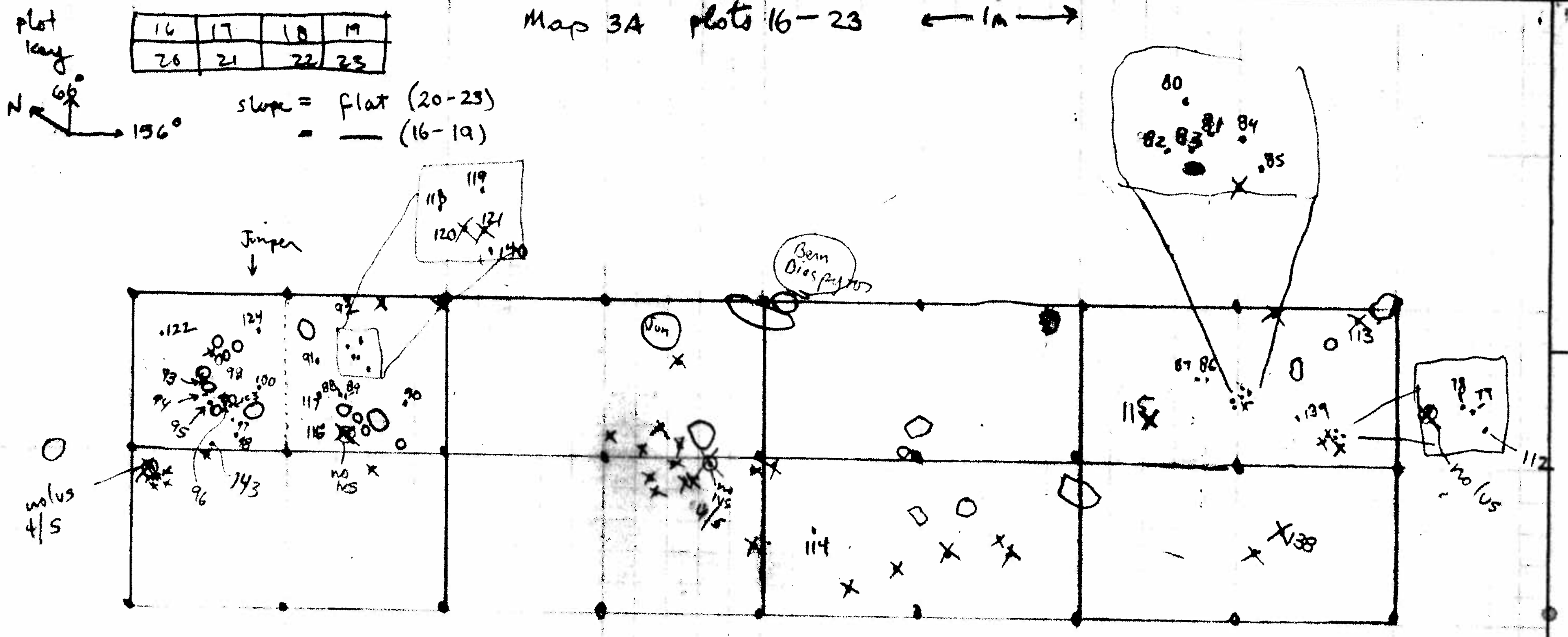


plot	22 NOV 93 (w-blu)	29 Dec 93 (O-W)	8 Feb 94 (blu-W)
6	1	3	5
7	1	0	-
8	0	0	-
9	0	0	-
10	0	0	-
11	3	3	4
12	7	10	8
13	0	0	-
14	0	0	-
15	0	0	-
TOTAL	12	16	

← TRAIL →

Barton Creek Floodplain

Map 3A plots 16 – 23



← trail →

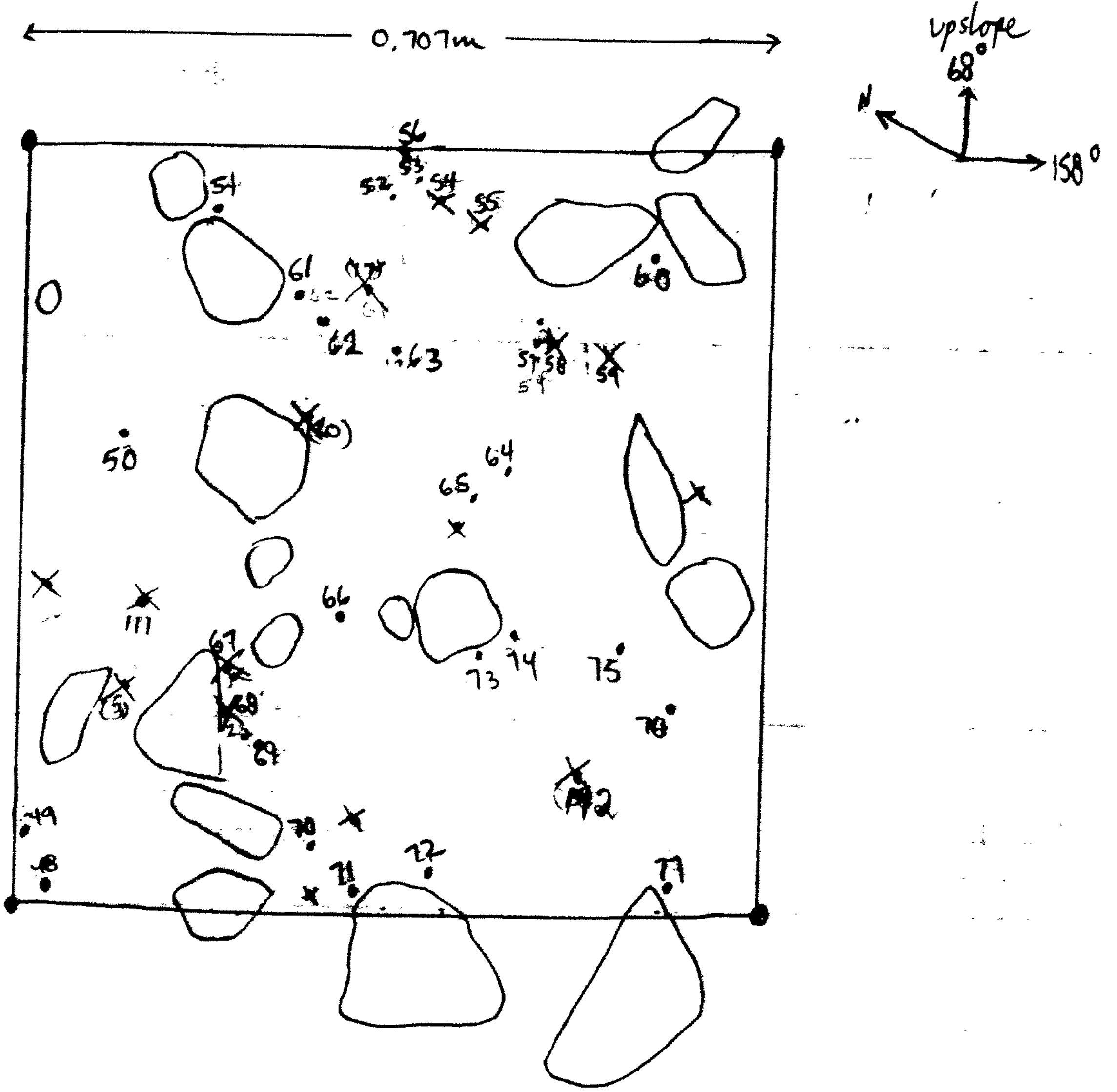
← river → downstream

plot	22 NOV (w-blu/*o-w)	29 DEC (w-g)	8 Feb (blu-w)
16	22	28	25
17	4	*4	3
18	1	1	0
19	15	17	17
20	8	5	5
21	6	8	9
22	4	3	3
23	2	1	1
TOTAL	62	62	63

census date + wire color

Barton Creek Floodplain

Map. 3C plot 24 (0.5m²)

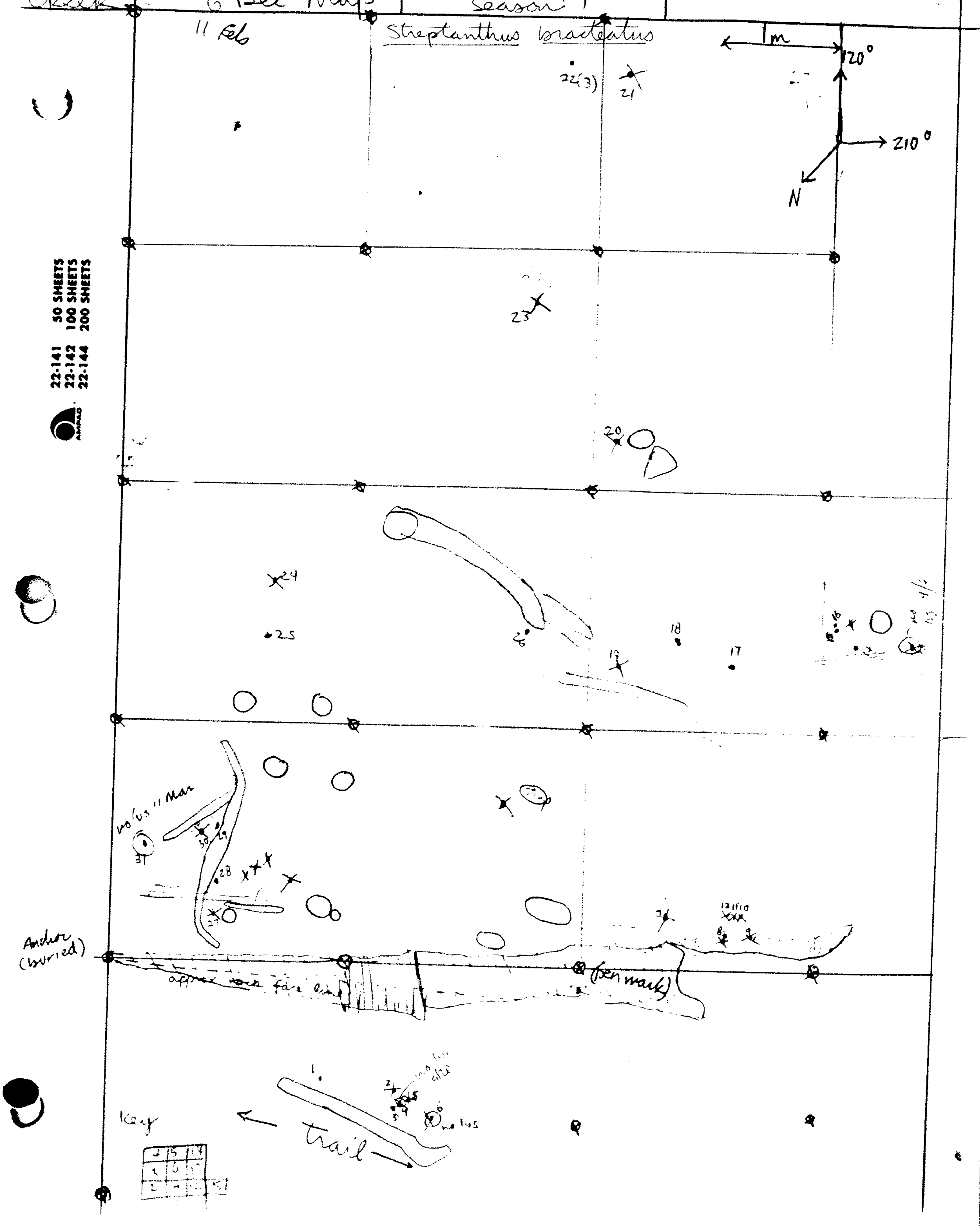


census date	#	wire color
23 NOV 93	37	o-w
29 Dec 93	37	w-g
8 Feb 94	35	–
11 Mar 94	35	–
4 April 94	35	gr-W

Bee Creek | 5 Jan Map 6 Bee Map | 1993-94 Season | Bee Creek

11 Feb

Streptanthus bracteatus



Walburn Dr. | 1993-94 MAP | Streptanthus bracteatus

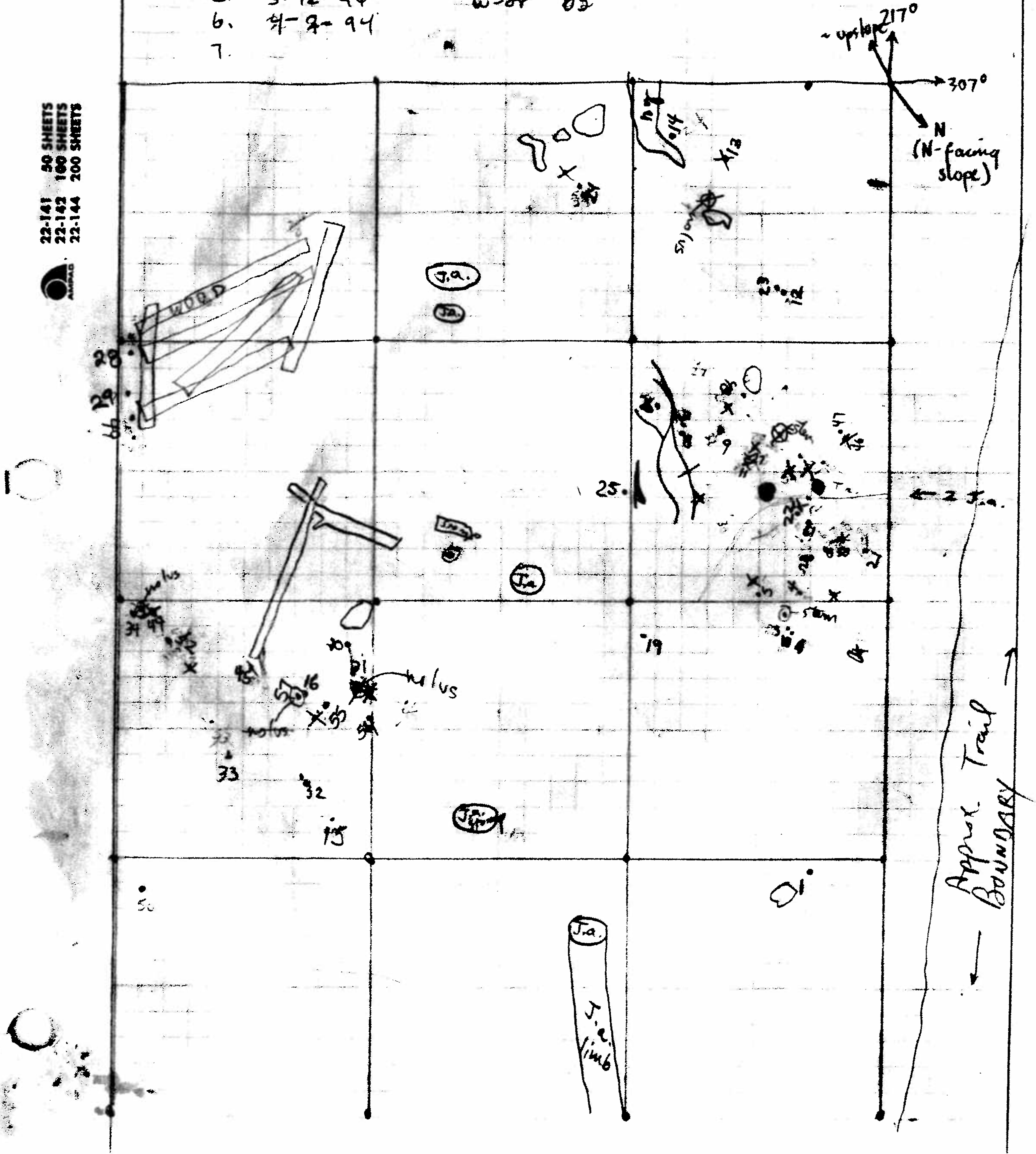
Plot key

12	8	4
11	7	3
10	6	2
9	5	1

	CENSUS DATES	WIRE COLOUR	#
1.	11-15-93	O-W	155 (#1-94)
2.	12-13-93	w-gr	55
3.	1-15-94	W-blu	57
4. ●	2-12-94	blu-w	66
5.	3-12-94	w-or	85
6.	4-9-94		
7.			

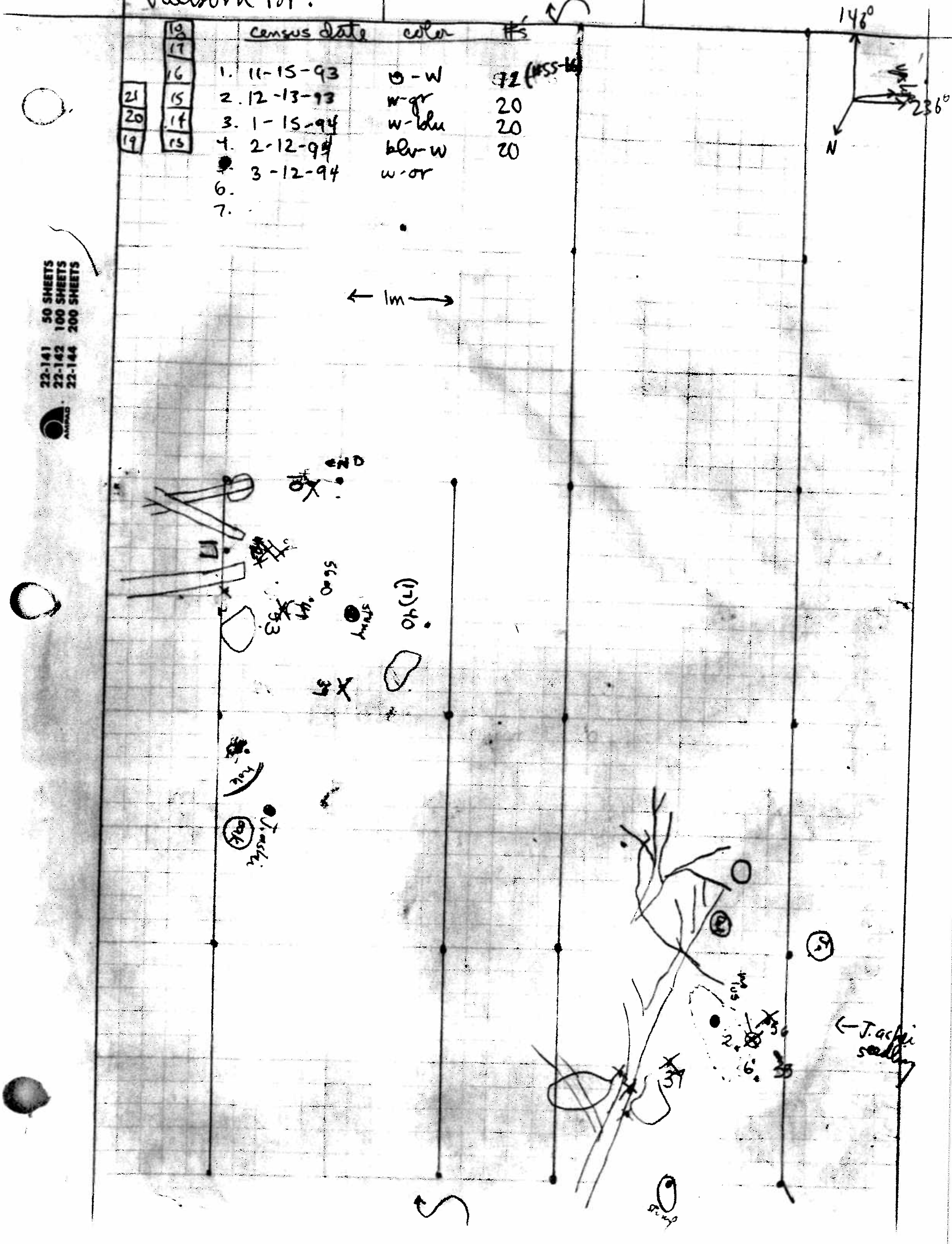
O = seedling

← 1m →



Vallourn for.

census date		color	#'s
1.	11-15-93	o-w	72 (#55-16
2.	12-13-93	w-gr	20
3.	1-15-94	w-blu	20
4.	2-12-94	blu-w	20
5.	3-12-94	w-or	
6.			
7.			

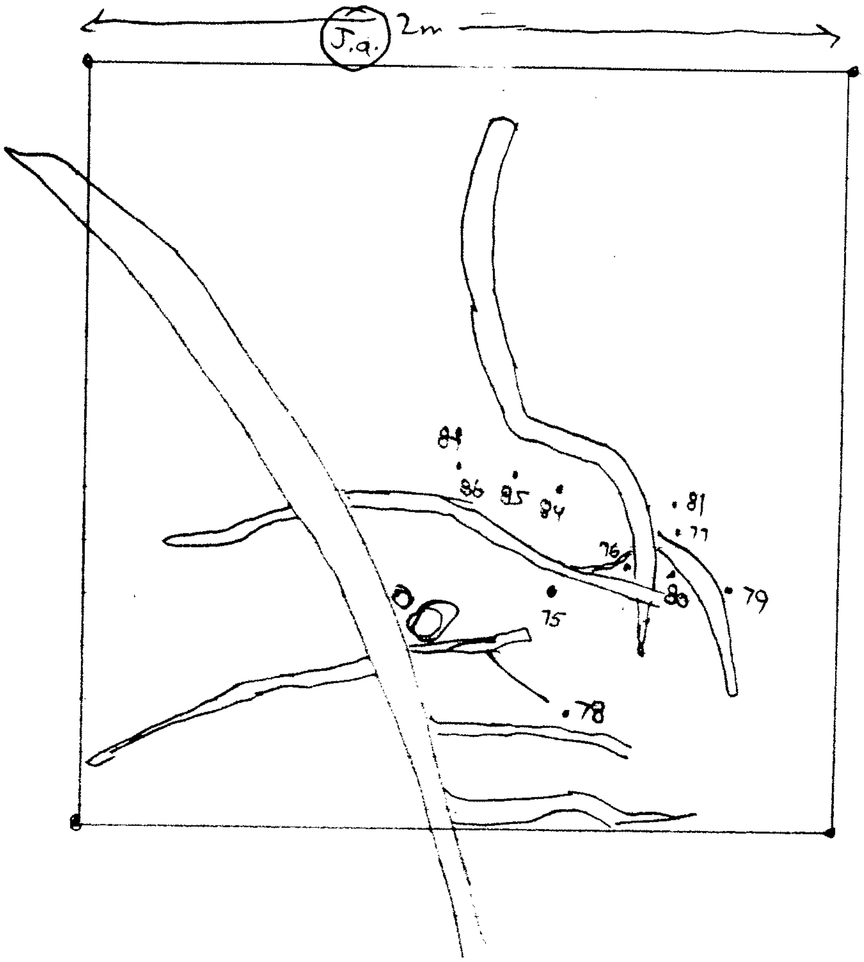


10 oct 94

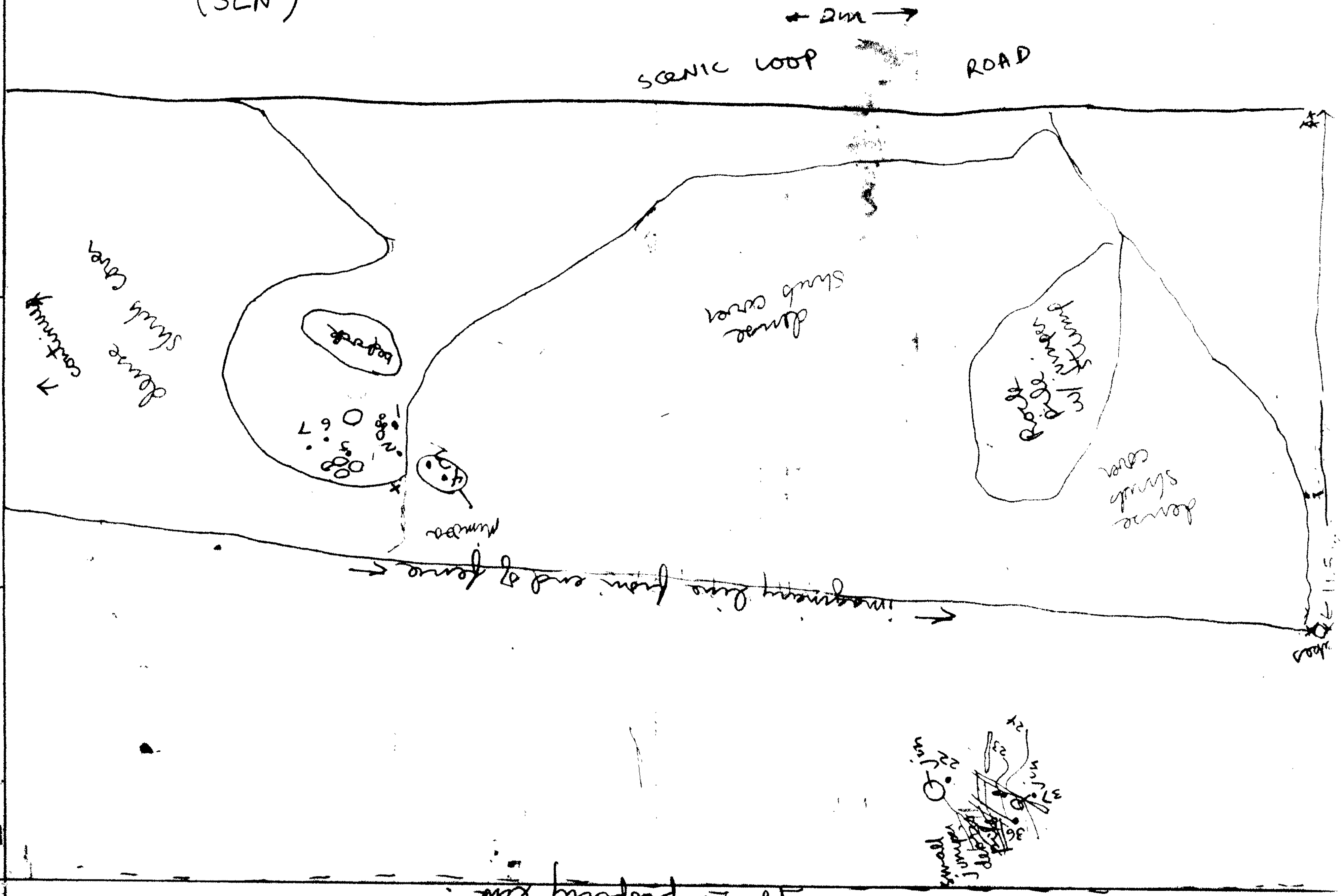
10 Oct 94

Valburn Dr. 1994 adult plant locations # 75 - 86

<u>plot 22</u>



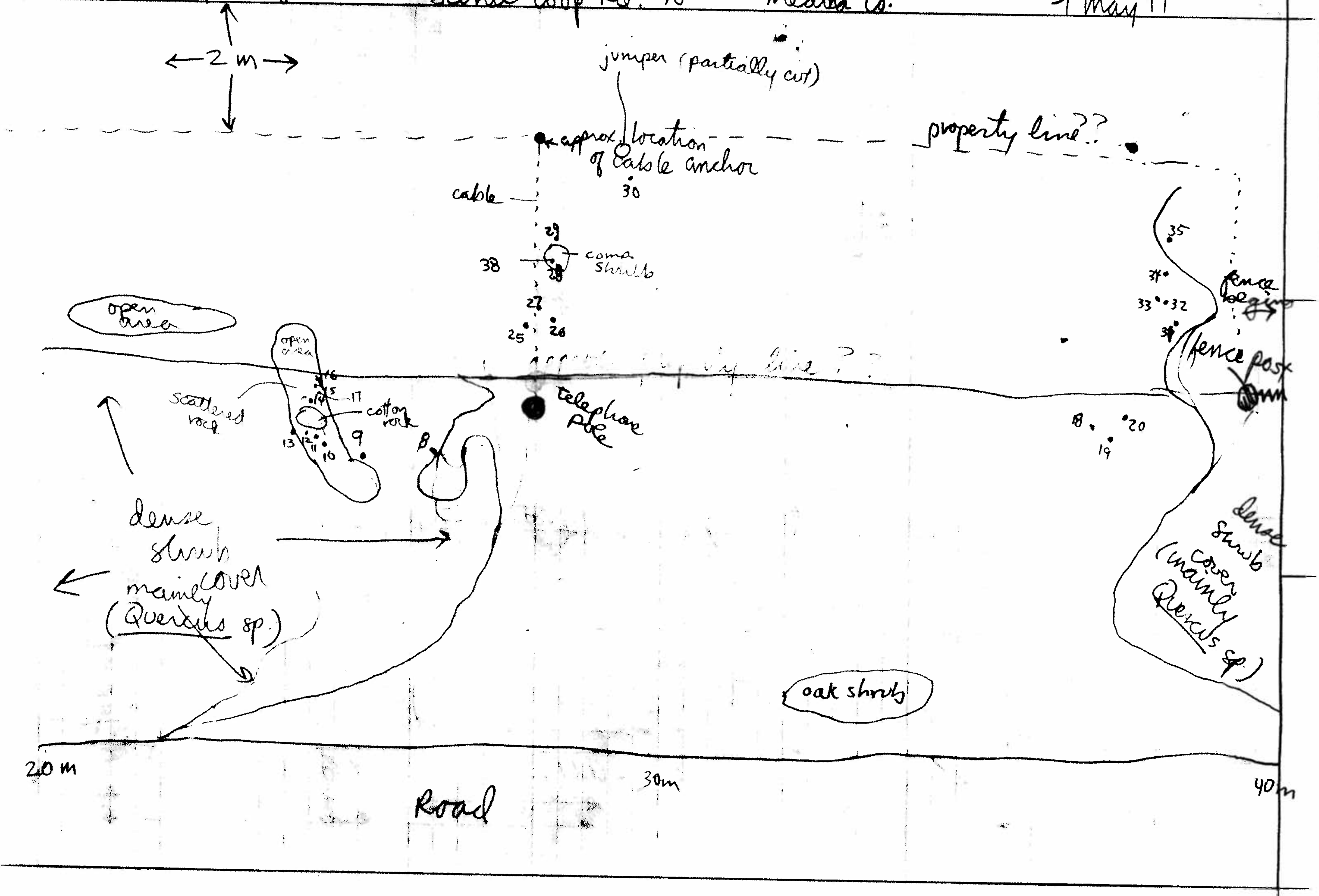
Scenic Loop North pop'n   Medina Co.   7 May 94   p. 1 of 2
("SLN")



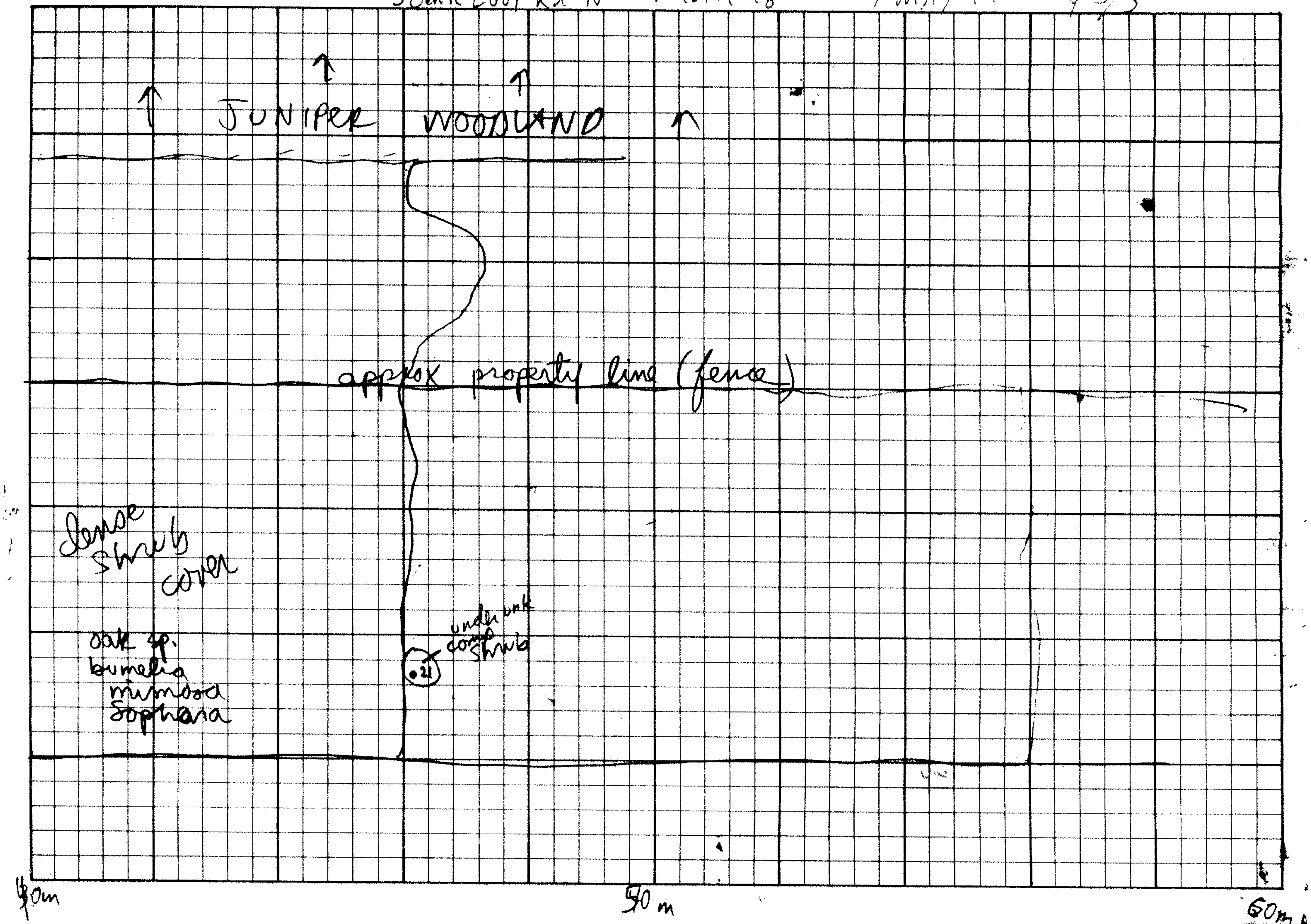
X = stake

(over for page 3)

P. 2 of 3 Scenic Loop Rd. N Medina Co. 7 May 94



Scenic Loop Rd N   Medina Co   7 MAY 94   p 3/3

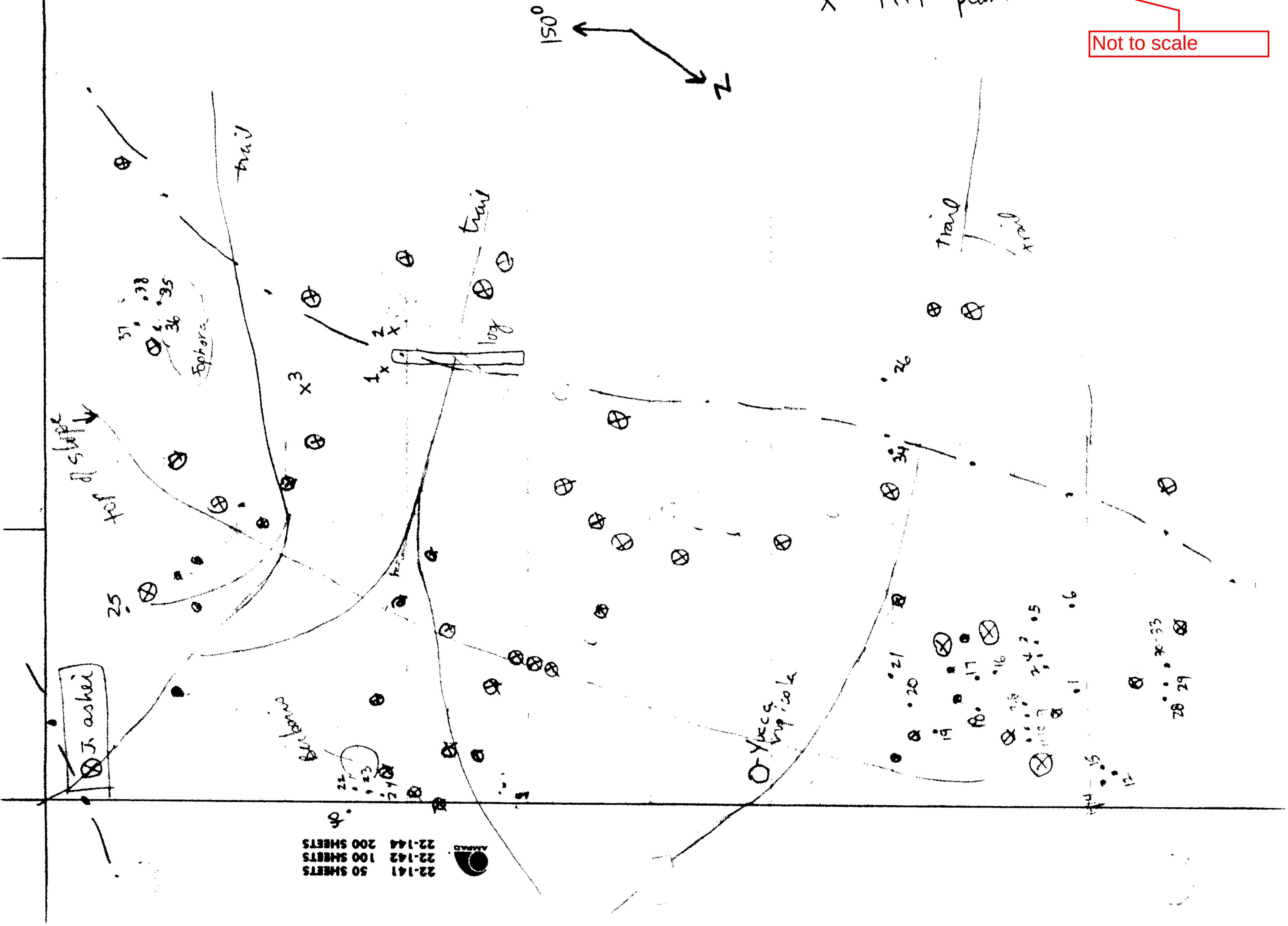


o = TAG MAPPED 4-29-93 APPROXIMATE LOCATIONS - NOT TO SCALE

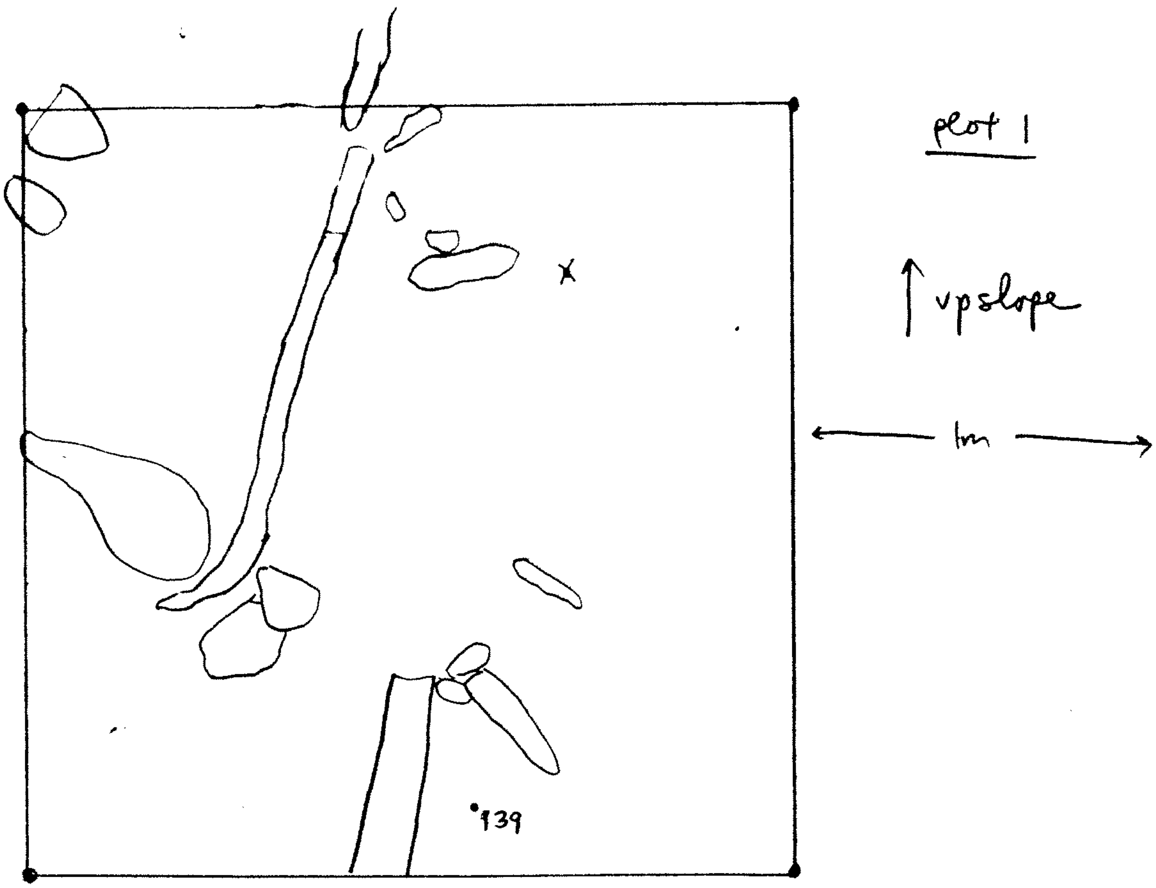
GARDNER STATE PARK

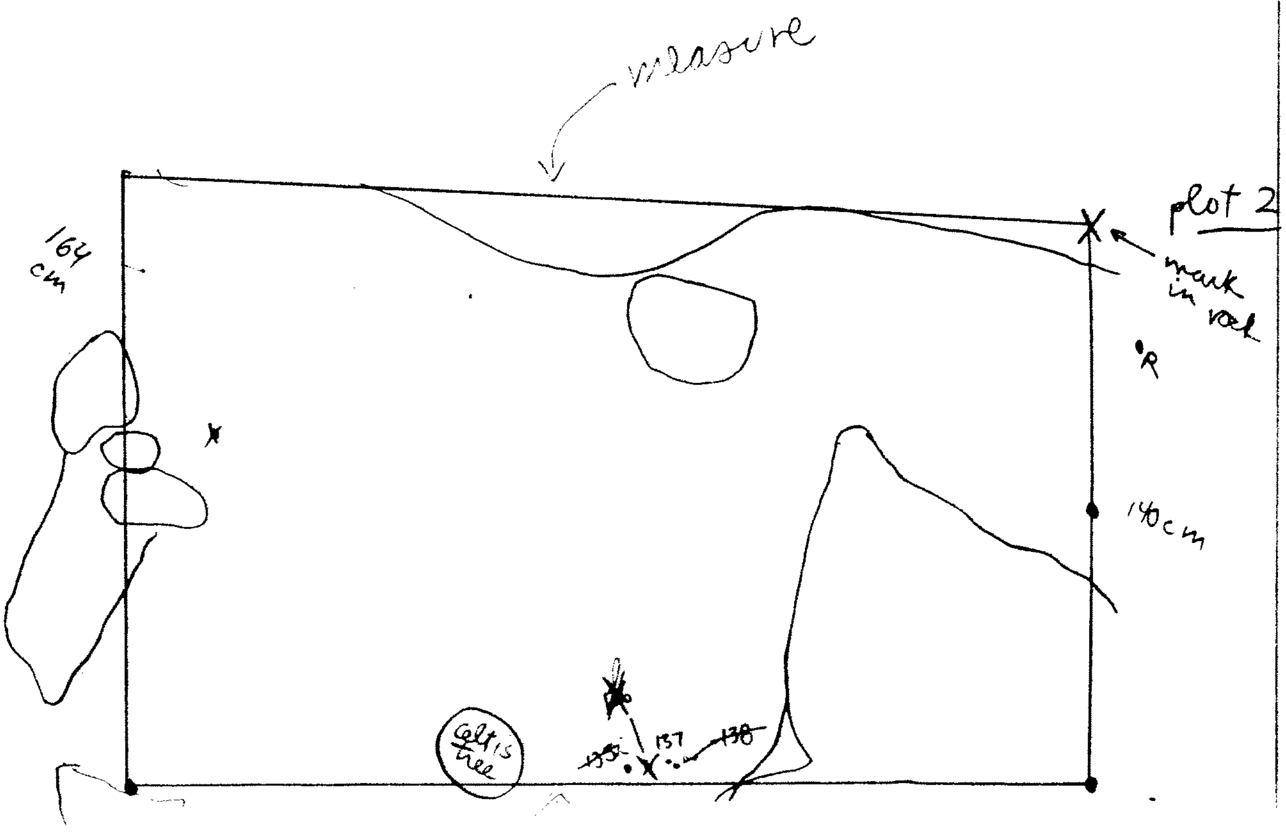
X = 6 May 1994 plants

Not to scale

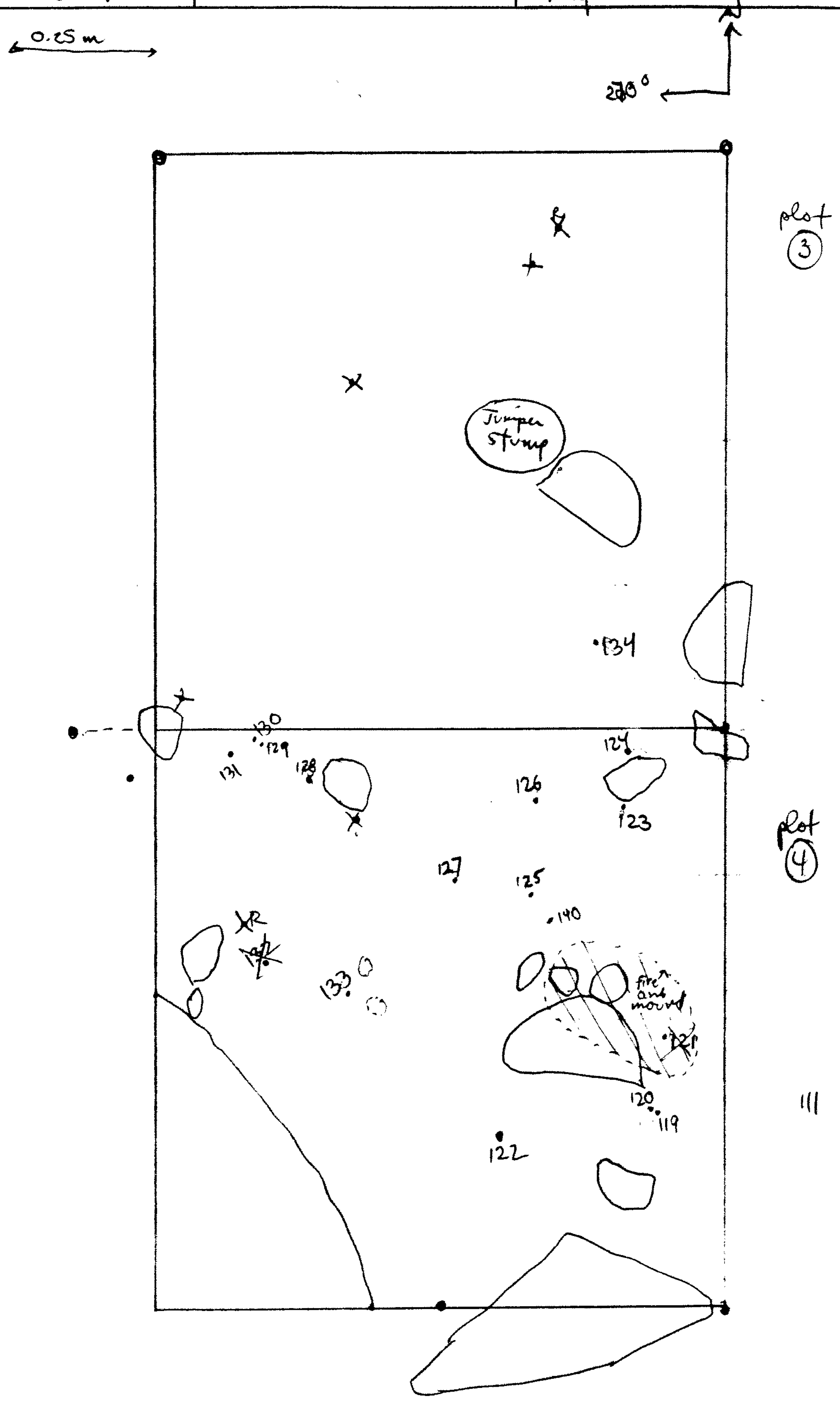


Map 2A | Barton Creek | 1994-95

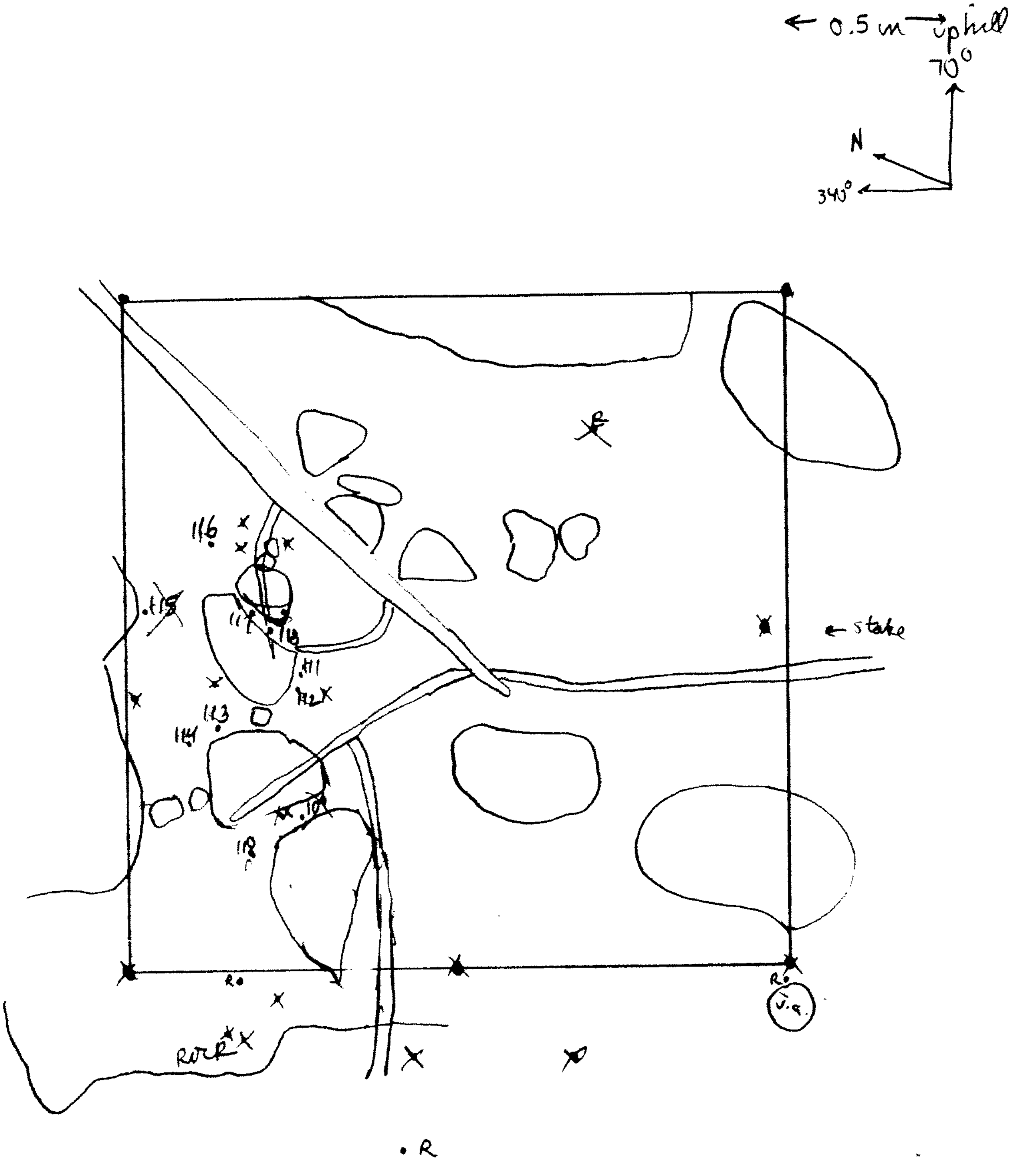




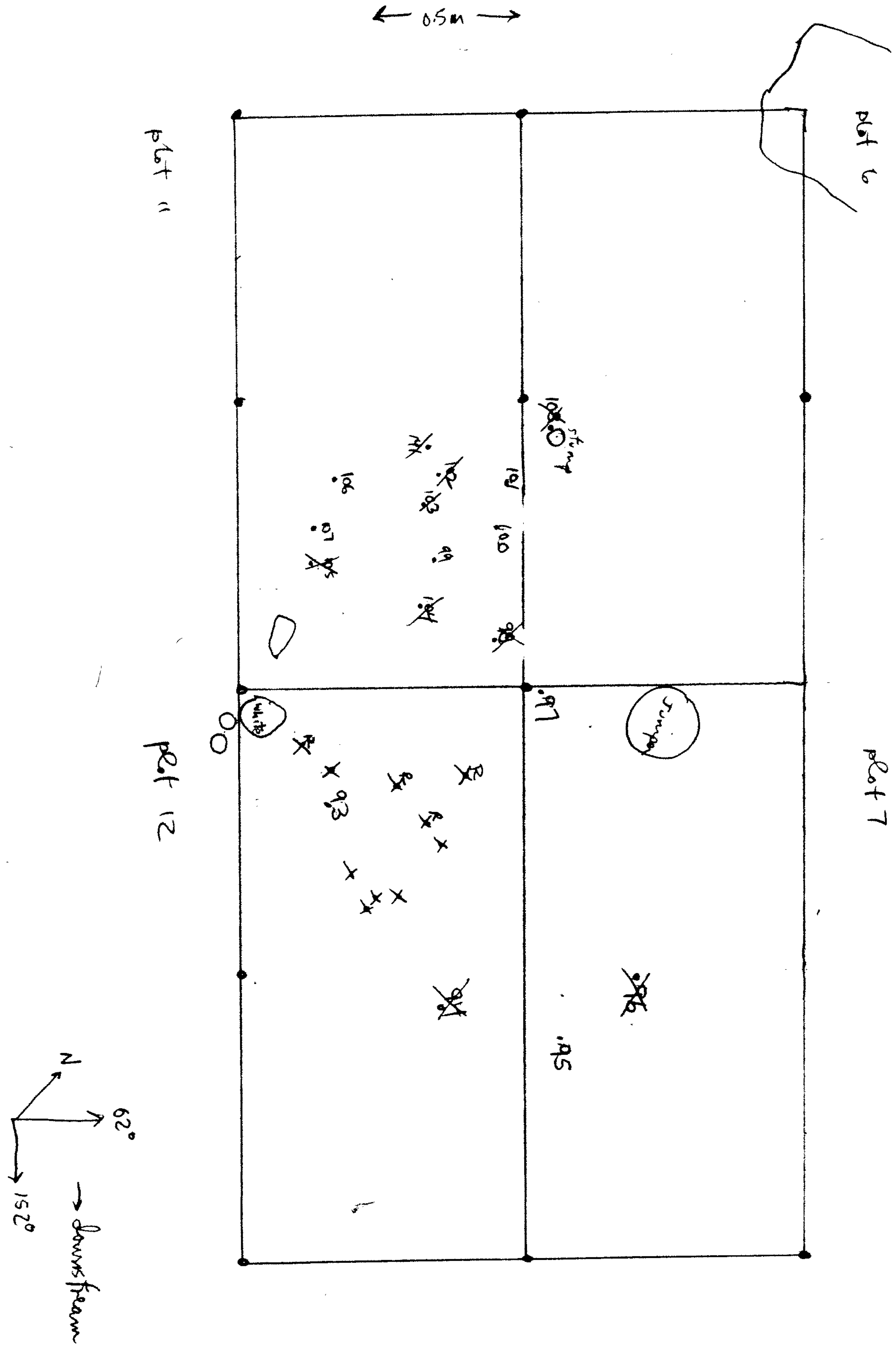
Barton Creek | 1994-5 | Map 2B



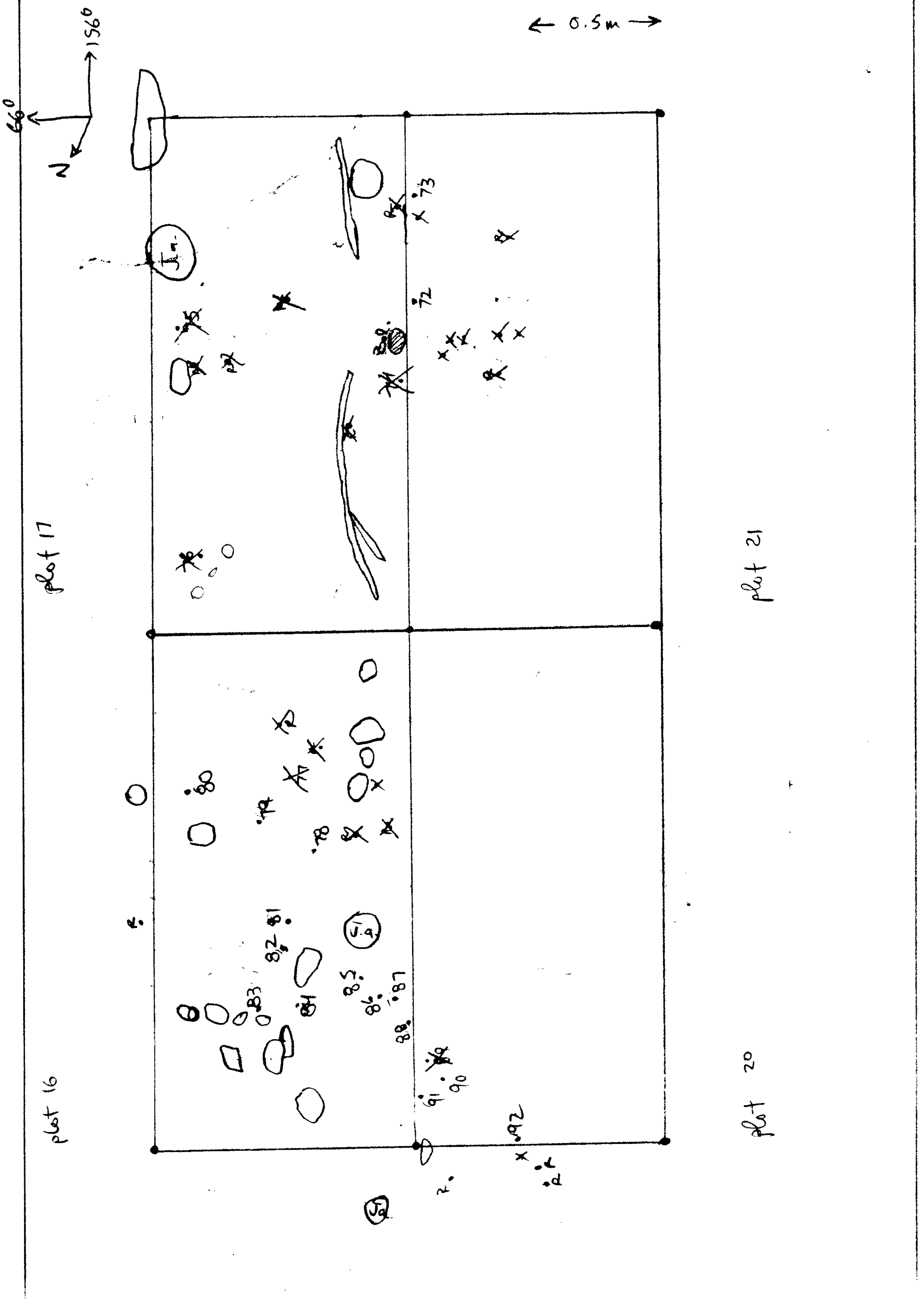
Barton Creek Map 2C | plot 5



Barton Creek | Map 3A | plots 6-7, 11-12

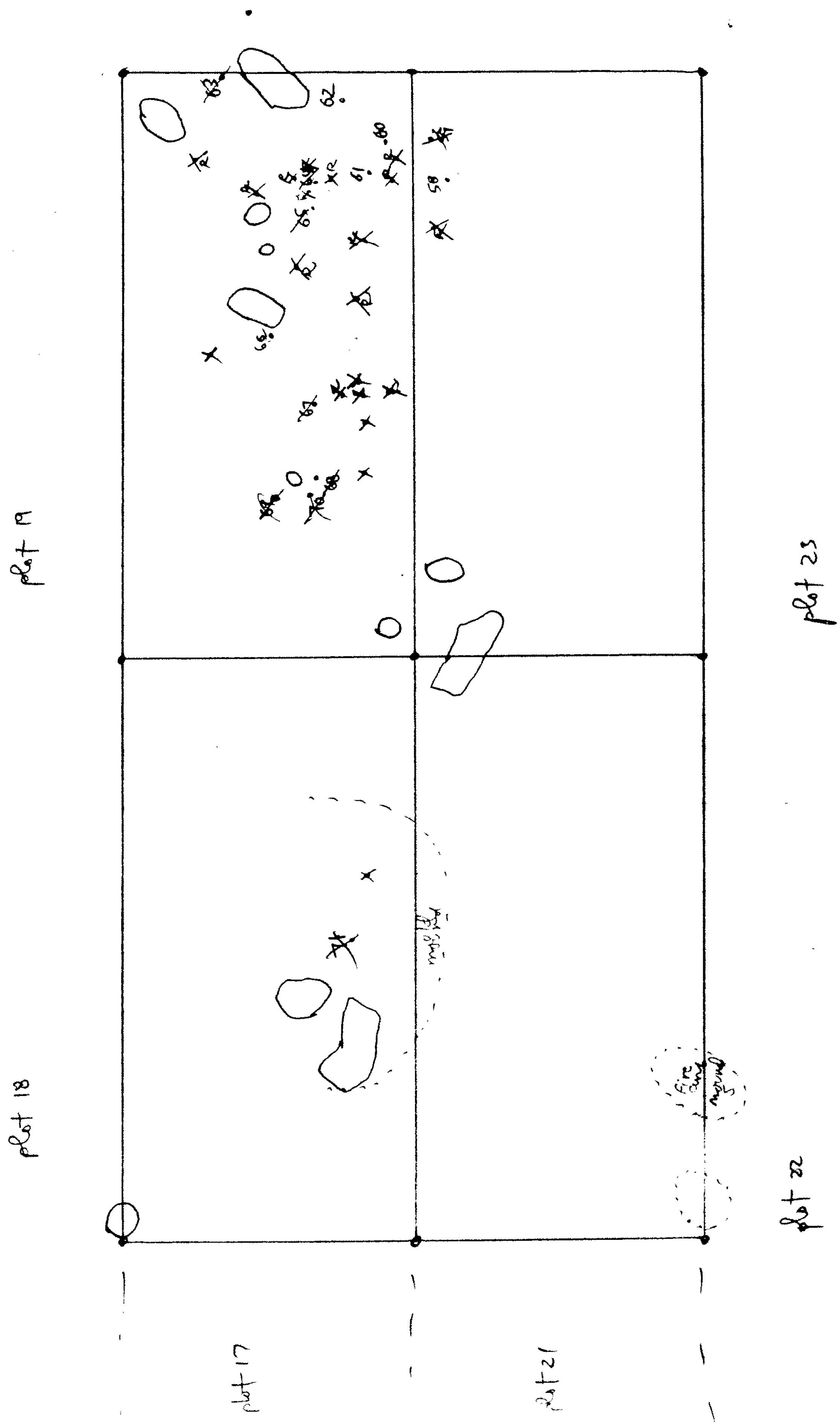


Burton Creek | Map 3B | plot 16-17, 20-2

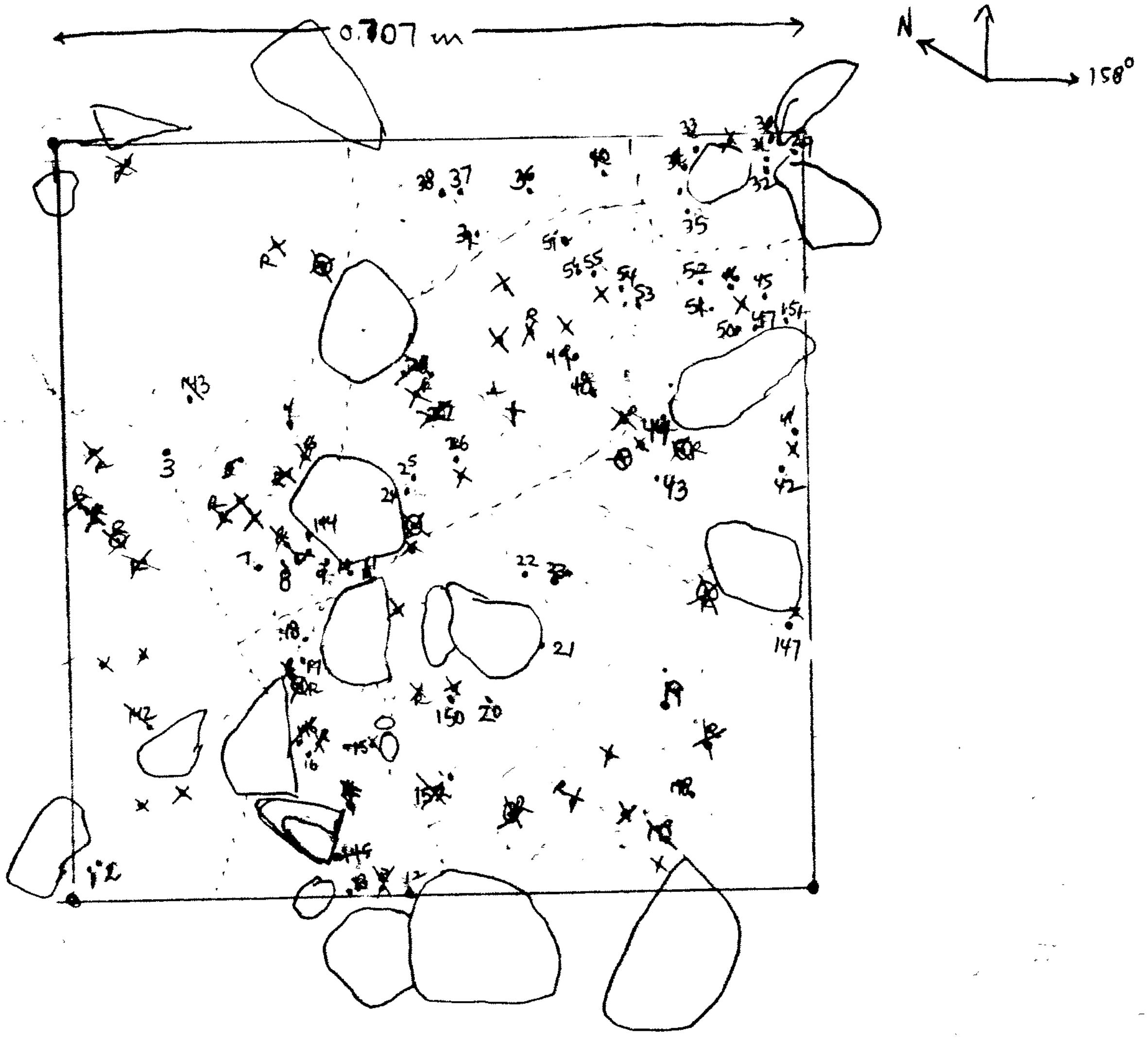


Barton Creek | Map 3C | 1994-95

plots 18-19, 22-23

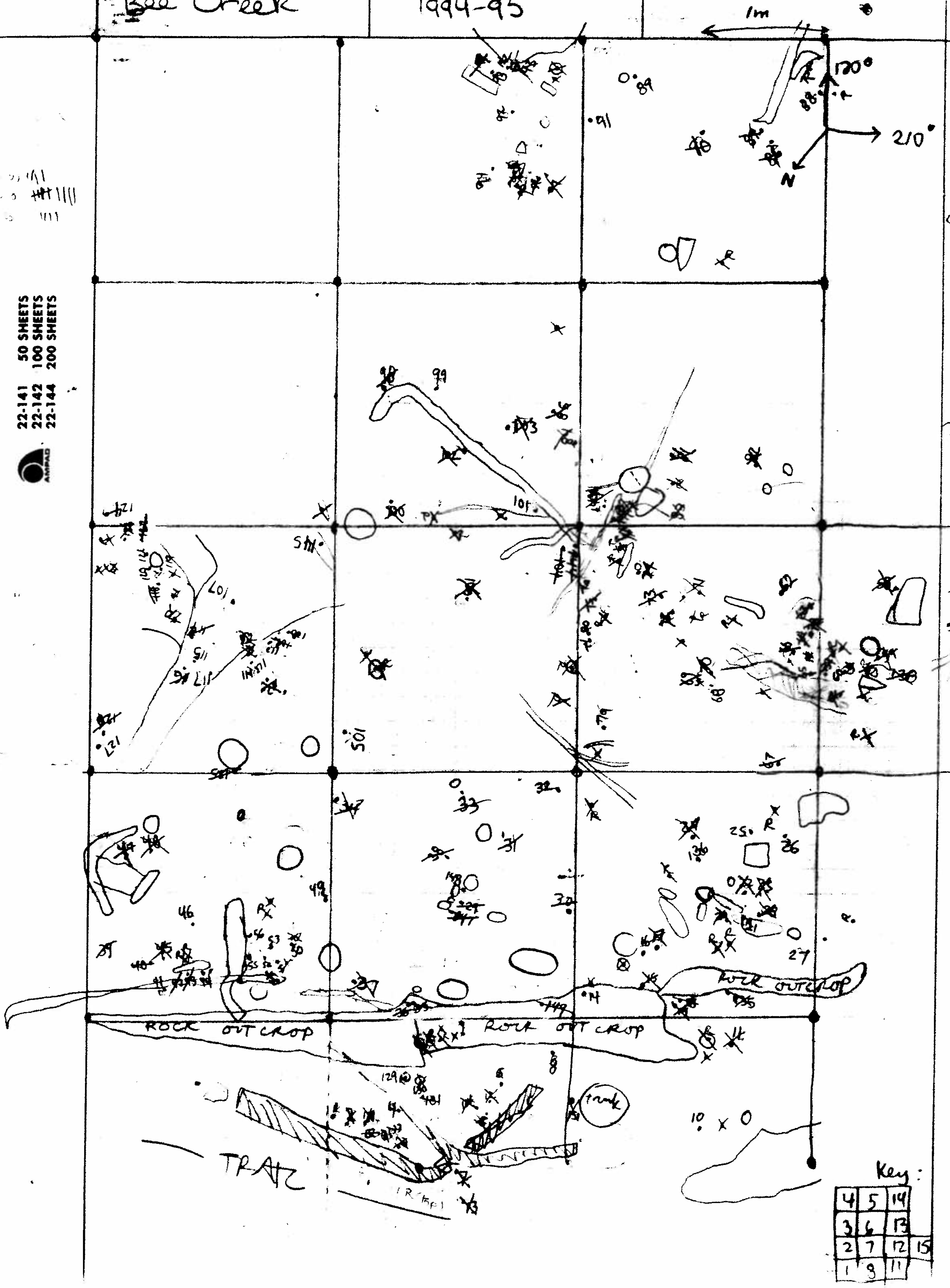


Barton Creek | Map 3D | plot 24
(0.5m²)

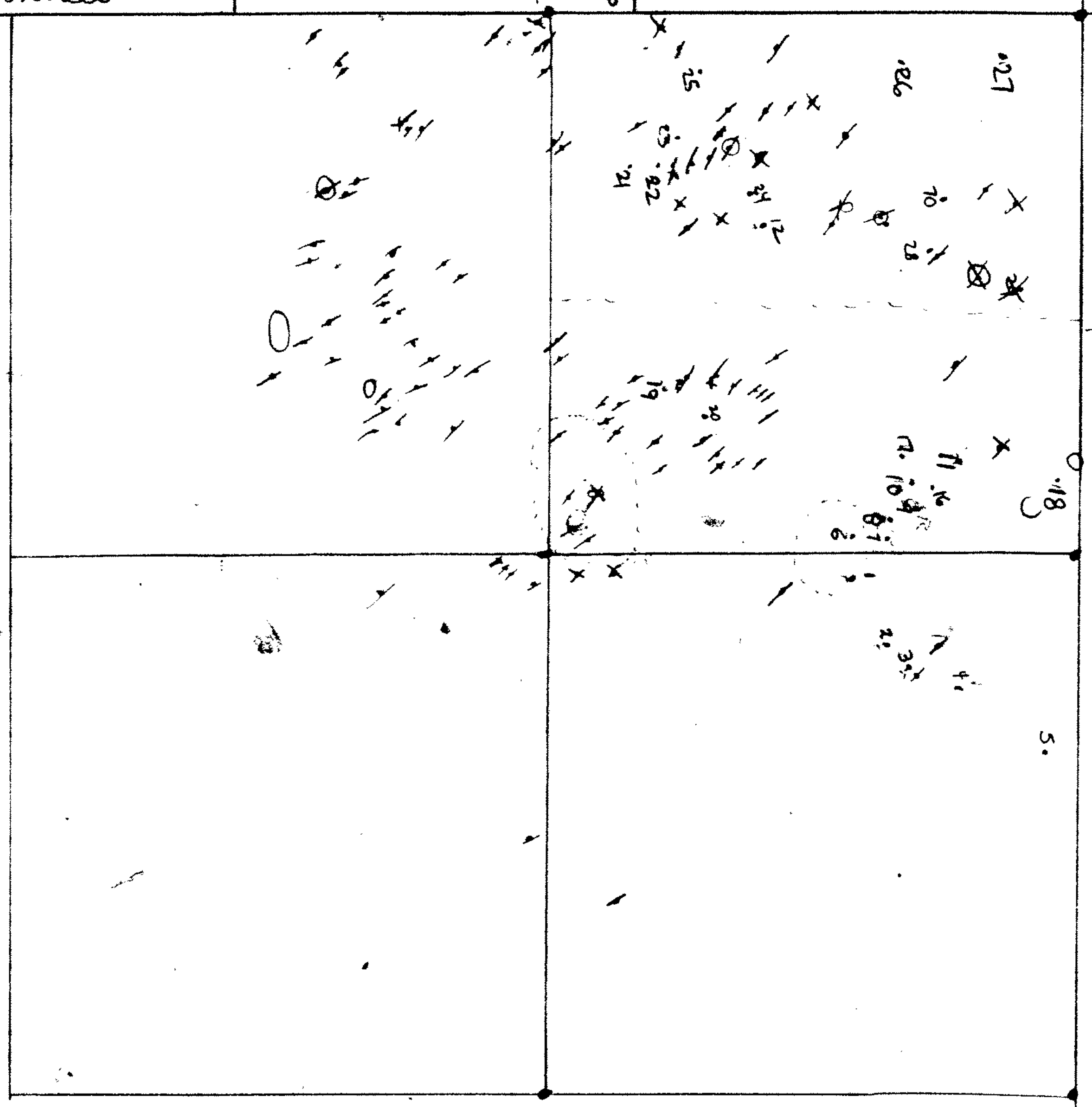


R
dead R

Bee Creek 1994-95

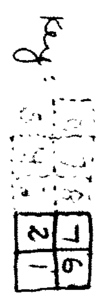


Mt Bonnell 1994-95 p. 182



tree cut
moved (for tor proof)

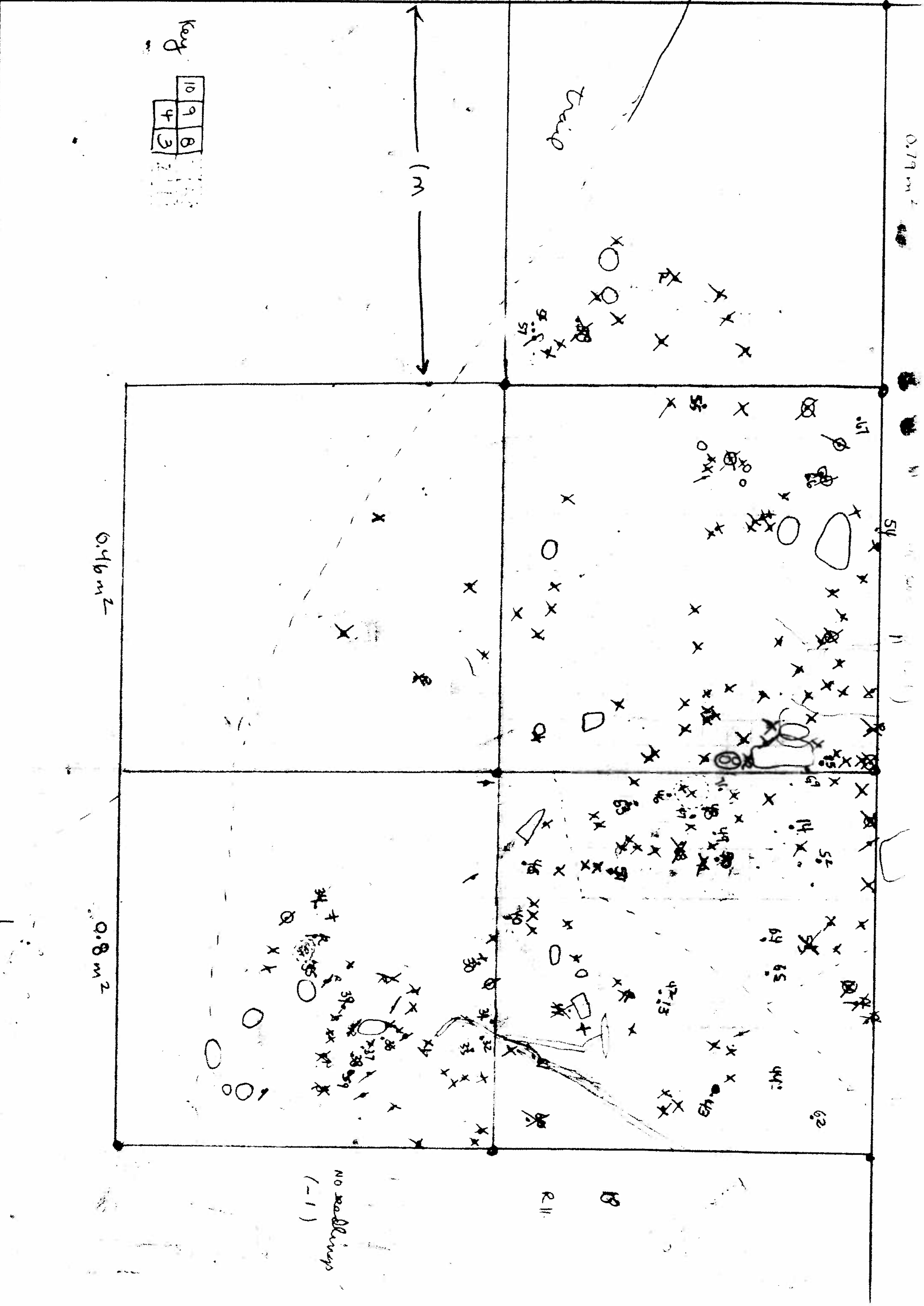
Key:



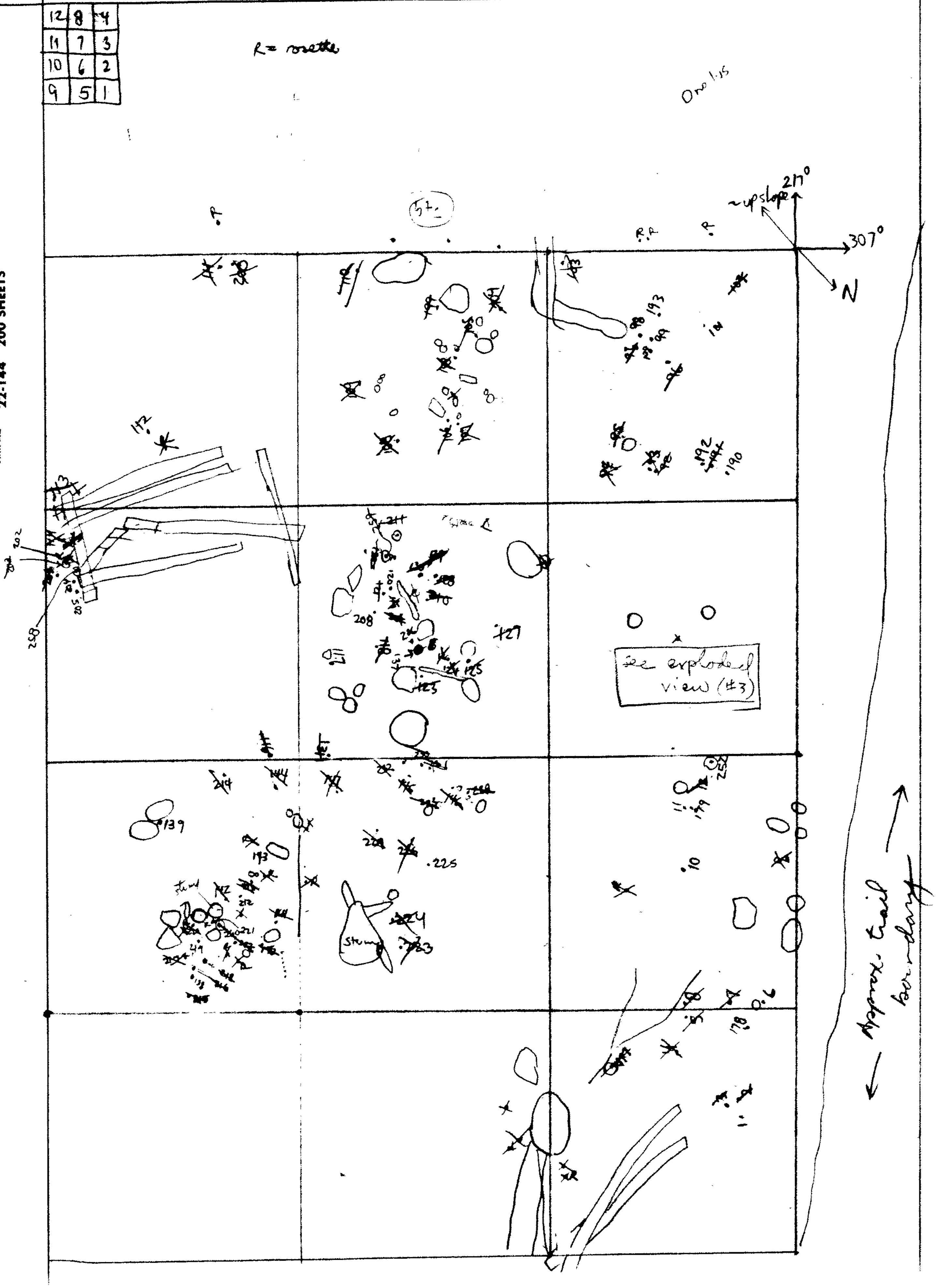
Mt. Bonnell

Page 2 of 2
1994-95

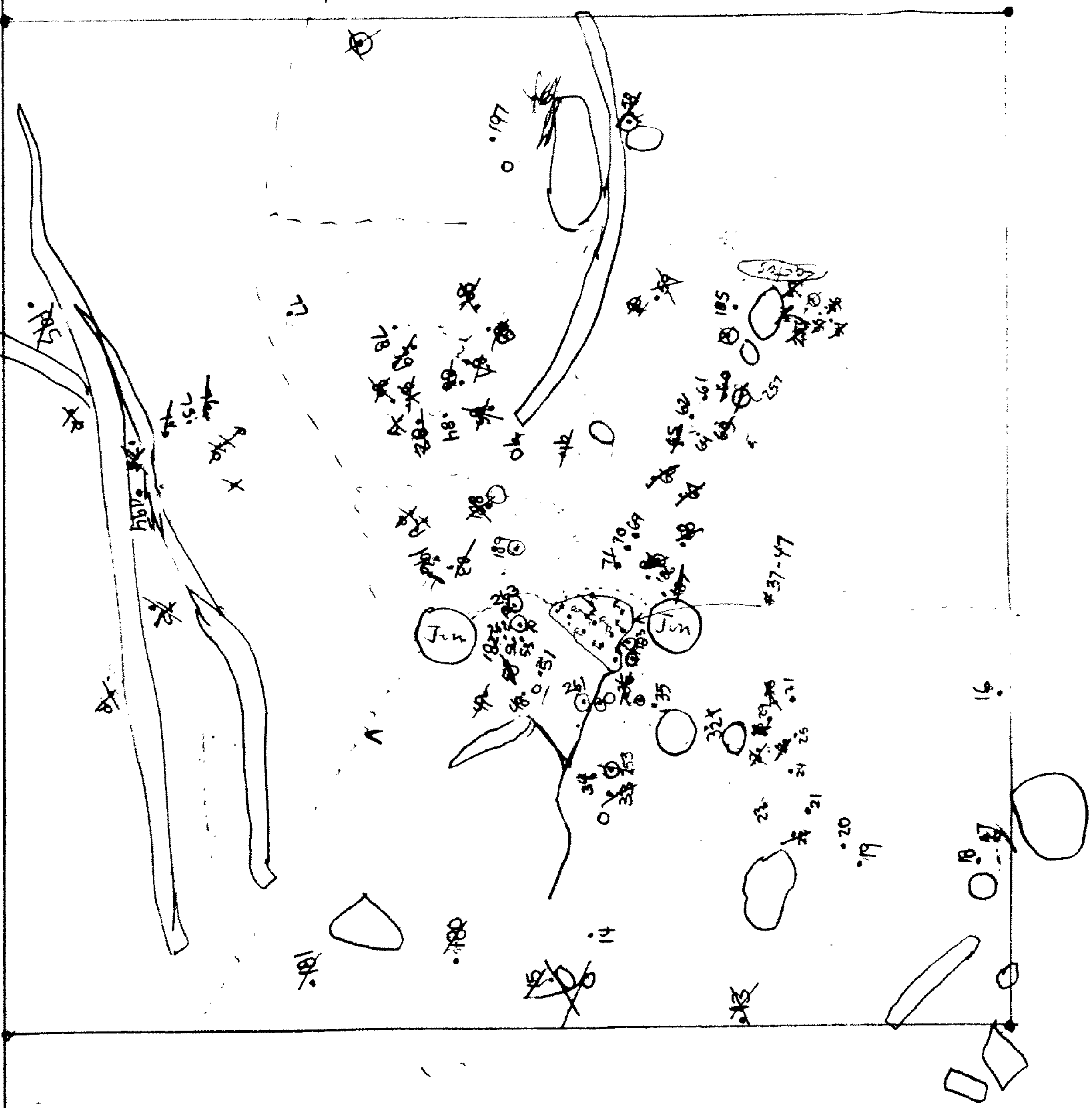
start 10 Oct 94



Valburn Dr. 1994-95

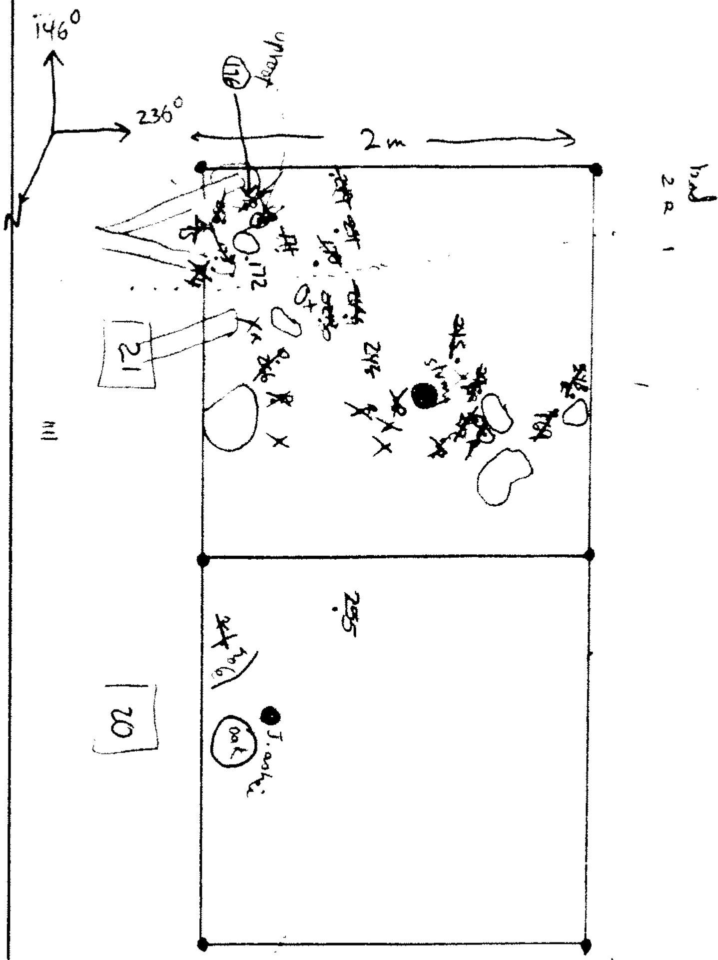


Valburn Dr | 1994-95 | plot 3

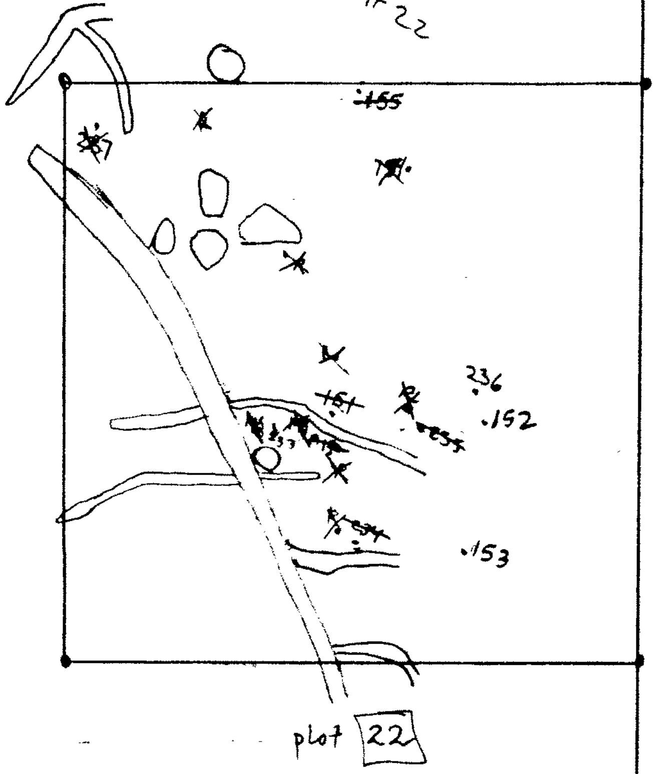


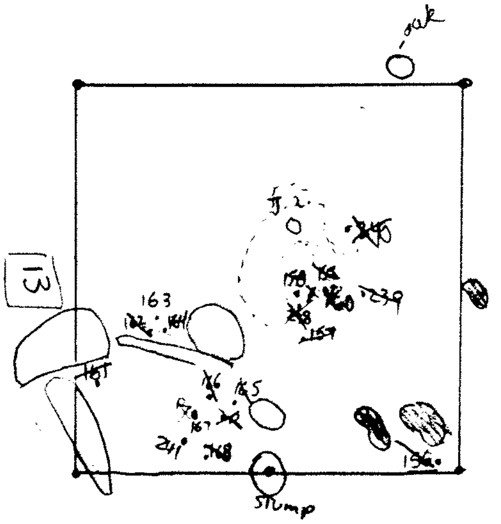
Seed → R

Valburn Dr | 1994-95 | plots 13, 20-22



17 Nov
39 seedlings upslope from #22





(Brush clearing in plot 13
in summer of 1994)

Date: December 6, 1993

To: Mr. Ron Sparks, Chairman, Austin Parks and Recreation Task Force
From: David B. Zippin, University of Texas Botany Department

Re: Barton Creek Management Plan

Thank you for the opportunity to give my input for the development of a Management Plan for the Barton Creek Greenbelt. I apologize for not presenting these comments to you in person. I had planned to attend the workshop on December 7, but another commitment forced me to cancel at the last minute.

I have been working in the upper reaches of the Greenbelt (near the Camp Craft entrance) for over a year, monitoring populations of the bracted twist-flower *Streptanthus bracteatus* as part of my dissertation research. I will continue to work in the greenbelt for another two years. The following are suggestions for inclusion in the Management Plan for the Greenbelt.

1. EXOTIC SPECIES REMOVAL AND MONITORING

Barton Creek has a growing exotic plant problem due to its proximity to housing developments and its very wet and favorable soils. Species such as Japanese privet (*Ligustrum japonicum*) and chinaberry (*Melia azedarach*) are already common sights along the trail. These species pose a threat to native vegetation along Barton Creek because their eventual spread will mean displacement of native plants and animals. The Barton Creek greenbelt is unique among Austin's habitats (e.g. it has a high diversity of woody plants). This biological diversity is jeopardized by the presence of these exotic plants.

Recommendations: Identify, tag, and remove exotic trees soon, before further spread makes eradication economically unfeasible (currently, they are not very abundant). Identify other potentially invasive exotics that could infest Barton Creek and train personnel to recognize them. Species such as giant reed (*Arundo donax*) and tamarisk tree (*Tamarix* sp.) are examples of extremely invasive exotics that are found in habitats similar to that in Barton Creek. These species would require immediate removal.

2. JUNIPER CONTROL AND MONITORING

Grassland areas along Barton Creek and near the Camp Craft Road trail junction are being invaded by cedar (*Juniperus ashei*) seedlings. Other woody plants such as yaupon (*Ilex vomitoria*) are also spreading, especially underneath oak trees, which serve as foci for seed dispersal. This conversion from grassland to woodland is a "natural" process in central Texas. However, grassland habitats in local preserves add further diversity and greater biological value and are becoming increasingly rare. If this habitat is to be maintained, these woody plants must be periodically removed.

Recommendations: Identify areas to be maintained as open grassland or grassland with oak overstory. Periodically burn these areas, or if that is not feasible, hand clear cedar and other unwanted woody plants.

3. RARE PLANT HABITAT MANAGEMENT

Barton Creek harbors the largest known population of the bracted twist-flower. In order to ensure the long-term persistence of this species in the greenbelt, there are two major factors to consider, deer behavior, and human access. From data I collected last spring, it appears that the population of bracted twist-flower at Barton Creek experiences low to moderate levels of deer browsing (compared to other twist-flower populations). This is likely due to the steep terrain and the frequent human presence on the trails, both of which limit deer movement. Creating conditions that increase deer presence along the creek where these plants are found should be avoided.

The densest concentration of bracted twist-flower plants in Barton Creek are found from 1-10 feet from the trail. Human impact may not pose an immediate risk (the trail has been there for many years). However, trail use will only increase in the future, which will in turn increase the risk of trampling by foot or mountain bike. Moreover, the issue is complicated by the possibility that the trail may actually enhance the population by providing a high light environment. My research will hopefully resolve this issue. Until the habitat requirements of this species is worked out, trampling and flower picking remains the most serious threat to this population.

Recommendations: Clearing of woody plants along the trail should be kept to a minimum near rare plant populations (excessive clearing occurred in the Fall of 1993), as this facilitates off-trail riding and walking. A long-term solution to the human access problem would be to re-route the main trail closer to the creek (at the same elevation) and revegetate the old trail with grasses and low shrubs (to maintain the high light levels).

No new paths or roads should be constructed anywhere near rare plant populations; this would increase deer access. The use of deer feeders by homeowners along the fringes of Barton Creek (I have confirmed at least one instance of this) must be discouraged, perhaps through an educational mailing campaign. Deer feeders provide an important food source only in the winter months when other forage is scarce and maintains an abnormally high deer population.

I encourage you to include provisions for long-term monitoring of the bracted twist-flower. This could be as simple as just mapping the extent of subpopulations once per year. The data I am collecting will give us a general idea of the population trends of this species. However, because this population is so important, and because population fluctuations beyond the time scale of my work are very likely, long-term monitoring is warranted.

I hope these suggestions are helpful in your efforts to produce the Barton Creek Greenbelt Management Plan. Thank you for the opportunity to aid in this important effort. If you have any questions regarding my comments, please call me at 471-4546. Since I was unable to attend the December 7 meeting, I would appreciate receiving any documents that were distributed at that time.

Sincerely,

David Zippin

THE DEPARTMENT OF BOTANY
THE UNIVERSITY OF TEXAS AT AUSTIN

Austin, Texas 78713-7640 · Phone (512) 471-5858 · Fax (512) 471-3878

3 April 1996

Ms. Jackie Davis, Biologist
Environmental and Conservation Services Department
City of Austin
P. O. Box 1088
Austin, TX 78767

Dear Ms. Davis,

I am writing in regards to the effects of the current drought on the bracted twistflower (*Streptanthus bracteatus*) in Austin, Texas. I have been monitoring five populations in Austin (out of only six known to exist within the City) since 1992 as part of my dissertation research at the University of Texas at Austin. The status of *S. bracteatus* this year is quite unique and warrants your attention.

On March 8 and 11 of this year, Gena Janssen, a Texas Parks and Wildlife Biologist, and I found no plants at one site, three plants at three of the sites, and only about twenty plants at the fifth (the most mesic site). Furthermore, all of the plants were much smaller than usual for that time of year. There is no additional recruitment into populations after January (this is a winter-germinating annual), so the populations will remain absent or small even if we receive more rain. For perspective, at these same sites at the same time last year there were over 1,000 plants.

There is no cause for alarm about the long-term status of this species (severe droughts such as this one result in very low germination and survivorship for many species), but it does pose problems for biological surveys in the Austin area this spring.

I bring this to your attention so that you can take this into account when the ESSO surveys for this species come in this spring with negative findings—it will be nearly impossible to find a new population this year. Even if one is found, its size and extent will be greatly underestimated.

I realize that you cannot (and probably should not) delay a project until next spring solely to perform an adequate survey for this species. However, if a project on potential bracted twistflower habitat may still be in the planning stages next year, I urge you to strongly recommend or require an additional focused survey for this imperiled species contingent on that delay.

Please circulate this notice to others in your department who may be reviewing ESSO's. If you have further questions, please call me at 471-4546 or 442-0083 or email me at david.zippin@mail.utexas.edu. Gena Janssen will be taking over the task of monitoring this species in the Austin area beginning this spring as part of TPWD's candidate monitoring program. She can be reached at 912-7011.

Sincerely,

David Zippin
Ph.D. Candidate

cc: Gena Janssen

David B. Zippin Section 6 FY 95-96 Expenses 3-1-96

Item	Date	Purchased from	Amount	Cost each	Total
SUPPLIES/OTHER					
Quantum Sensor	11-1-95	LI-COR	1	$290.00	$290.00
Terminal Block	11-1-95	LI-COR	1	$95.00	$95.00
SYSTAT leasing renewal	11-5-95	UT Comp Center	1 year	$75.00	$75.00
Mounting & Leveling Fixtures	11-15-95	LI-COR	4	$38.00	$165.00
SPSS Manuals	11-20-95	University Co-op	6		$191.87
SPSS Manuals	1-16-96	University Co-op	2		$76.00
Computer cable	1-20-96	LI-COR	1	$60.68	$60.68
Plastic Tarp	1-25-96	Home Depot	2	$42.50	$85.00
Gloves and masks	1-25-96	Home Depot			$22.95
Paper	1-27-96	Office Depot	1	$9.50	$9.50
Trailer Rental	1-29-96	Austin Tint Co.	2 (2 days)	$33.00	$66.00
Copies		UT Botany Dept.			$50.00
				TOTAL	$1187.00
SALARIES & FRINGE BENEFITS					
DAVID ZIPPIN					
salary	6-30-96				$1150.00
salary	7-31-96				$1150.00
salary	8-31-96				$1150.00
fringe	6-30-96	health insurance + OASI			$186.31
fringe	7-31-96	health insurance + OASI			$186.31
fringe	6-30-96	health insurance + OASI			$186.31
TROY DAVIS			HOURS		
salary + fringe	11-15-95		30.0	$7.00/hr	$227.64
salary + fringe	11-30-95		30.0	$7.00/hr	$227.64
salary + fringe	12-15-95		12.0	$7.00/hr	$91.06
salary + fringe	1-31-96		30.0	$7.00/hr	$227.64
salary + fringe	2-15-95		27.0	$7.00/hr	$204.88
salary + fringe	2-29-96		30.0	$7.00/hr	$227.64
				TOTAL	$5215.42
TRAVEL					
				TOTAL	$0.00

GRAND TOTALS

TOTAL: SUPPLIES	$1187.00
TOTAL: SALARIES	$5215.42
TOTAL: TRAVEL	$0.00
GRAND TOTAL SPENT	**$6402.42**
FY 95-96 Budget	$6,421.00
TOTAL REMAINING	***$18.58***

David B. Zippin

Section 6 FY 95-96 Expenses

3-1-96

Item	Date	Purchased from	Amount	Cost each	Total
SUPPLIES/OTHER					
Quantum Sensor	11-1-95	LI-COR	1	$290.00	$290.00
Terminal Block	11-1-95	LI-COR	1	$95.00	$95.00
SYSTAT leasing renewal	11-5-95	UT Comp Center	1 year	$75.00	$75.00
Mounting & Leveling Fixtures	11-15-95	LI-COR	4	$38.00	$165.00
SPSS Manuals	11-20-95	University Co-op	6		$191.87
SPSS Manuals	1-16-96	University Co-op	2		$76.00
Computer cable	1-20-96	LI-COR	1	$60.68	$60.68
Plastic Tarp	1-25-96	Home Depot	2	$42.50	$85.00
Gloves and masks	1-25-96	Home Depot			$22.95
Paper	1-27-96	Office Depot	1	$9.50	$9.50
Trailer Rental	1-29-96	Austin Tint Co.	2 (2 days)	$33.00	$66.00
Copies		UT Botany Dept.			$50.00
				TOTAL	$1187.00
SALARIES & FRINGE BENEFITS					
DAVID ZIPPIN					
salary	6-30-96				$1278.00
salary	7-31-96				$1278.00
salary	8-31-96				$1278.00
fringe	6-30-96	health insurance + OASI			$186.31
fringe	7-31-96	health insurance + OASI			$186.31
fringe	6-30-96	health insurance + OASI			$186.31
TROY DAVIS			HOURS		
salary + fringe	11-15-95		30.0	$7.00/hr	$227.64
salary + fringe	11-30-95		30.0	$7.00/hr	$227.64
salary + fringe	12-15-95		12.0	$7.00/hr	$91.06
salary + fringe	1-31-96		30.0	$7.00/hr	$227.64
salary + fringe	2-15-95		27.0	$7.00/hr	$204.88
salary + fringe	2-29-96		30.0	$7.00/hr	$227.64
				TOTAL	$5599.42
TRAVEL					
				TOTAL	$0.00
GRAND TOTALS					
TOTAL: SUPPLIES					$1187.00
TOTAL: SALARIES					$5599.42
TOTAL: TRAVEL					$0.00
GRAND TOTAL SPENT					**$6786.42**
FY 95-96 Budget					$6,421.00
TOTAL REMAINING					***($365.42)***

Bluffs of Cat Mtn.

Chuck, [April 2, 15 or 17]

None of the plants were flowering at the time of our survey, however, many had developing scapes and/ inflorescences.

If you need help locating these areas, let me know.

Lee

Survey Date??

1992