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Does Browsing Matter? : Predation and Population Declines in the Federally Endangered Schweinitz's Sunflower (Helianthus Schweinitzii T&G)

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To the Dean of the Graduate School:

We are submitting a thesis written by Bryan Benson England III entitled "Does Browsing Matter? Predation and Population Declines in the Federally Endangered Schweinitz's Sunflower (*Helianthus schweinitzii* T&G)."

We recommend acceptance in partial fulfillment of the requirements for the degree of Master of Science in Biology.

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DOES BROWSING MATTER? PREDATION AND POPULATION DECLINES IN THE FEDERALLY ENDANGERED SCHWEINITZ'S SUNFLOWER (*HELIANTHUS SCHWEINITZII* T&G)

A Thesis

Presented to the Faculty

Of the

College of Arts and Sciences

In Partial Fulfillment

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Of

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By

Bryan Benson England III

ABSTRACT

Herbivory is a ubiquitous ecological process, yet its importance to plant community ecology and conservation biology is controversial. When Schweinitz's sunflower (*Helianthus schweinitzii* T&G) was listed as a federally endangered species in 1991, "Predation and Parasitism" were considered "not applicable" as threats, and it was the lack of large herbivores that was repeatedly identified as a threat to this species' survival. Two decades later, persistent negative population trends in many protected populations and anecdotal reports of "heavy browse pressure from white-tailed deer" led to suggestions that herbivory by deer could be impeding the recovery of this species. To test for the existence of heavy deer browsing and the hypothesized relationship between high levels of browsing and sunflower population declines, this study tracked over 1,000 individual Schweinitz's sunflower stems from seven populations in York (SC) and Mecklenburg (NC) counties during the growing season of 2013 to assess browsing herbivore impacts across a range of populations with previously reported declining and non-declining population trends. Herbivore damage was observed at all sites monitored, and Schweinitz's sunflower sites with declining population trends displayed significantly higher frequencies of stem-browse events than did non-declining populations, with the mean stem-browse frequency for declining populations being over twice that of non-declining populations (stem-browse frequency at declining-population sites $\bar{x}$=57%, SD=22%, n=3; at non-declining sites $\bar{x}$=20%, SD=11%, n=4; t(5)=2.89, p=.017 (one-tailed)).

The hypothesis that high browse frequencies are likely to cause declining Schweinitz's sunflower populations trends was supported by this result, but the hypothesis that deer, specifically, were the primary cause of stem-browse damage was not supported at all sites. Overall, the majority of all stem-browse damage was consistent in appearance with damage by white-tailed deer, but some damage attributable to small mammals (lagomorphs or rodents) and, rarely, to insects, was also observed at most sites. At one site small mammal damage was the dominant browse-type seen, exceeding damage by deer, in a declining population where the local damage had previously been described as "heavy browse pressure from white-tailed deer". These results suggest that conservation managers should consider impacts from herbivores (including but not limited to deer) as significant threats to the survival of Schweinitz's sunflower populations in order to increase the success of recovery efforts for this endangered species.

ACKNOWLEDGMENTS

This study would not have been possible without the support of many people in the conservation community, particularly those who provided me permission to collect data from the Schweinitz's sunflower sites studied and helpfully answered my questions about the history and management of these sites. This includes staff from organizations including the Mecklenburg County Park and Recreation Department, the South Carolina Department of Transportation, the Anne Springs Close Greenway, the South Carolina Department of Natural Resources, and the York County Culture and Heritage Museums. In the course of this work I never encountered anyone, from front desk receptionists to road crews, who was not friendly and supportive of this project. Schweinitz's sunflowers may be somewhat mysterious to the public, but it is this base of popular support for the preservation of our natural heritage that keeps so many of our parks and public lands in existence, and offers hope for the continued preservation of this species.

I would like to thank the faculty and staff of Winthrop University for their support, and particularly my committee reviewers, for their very helpful comments.

I would like to thank my family for their patience and love, particularly my wife, Abigail, and children, as this project has taken longer than any of us expected, and my wife's family, who have from the beginning seen this project as a "leap of faith" that I would, eventually, complete.

Finally, I would like to thank God for allowing me to live long enough to see this project to completion.

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INTRODUCTION

"Damage to plants by herbivores is ubiquitous and sometimes severe", while the ability of plants to tolerate herbivory is variable (Rosenthal and Kotanen 1994, p.145). In contrast to the case for woody plants, where defoliating invertebrates are thought to be the dominant herbivores, it has been claimed that the "most common type of herbivory experienced by herbaceous plants is grazing by vertebrates" (Haukioja and Koricheva 2000, p.556). In eastern North America, the vertebrate herbivore most frequently recognized as producing pervasive, ecosystem-altering impacts through its herbivory is the white-tailed deer (*Odocoileus virginianus* (Boddaert)), thus earning it the label of a "keystone" herbivore (McShea and Rappole 1992; Waller and Alverson 1997).

White-tailed deer are generalist herbivores, yet they are also quite selective browsers, with the ecological result that deer-preferred plant species show declines while less-preferred species may proliferate when browse pressure from a rising deer population acts to shift plant community compositions (Rooney and Waller 2003; Frerker et al. 2014).

While some ecologists continue to minimize the potential for herbivores to threaten endangered species (e.g., "predation is unlikely to be a common threat to plants [on the US endangered species list]" Davis 2009, p.182), many conservation biologists have been alarmed for decades by the large number of rare plants observed among those species experiencing increasingly intense deer browsing. A 1992 survey identified 98 plant species listed for conservation concern at the state or federal level which were experiencing damage by deer, with populations of multiple rare species described as experiencing 100% losses of their flower production in some years due to deer herbivory (Miller et al. 1992). Declines in many additional rare species have been attributed to deer herbivory since Miller and colleagues' survey drew attention to the issue.

One such species is Schweinitz's sunflower (*Helianthus schweinitzii* Torrey & Gray), a federally endangered herbaceous perennial known only from the Piedmont region of North and South Carolina. While currently reported from 15 counties, the majority of known populations are found in two concentrations, with one focused around the Uwharrie Mountains of central North Carolina (Randolph and Montgomery Counties), and a more southerly concentration straddling the North Carolina-South Carolina border between Mecklenburg (NC) and York (SC) counties (Bibb 2010). Initial assessments did not mention herbivory as a cause of this species' endangerment or as a threat to its recovery (Murdock 1991; Weakley and Houk 1994), but the most recent federal review of the species' status suggested a different picture:

> "Since that time [1994], there are some indications that deer browse may be significantly affecting the survival of transplanted individuals and some native, resident populations. However, the severity and geographic scope of this threat needs further investigation. This threat may now constitute a significant threat to the species if left unaddressed" (Bibb 2010, p.10).

This thoroughly hedged ("some indications...may be significantly...needs further investigation") yet ominous conclusion was sourced only with a reference to personal communication with a single North Carolina Department of Transportation employee (the possibility of deer browsing affecting populations at the species' southern limit in South Carolina was not addressed). Such hesitation likely reflects the fact that, as Miller and colleagues (1992) bluntly put it, "verifying white-tailed deer impacts on threatened and endangered plants is difficult" (p.72). The difficulty comes from the rarity of directly observing deer browsing on rare plants, and while observing "signs of browsing on the plant may be the next best evidence available...unless the plant or plant populations are checked frequently, browsing can often be overlooked or mistaken for browsing by other herbivores such as rabbit or woodchuck" (Miller et al. 1992, p.72). Even when observations from a particular site are available, it is difficult to generalize them to other populations of an endangered plant since, as Miller and colleagues also noted, individual site characteristics (site size, shape, and habitat connections) are likely to significantly influence plant-animal interactions (such as herbivory), and larger-scale geographic considerations may also be influential (i.e., "Plants may be especially vulnerable to depredation on the outer limits of their range" (Miller et al. 1992, p.72)).

To address these difficulties and investigate the potential threat posed by deer browsing to the federally endangered Schweinitz's sunflower, this study intensively monitored seven Schweinitz's sunflower populations at the southernmost limit of that species' range in York County, South Carolina, and adjacent Mecklenburg County, North Carolina, throughout the growing season of 2013. The resulting data from repeated checks on over 1,000 individual

Schweinitz's sunflower stems (totaling over 4,000 stem measurements) document browsing both qualitatively and quantitatively, and allow the first detailed characterization of the frequency, seasonality, severity, and herbivore species responsible for browse damage at multiple Schweinitz's sunflowers sites.

While all seven sunflower sites were monitored during the same season by the same individual (the author), the results from this study will be presented in two parts: Part I describes, in close detail, observations recorded at Dodge City Prairie restoration in 2013. Part II describes the overall monitoring project and the results from all seven monitored sites, inclusive of Dodge City.

The reasons for describing Dodge City in detail are several:

1) Providing a detailed description of the monitoring method employed at Dodge City exemplifies the techniques used at the other sites, reducing the need for exhaustive descriptions of methods from each site individually, other than to note how methods were adjusted due to logistical issues that were unique to each site.

2) The Dodge City site was unique in that a suspicion of "heavy browse pressure from white-tailed deer" (Lampell 2013, p.8) was specifically reported for this site prior to this study, justifying site-specific hypotheses. All other sites were selected without any advance reports indicating what level of browsing or browse agents should be expected.

3) The Dodge City site has a unique history as a site which has already experienced a total failure of one introduction of transplanted Schweinitz's sunflowers and available data suggested that a second batch of sunflowers transplanted to Dodge City was heading towards a similar fate in 2013 (this

second transplanted population did, in fact, fail completely by 2016-2017, pers. obs.). The failure of a mitigation transplantation project of an endangered species is a significant event, not only because it represents total loss of the population that was being transplanted, but also because of the loss of all the resources expended in the transplant effort. Understanding why such failures occur is a major concern, and the monitoring of Dodge City in 2013 offered a rare, detailed glimpse of a transplanted population in the process of extirpation.

Studies in the field of conservation biology and restoration ecology have found failure to be the most common outcome of rare plant translocation efforts, yet descriptions of unsuccessful transplant projects are known to be drastically underrepresented in the published literature, due to what has been described as a "strong inclination not to publish negative or discouraging experimental results", despite the great need for detailed communications about unsuccessful projects to advance the field as a whole (Drayton and Primack 2012, p.299; Godefroid et al. 2010; Knight 2009; Menges 2008; Fahselt 2007; Redford and Taber 2000). Therefore, the detailed discussion of the Dodge City site in Part I is offered in recognition of the site's unique status as a twice-failed transplant project and the much-discussed need for more reporting on unsuccessful conservation projects.

The Dodge City site was selected for intense monitoring for the reasons described above, with the understanding that explaining the broader trend of population declines in southern Schweinitz's sunflower populations -- the goal of Part II of this study -- would necessarily require data from more than one site. Even if Dodge City was found by observation to be both a declining and heavily browsed population, as hypothesized, this could still be attributed to mere coincidence. To test a hypothesis that higher levels of browsing consistently correlate with, and presumably cause, population declines in Schweinitz's sunflowers, robust measurements of browsing levels would be needed from a sufficient number of both declining and non-declining sunflower populations to allow for a statistically powerful test. This is particularly important given the skepticism which some ecologists hold against the possibility of predation as a threat to endangered plants in general (e.g., Davis 2009), a view which was specifically evident in the early recovery plans for Schweinitz's sunflower which described predation as "not applicable" as a threat to the species (Murdock 1991, p.21689).

Part II of this study describes the monitoring procedures followed for seven natural and restoration Schweinitz's sunflower populations (including five in South Carolina, and one additional site in southern North Carolina close to Dodge City Prairie) that represent a mix of previously reported population trends. This data set was tested against the previously reported population trends for these Schweinitz's sunflower sites to assess the significance of the relationship between higher browse rates and declining Schweinitz's sunflower populations.

HYPOTHESES

For Part I: Dodge City Prairie

1: That browsing of Schweinitz's sunflowers at Dodge City Prairie is occurring.

2: That white-tailed deer are the primary agent of browsing on Schweinitz's sunflowers at Dodge City Prairie.

3: That browsing of Schweinitz's sunflowers at Dodge City Prairie is "heavy" (defined here as >50% of stems experiencing apical browsing during a season, cf. terminology in Pierson and deCalesta 2015).

For Part II: Southern (York-Mecklenburg) Schweinitz's sunflower populations generally

4: That variation in browse frequencies across southern Schweinitz's sunflower populations corresponds with previously reported variation in population trend in these populations, with higher browse frequencies corresponding significantly with declining population trends.

BACKGROUND

--Debates in Historical Ecology--

The botanist enquires where a given cultivated plant grows spontaneously, or what was its wild original ; and he has to judge, as well as he can, where it is truly indigenous or where a reversion from a cultivated to a wild condition. This, as respects weeds and the like, is a difficult matter, even in a newly settled country like North America...

Plentifulness is of no account ...The several lines of evidence, — botanical, archaeological, palaeontological, historical, and linguistic — may be used to supplement or correct each other.

--Asa Gray and J. Hammond Trumbull on DeCandolle (1883)

1. A Distribution without an Explanation.

In the decades following its listing as a federally endangered species in 1991, Schweinitz's sunflower (*Helianthus schweinitzii*) attracted research attention from a number of ecologists and conservation biologists, attention such as this previously obscure species had never before received, despite its rather early introduction to the scientific world in the 1848 *Flora* of John Torrey and Asa Gray. The more clearly the species was understood, the more puzzling it appeared, in that both its distribution and its habitats defied the usual pattern for a rare species. It was found to be restricted to a rather small number of sites in the central Piedmont of North and South Carolina, a region long noted for its lack of endemic species (e.g., Curtis 1860). While geographic restriction is not, by itself, an unusual thing for a rare plant, generally plants are geographically restricted because they have specialized habitat requirements which occur in very few places (for example, a plant may specialize in rock outcrops of an unusual chemical composition), or because they occur in an isolated example of a habitat with no ability to disperse to other similar, but distant, locations.

Far from requiring an extremely specific, rare habitat, most populations of Schweinitz's sunflowers occur on roadsides, under powerline rights-of-way, and in other human-disturbed marginal areas. According to a recent federal review, 90% of all Schweinitz's sunflower populations occur in managed right-of-way areas, chiefly along roadsides and under powerlines (Bibb 2010). Such human-disturbed habitats are ubiquitous throughout the Carolina Piedmont, and indeed throughout the southeast – so why isn't the Schweinitz's sunflower?

Other than avoiding dense shade, Schweinitz's sunflower population sites have little in common. Some are roadside populations occurring on dry clay-soil slopes with a nearly complete lack of other wildflowers, and yet the Schweinitz's sunflowers in these sites appear to be blooming and multiplying. Other Schweinitz's sunflower populations are found in botanically rich (and often seasonally wet) sites where they are seen coexisting with a dense and highly diverse wildflower assemblage including other rare species of conservation concern. These open, wildflower-rich areas have been dubbed "Piedmont prairies", and such sites resemble roadsides in that nearly all Piedmont prairie sites have been kept open and free from trees by periodic human disturbances such as mowing. Although the Schweinitz's sunflower is often identified as a Piedmont prairie associated species, no other Piedmont prairie associated species is restricted only to the Carolina Piedmont. Davis and colleagues (2002) produced a list of 277 plant species which they identified as being either strongly or weakly associated with Piedmont prairies. Most of these species are widely distributed, and are not considered globally rare. Only four of their 277 species were noted as having a federally-recognized conservation status, or as being candidates for a federal status: the Schweinitz's sunflower, Smooth Coneflower (*Echinacea laevigata*), Georgia Aster (*Symphyotrichum georgianum*), and Heller's Bird-foot-trefoil (*Acmispon helleri*). Even compared to these rarest-of-all Piedmont prairie species, the Schweinitz's sunflower stands apart for its extremely restricted distribution.

Table 1. Known distributions of four rare Piedmont prairie associated species (data from Weakley 2015).

Species Name	Fed. Status	VA	NC	SC	GA	AL	FL
Helianthus schweinitzii	Endg.		Pd	Pd			
Echinacea laevigata	Endg.	Mt, Pd	Pd	Mt, Pd, Cp	Mt	Mt, Cp	
Symphyotrichum georgianum	Cand.		Pd	Mt, Pd	Mt, Pd, Cp	Mt, Pd	Cp
Acmispon helleri (=*Lotus helleri*)	Cand.	Pd	Pd	Pd	Pd		
Province: Mt=Mountains; Pd=Piedmont; Cp=Coastal Plain							

As seen in Table 1, even the rarest Piedmont prairie species (other than Schweinitz's sunflower) always have distributions that extend either northward into at least the Piedmont of Virginia, and/or southward into the Piedmont of Georgia and Alabama. Also, most Piedmont prairie species are not specifically restricted to the Piedmont province but occur in pockets of open prairie-like habitat scattered across the Mountain and Coastal Plain regions of both Carolinas and neighboring states as well. Why is it only the Schweinitz's sunflower that is so geographically restricted? And what was its habitat in pre-modern times, before highway and powerline right-of-ways criss-crossed the Piedmont?

2. Historical Botany Draws a Blank

Normally to answer a question about what a particular plant was doing in the recent past, one can turn to the works of earlier generations of botanists and the herbarium specimens they have left behind. All sunflowers are native to North America, and Eastern North America can boast five centuries of botanical study. The common sunflower (*Helianthus annuus*) was introduced to European botanists early in the 16th century, with the first known illustration appearing in 1544 in the work of Leonard Fuchs, well before the naming of the genus by Linnaeus in 1753. Thus when James Hariot in the 1580's wished to describe the cultivation of sunflowers by Algonquian tribes he observed living along coastal North Carolina (at that time called Virginia), Hariot already knew sunflowers by a

European name, as the "*Planta Solis*" (Hariot 1588) -- a Latin equivalent of the Greek-derived name *Helianthus* which Linnaeus would later use for the genus.

Unlike the common sunflower, Schweinitz's sunflower had to wait additional centuries to receive a Latin specific name, when it appeared in the second volume of John Torrey (1796-1873) and Asa Gray's (1810-1888) *Flora of North America* (1842). Torrey and Gray based their species description on specimens they received from two sources: Moses Ashley Curtis (1808-1872) in Mecklenburg County, North Carolina, and Lewis David de Schweinitz (1780-1834), from "near Salem," North Carolina. Both Curtis and de Schweinitz were highly-regarded American botanist-mycologists, and the species was named to honor the recently deceased Schweinitz. While Torrey and Gray included brief habitat descriptions with most of the sunflower species in their *Flora*, no such description appeared with *H. schweinitzii*. Torrey and Gray never actually saw a live or complete specimen (having been sent only pressed upper stems), and thus while noting the specimens' small flowers and narrow leaves, they could not report a habitat or even precisely describe the plants' height (they wrote "apparently three to six feet", although *H. schweinitzii* can grow to over ten feet – one of the tallest perennial forbs in eastern North America). They were also unaware of its most distinctive feature – its thick, tuberous roots, often described as "carrot-like" (Murdock 1991). Without knowledge of this detail it was easy for botanists to confuse *H. schweinitzii* with other *Helianthus* species that display similar leaves and flowers, but lack tuberous roots.

After Torrey and Gray (1842), Alvan Wentworth Chapman (1809-1899) was the next botanist to mention the species, in his *Flora of the Southern United States* (1860). Chapman also provided no habitat description, and citing Curtis, located the plant as coming from the "Upper districts of North Carolina". Curtis himself, in the third part of his *Geologic and Natural History Survey of North Carolina* (1867), reported *H. schweinitzii* from the "Mid. Dist." -- a term he used to describe what we today call the Piedmont. By not identifying it with a particular county, Curtis apparently believed the species to occur in multiple counties. Unlike Torrey and Gray, Curtis presumably knew and could have recorded the habitat where he collected this species, but unfortunately Curtis rarely provided habitat information for species listed in his *Survey*. Thus we lack any first-hand habitat description for the early collections of the species.

In his *Descriptive Botany* (1879) Alphonso Wood (1810-1881) reduced *H. schweinitzii* to a synonym of the widespread *H. microcephalus*, but Asa Gray retained it as a full species in his *Synoptical Flora* (1884). Wood's action is significant because it shows how northern botanists, who had only a fragmentary impression of *H. schweinitzii*, were coming to think of the species. Gray (1884) acknowledged a similarity with *H. microcephalus* (which he called *H. parviflorus*), and particularly saw a resemblance to a new variety Gray called *H. parviflorus* var. *attenuatus* (reported from "dry woods" in Tallulah Falls, Georgia). This variety Gray described as "connecting" *H. parviflorus* with *H. schweinitzii*. Today *H. parviflorus* var. *attenuatus* is recognized as a very rare endemic species under the name *H. smithii* Heiser, known only from Tennessee, Alabama, and Georgia, and which is not thought to be very closely related to *H. schweinitzii*. Both species have narrow, mostly sessile leaves that can be rough on both surfaces as well as small flower heads, so the resemblance (without the root) of *H. smithii* to *H. schweinitzii* was real. Gray's *Synoptical Flora* (1884) was notable for reporting the first habitat description given for *H. schweinitzii* ("dry ground") and also for expanding the species' range to "W. North Carolina to Middle Georgia". Today no specimen of genuine *H. schweinitzii* is recognized from either Georgia or the western mountains of North Carolina, and this westward range expansion appears to have been based on misidentifications (likely including *H. smithii*). This consequently means that even this simple habitat description of "dry ground" cannot be taken as reliably referring to true *H. schweinitzii.*

The confusion of *H. schweinitzii* with *H. smithii* spread from this point as Charles Mohr (1824-1901) next reported *H. schweinitzii* as "infrequent" (meaning moderately common), in the "dry borders of woods" in the "Mountain region" of his state in his *Plant Life of Alabama* (1901). After this John Kunkel Small (1869-1938) in the first and second editions of his *Flora of the Southeastern United States* (1903, 1913) added Mohr's report to Gray's and thus reported *H. schweinitzii* from "dry soil, North Carolina to Georgia and Alabama." In his *Manual of the Southeastern Flora* (1933), Small slightly expanded his habitat description to "Dry, often sandy and rocky woods, various provinces, Ga. to Ala. to N.C." Despite the presence of some habitat information in all these reports, all mentions of *H. schweinitzii* and its habitat from Gray's *Synoptical Flora* (1884) through Small's work now must be presumed distorted by confusion with plants presently recognized as belonging to other *Helianthus* species, leaving the actual habitat of *H. schweinitzii* during the late 19th and early 20th centuries unrecorded.

In this period Elba Emanuel Watson (1871-1936) is noteworthy for his *Contributions to monograph on the genus Helianthus* (1929), which made a greater effort to describe the underground characteristics of many *Helianthus* species, and Watson claimed to have "examined the roots of countless thousands of perennial sunflowers in their natural habitat." This approach might have thrown light on *H. schweinitzii* sooner by revealing its distinctive tuberous roots, except that Watson was unable to locate any new, complete, *H. schweinitzii* specimens in the wild from which he could have made this discovery. Watson did carefully examine the (rootless) preserved type specimens collected by de Schweinitz "near Salem", and working strictly from these herbarium specimens Watson broke with Gray, Mohr, and Small by rejecting the identification of the *H. schweinitzii* with any sunflowers collected from Alabama or Georgia, and narrowly restricted the species to only specimens from North Carolina. Watson searched the vicinity of "Salem, North Carolina" during the summer of 1925, but failed to find the *H. schweinitzii* he was searching for. From this Watson concluded that the species was "evidently rare." This conclusion may have been correct, but since *H. schweinitzii* blooms later than most *Helianthus*, chiefly in September and October, summer was not the ideal time to conduct a search, although Watson could not have known this from the incomplete documentation on the herbarium specimens available to him.

The views in Watson's monograph on *Helianthus* were not fully accepted (e.g., Small 1933 cites Watson, but does not follow Watson's restriction of *H. schweinitzii* to North Carolina), and it fell to Charles Bixley Heiser Jr. (1920-2010) to reinvigorate study of the genus in the years following World War II. Heiser's early work began with a series of detailed reports on experimental crosses and hybridization tests between putative *Helianthus* species which strove to find an empirical basis for species delimitation, culminating in an exhaustive monograph *The North American Sunflowers* (Heiser et al. 1969). Heiser collected extensively, often bringing back live plants to his gardens for further observation and growth under experimental conditions, and he diligently reviewed all available type materials. Heiser sought *H. schweinitzii* from the region of the original type specimens in the central North Carolina Piedmont, where he found sunflowers he believed to be a match growing on roadsides, and he noted the presence of tuberous roots as a distinctive feature. Heiser concluded that without knowledge of this feature, the species had been widely misidentified and over-reported. In a 1964 paper, Heiser and D. M. Smith described *H. schweinitzii* as “occurring in only a few localities in North Carolina”, vindicating Watson by bringing the species back to the range and specimens of Torrey and Gray (1842).

Heiser reported the chromosome count of *H. schweinitzii* as n=51 (2n=102), classing it as a hexaploid from the *Helianthus* base count of n=17 (somatic cells typically diploid 2n=34). This also helped to distinguish *H. schweinitzii* from *H. smithii* which Heiser elevated from a variety to full species status and reported as being a tetraploid n=34 (2n=68) (Heiser and Smith 1964).

The identification of *H. schweinitzii* as a hexaploid has since been challenged (Matthews et al. 1997), but at that time Heiser and D. M. Smith used their polyploid chromosome count to speculate on a possible origin for *H. schweinitzii* through the hybridization of *H. microcephelus* and *H. giganteus*, although they did not explain precisely how these two diploid species might have combined to produce a hexaploid species as they reported *H. schweinitzii* to be.

Even with recognition of its distinctive tuberous roots, *H. schweinitzii* continued to be confused with other species in the post-World War II years (including sometimes by Heiser), leading to mistaken reports that once again inflated the species' geographic and ecological range beyond the Carolina Piedmont -- but this time toward the east rather than toward the west. Albert E. Radford and colleagues (1964, 1968) reported localities of *H. schweinitzii* from both the North Carolina coast and from the central South Carolina sandhills, and from the inclusion of these collections they reported the habitats for the species as "upland woods, thickets and pastures". These specimens were also included as locations for *H. schweinitzii* in Heiser's 1969 monograph, where Heiser added an additional report from the northeastern coastal region of South Carolina. In this monograph Heiser conspicuously refrained from offering any generalizations regarding the habitat of *H. schweinitzii*.

All these locations from outside the Carolina Piedmont have since been rejected as misidentifications (see Matthews et al. 1997 for discussion), but backed by the authority of Heiser and Radford et al., these coastal and sandhill region specimens were cited for years in descriptions of *H. schweinitzii* (from

Heiser et al. 1969 through Kral 1983), perpetuating an ecologically confused and falsely wide-ranging view of the species and the habitats in which it occurs. This led to much confusion in the literature, as seen in Gershenzon and Mabry's (1984) phytochemical study titled "Furanoheliangolides from *Helianthus schweinitzii*" based on Coastal Plain plants that are now considered not to have been proper *H. schweinitzii* at all, but *H. floridanus*.

Although a consensus that *H. schweinitzii* is restricted to the Carolina Piedmont has generally held since the species' recognition as a federally endangered species in 1991, misidentifications and mistaken range expansions continue to appear. Reed Noss' recent book, *Forgotten Grasslands of the South: Natural History and Conservation* (2013), errs in listing Schweinitz's sunflowers among the species to be found at Difficult Creek Natural Area Preserve located in the southern Piedmont of Virginia. Although the Difficult Creek site is a highly diverse locality with many rare and endemic Piedmont prairie associated species (including *Echinacea laevigata*), Schweinitz's sunflower is not known to occur there, just as it is not known to occur anywhere in the state of Virginia and is not included among the Virginia Natural Heritage Program's most recent comprehensive list of rare plants known from that state (Townsend 2016).

The botanical history of *H. schweinitzii* reads a bit like a comedy of errors, but the end result is that we have not a single description of the habitat of a truly tuberous-rooted *H. schweinitzii* dated to before the Second World War, and very few reliable habitat descriptions even from decades thereafter. Thus the pre-modern “natural” habitat of the species remains unknown (never mind its prehistoric habitat), as does the reason for its unique geographic range (confined to oddly selective portions of the Piedmont in North and South Carolina).

Perhaps it took so long to recognize *H. schweinitzii* as a Carolina Piedmont endemic because botanists did not expect the Carolina Piedmont region to posses unique endemic plants. As Moses Curtis, one of the original discoverers of *H. schweinitzii,* once wrote:

> 'In this district [the North Carolina Piedmont] the forests are characterized by a predominance of Oaks, as the lower [Coastal Plain] is by Pines. It is far less productive of rare and peculiar plants than either of the others [the Mountain and Coastal Plain regions]… I cannot recall any one species which can be considered as giving a character to this district distinct from that of the States lying north or south of it.' (Curtis 1860, p.xi)

Peculiar or not, Schweinitz's sunflowers must have existed in some sort of habitat before the creation of the maintained right-of-ways where 90% of all populations exist today. With an absence of any reliable historical records to act as a guide, the interest created by listing *H. schweinitzii* as an endangered species stimulated numerous (often contradictory) speculative attempts to explain the historical ecology of this species, which will be examined next.

3. Review of Hypotheses 1991-2002: The first ten years

3a. Murdock's Bison and Natural Fire Model, and Critique

In the 1991 ruling that made Schweinitz's sunflower a federally endangered species (Murdock 1991), the US Fish and Wildlife Service clearly appreciated the relevance of historical ecology to the conservation of this species. The short (five page) ruling included quotations from two mid-19th century historians who described the York County region of South Carolina in the 1700's as having once had much "open prairie" and a formerly great abundance of game, including bison, elk, and deer (the sources Murdock quotes are John Henry Logan's (1821-1885) *A history of the Upper Country of South Carolina* (1859), and Elizabeth Ellet's (1818-1877) *Domestic history of the American Revolution* (1850), with Logan (1859) quoted directly and Ellet (1850) quoted indirectly through Douglas Summers Brown's (1903-2007) book of local history, *A City Without Cobwebs: A History of Rock Hill, South Carolina* (Brown 1953)).

This was an unusual approach for the *Federal Register* – most listing statements for endangered plants do not invoke 19th century amateur historians – yet these quotes (from writers who were not first-hand witness to the 18th century scenes they claimed to describe) were used as the basis for Murdock's claim that "natural fires, as well as large herbivores, including elk and bison, are part of the history of vegetation in this species' range". Murdock then claimed that "extirpated populations [of Schweinitz's sunflowers] are believed to have succumbed as a result of suppression of natural disturbance (fire and/or grazing)", among other causes of habitat destruction. Murdock concluded by claiming, definitively, that "fire suppression and absence of grazing by large native herbivores are a serious problem for this species" (p.21689).

The model of ecological history proposed in this federal listing statement is, in retrospect, problematic. It was notable for its total omission of any acknowledgement of anthropogenic ecological influence in pre-modern times. This was particularly strange since Murdock quoted from two historical sources who extensively discussed historical Native Americans in the exact region under consideration (e.g., throughout Logan 1859; and Brown authored an entire book specifically on the Native Americans of York County, *The Catawba Indians: The People of the River* (Brown 1966)), yet there was no mention of Native Americans in Murdock's statement. This view, that Native American influences need not be considered, or even mentioned, was not unique for its time. The guiding document for the classification of "Natural Communities" then used by the North Carolina Natural Heritage Program (Schafale and Weakley 1990) began with a discussion on the question of "naturalness", and whether there was any difference between taking the pre-European North Carolina circa 1500AD as a standard for naturalness, versus making the hypothetical conditions of a totally human-free Earth as the standard for "natural" conditions. The conclusion:

> "In practice, very rarely, if ever, do we know both the presettlement and potential natural state and know them to be different from each other. Because of our limited knowledge and our imperfect examples, the difference between the two views is seldom of major practical importance." (Schafale and Weakley 1990, p.1)

Under this view, "very rarely, if ever" do we have reason to think that there would be any difference between a historical ecology that includes Native Americans, and an ecology that is 100% *Homo sapiens* free.

Murdock's omission of Native Americans from the historical ecology of

Schweinitz's sunflower can be understood in the context of this view, thusly presented by the leading governmental conservation agency in the state of North Carolina. A full discussion of the motives and views historically taken by ecologists, particularly government ecologists, on Native Americans is beyond the scope of this work, but it can safely be said that the approach geographer William Denevan (1992) called "the pristine myth", which explicitly treated Native Americans as "transparent in the landscape", was widely employed by many authoritative sources through the 1990's.

In contrast to the invisibility of Native Americans, the hypothesized historical grazing by large native herbivores was mentioned at least five separate times in the Schweinitz's sunflower listing statement, usually together with "natural fires". Although this was not stated, the emphasis on extirpated grazing herbivores may have been felt necessary because both Logan (1859) and Ellet (1850) agreed (and this was a first-hand observation) that the prairie-like clearings remembered in local tradition from the 1700's did not persist but had succeeded to forest by the time of their writing in the 1850's. If the clearings reportedly present in the 1700's had been maintained by "natural fire" alone, it would be difficult to account for this rapid disappearance, since forest fire suppression technology in the early 1800's was practically non-existent. Whatever the "natural fire" frequency in the 1700's may have been, it is implausible that it would have changed so dramatically in such a short time. The rapidity of this succession from prairie to forest drew comment from other writers before Ellet and Logan, and Logan quotes from William Henry Foote's *Sketches* *of North Carolina* (1846) which describes the region's rapid conversion:

> "Emigration was encouraged and directed very much in its earliest periods, by the vast prairies, with pea-vine grass and canebrakes, which stretched across the States of Virginia and Carolina. There are large forests now in these two States, where, a hundred years ago, not a tree, and scarce a shrub could be seen". (Foote 1846, p.79)

Such a dramatic change demands an explanation, and given the obvious inadequacy of attributing the change to suppression of natural fire alone, Murdock's effort to identify some other process becomes understandable, although contemporary archaeologists, had Murdock consulted with them, would have found the emphasis on grazing buffalo and elk misplaced. In a 1990 article tellingly titled "The Bull in the North Carolina Buffalo" H. Trawick Ward systematically discredited the idea that ecologically significant numbers of American buffalo (*Bison bison*) were historically present in the North Carolina Piedmont. Oral traditions about wildlife may be plentiful, but many such stories were little more than plagiarized tall tales (for example, Logan (1859) also described, in all seriousness, multiple witnessed accounts of deadly venomous "hoop" or "horn snakes", supposedly with a sting in their tail capable of killing trees overnight; although mentioned by many early writers, obviously no such snakes are now credited as having ever existed in the region), and there is, Ward claims, not a single scrap of Holocene bison bone that has ever been recovered from any North Carolina Piedmont archaeological site. Ward knows whereof he speaks, since he literally "wrote the book" on archaeology in North Carolina

(Ward and Davis 1999) and particularly specialized in Native American sites of the North Carolina Piedmont. If anyone would have been able to offer concrete physical evidence to support bison on the Carolina Piedmont prairies, it would have been Ward, who nonetheless concluded that there was "considerably more bull than bison in the North Carolina buffalo" (Ward 1990, p.29)

The existence of a diverse megafauna in the Carolinas during the Pleistocene is not in dispute, and multiple *Bison* species could have roamed the Piedmont during that time, but extirpations in the far distant past are not relevant to explaining the rapid disappearance of Piedmont clearings reported between the late 1700's and early 1800's. The fragmentary nature of the fossil record makes it difficult to say precisely when large Ice Age bison herds may have finally disappeared from the Carolinas, but it is interesting here to note results from a recent study (Moore et al. 2016) of artifacts from the Central Savannah River area which used immunological assays to test Paleoindian and later stone artifacts for reactions from proteins preserved in microfractures on the faces of the tools. That study found that a small percentage of the stone tools they tested from very early archeological periods (but none of the tools from later periods) tested positive for bovid protein (presumably bison), and these authors concluded that "these studies suggest that bison were present in the Southeast at least through the tenth millennium B.C. and possibly much later, with at least some remnant populations persisting into the early part of the Middle Archaic [roughly 6,000 years B.C.]" (Moore et al. 2016, p.142). This would leave the southeast free from even "remnant populations" of bison for well over 5,000 years before Europeans arrived. Given that Piedmont fields succeed to forest in a few decades, there is currently no archaeological basis whatsoever for attributing the "Piedmont prairies" observed by Europeans to bison.

The archaeological absence of bison in the Carolina Piedmont is supported by the historical record, particularly the written accounts from multiple Spanish expeditions who traveled throughout the southeast, including the Carolina Piedmont, in the 1500's, none of which reported seeing any live bison until they reached points near the Mississippi. These Spanish explorers were aware of bison in North America from earlier ventures in Mexico and Texas, and they hoped to find the beasts in the southeast to feed their soldiers, who were often on the brink of starvation. Some early 17th century accounts of the De Soto expedition claimed that the Spanish had continuously questioned the native peoples they encountered about bison as they traveled through the southeast, but even the brutally enhanced interrogation techniques employed by conquistadors could not extract directions to southeastern bison herds which apparently did not exist (Van Horne 2012).

In the absence of any Spanish bison accounts from the 1500 or 1600's, the stories of bison sightings we do have from the Carolinas date from a brief period in the early 1700's when English settlers appeared to describe small numbers of bison as wandering into the Carolinas from points to the north and west. Ward sees this phenomenon as related to the decline of Native American populations by that period resulting from diseases introduced by those earlier Spanish explorers, theorizing that a relaxation of hunting pressure in the south-central states and the lure of abandoned Native American village fields would have drawn some wandering bison briefly eastward, only to face a rapid extermination from westward-flowing 18th-century European hunters and settlers, leaving only their legend (and not a single bison bone) behind.

Alternatively, it is also possible that the reports of Carolina "buffelo" from the early 1700's were descriptions of feral cattle (*Bos taurus*), not American bison (*Bison bison*), as Van Horne (2012) argued was the best explanation for similar reports from Georgia in the same period. It was a world-wide conventional English usage in the 1700's to use the term "buffalo" to describe any wild cow or cow-like animal suitable to make "buff" (leather) hence use of the name "water buffalo" to describe the domesticated bovids found in Asia, and "Cape buffalo" to describe an unrelated wild bovid in Africa. Feral cattle were reportedly well established in southeastern Virginia by the 1690's, and in northeastern North Carolina by the 1730's (Sawyer 2010), and small feral herds persisted well into the 20th century (e.g., Wood et al. 1987). Some evidence suggests an earlier date for their establishment in North Carolina, as colonial laws from as early as 1673 were established "For prevention of uninterested person in huntinge & killinge wild or out-lyinge Cattle" in what was then known as "Albemarle County" of "Carolina", demonstrating that concerns over "wild" cattle pre-date the creation of North Carolina as a distinct colony (Clark 1906, p.138). Jamestown Colony in southern Virginia is known to have imported cattle as early as 1611, a vaguely reported short-lived Spanish mission in Virginia is said to have kept cattle in the 1570's, and there were also reports of cattle escaping from the (soon-to-be-lost)

Roanoke colony in North Carolina at around the same time (Sawyer 2009). If Carolina "buffalo" sightings from the early 1700's were in fact based on feral *Bos taurus* (with the tales perhaps embellished with details derived from travelers' stories based on actual American bison seen in other states), then this could explain the timing of such reports from the 1700's but not earlier, as well the many "buffalo" toponyms in the Carolinas, all in a manner that does not ignore the total absence of archaeological *Bison bison* bones in the Carolina Piedmont.

Under either of these scenarios (short-lived bison in-migration, or feral cattle confusion in the early 1700's), any bison in the Carolina Piedmont would have been far too few and short-lived to have been responsible for maintaining an ecosystem for a narrowly endemic sunflower species which is conspicuously not found in nearby states (such as Kentucky) where the historic presence of bison (and elk) has strong support.

It may be just as well that we do not have evidence for herds of American bison roaming the Carolina Piedmont prairies, since recent long-term experimental studies have found that bison grazing can actually increase the growth of woody shrubs and trees and hasten the conversion of mesic prairie to woodland (Briggs et al. 2002, 2005). Bison primarily feed on grass, and while they do ingest a wide range of herbaceous forbs (including sunflowers, Bergman et al. 2015), they avoid browsing on woody stems. In habitats where rainfall and soil conditions are sufficient to support woodland (as is true in the Carolina Piedmont, and on the margins of the western prairies) a high fire frequency can maintain an area as mesic prairie, but only as long as the fires can burn evenly and hot enough to thoroughly suppress woody plants. By selectively reducing the quantity of standing grass stems available to fuel prairie fires, and thereby reducing fire intensity and increasing fire patchiness, bison can indirectly protect woody plants from fire damage and thereby dramatically speed the conversion of mesic prairie to woodland. This finding from long-term experiments was not available to Murdock in 1991, and even in the late-1990's the same authors who would later demonstrate it had yet to suspect it (e.g., Knapp et al. 1999).

If "natural fire" was manifestly inadequate, and American bison scarce to non-existent (and possibly counter-productive to the maintenance of prairies), there still remains Murdock's suggestion of "elk" as contributing to the historic maintenance of Carolina Piedmont prairies. The archaeological situation for Carolina Piedmont elk is little better than that of Carolina Piedmont bison (Ward 1990), with elk bones being extremely rare in the Carolinas, and Murdock's own source, Logan, admits that by local tradition the "timid" elk disappeared from "upper Carolina" at an even earlier date than the buffalo and "scarcely a tradition lingers among the people to cast a gleam of light upon the early history of the elk in Upper Carolina" (Logan 1859, p.36). While vagrant elk periodically wandering into the Carolina Piedmont from neighboring states was certainly possible (and impossible to disprove), reliable evidence for ecologically significant herds of elk in the Carolina Piedmont simply does not exist.

With Piedmont herds of bison and elk dismissible as unsubstantiated, was there any possible natural agent demonstrably abundant enough to have had influence in the historic Piedmont prairies habitats presumed to have supported

Schweinitz's sunflowers in the days before roadsides and right-of-way clearings? While Murdock's selections placed the emphasis on semi-legendary tales of long-vanished herds of buffalo and elk, Logan's account clearly emphasized another species: "Of all the animals indigenous to this portion of the Cherokee country, the fallow deer was the most numerous and the most important" (Logan 1859, p.26). Logan does not merely relate hunter's tales of enormous deer herds in days gone by -- here he was able to draw upon colonial trade records gathered by other historians to describe how in the 1730's Charleston alone was exporting deerskins at an regular annual rate "above 200,000", and sometimes above 250,000 in a single year (Rivers 1850, p.73). Such numbers attest to the abundance of deer in the Carolinas in the early years of European settlement.

Archeological evidence agrees, showing white-tailed deer bones to be the most common animal remains found at many Carolina Piedmont sites from both the pre-contact and post-contact period (Ward and Davis 1999). The Town Creek Site in Montgomery County, North Carolina, is illustrative, as it is simultaneously one of the best studied Native American sites in the Carolinas, and it is located in the same county as the greatest concentration of Schweinitz's sunflowers. An analysis of faunal remains recovered there reported 7,033 identified pieces of faunal material, with 5,394 of them (77%) identified as white-tailed deer (Wilson and Hogue 1995), while no bison or elk remains were reported from Town Creek.

Working from River's (1850) deerskin export numbers from one South Carolina port (which surely underestimates the actual deer harvest as they do not include animals killed for local skin use, animals exported through other venues, or animals killed but not processed for their pelts), we find the typical annual deer-pelt harvest of 200,000 in the 1730's exceeds the total deer harvest estimated for the entire state of South Caroline in either 2015 or 2016 (195,000 and 172,000, respectively, in Ruth and Cantrell 2017). From this we can see that the current deer population in South Carolina, estimated at ~700,000 for 2016, is not necessarily so different from the deer population of 300 years ago. The current deer harvest numbers represent a decline from the peak year of 2002, when the harvest for South Carolina was estimated at 320,000 from an estimated peak deer population of ~1 million.

While colonial-era deer populations appear roughly similar to modern deer populations, we can also be sure that current deer numbers are dramatically different from the early 1900's when the total population for South Carolina is thought to have been less than 20,000 deer (less than 3% of the present population, concentrated in inaccessible swamps), or even in 1975, when the state's deer population was only half of what it is today.

The high levels of harvest for the colonial pelt trade continued for decades through the 1700's, but in the absence of enforced hunting seasons or other game-conserving restrictions, they did not prove sustainable over the long run, and Logan (1859) could write that "deer is now nearly extinct in the upper county [of Carolina]" and he predicted that while "a few may yet linger, but soon not a representative of the race [of deer] will be found east of the Blue Ridge" (Logan 1859, p.31-32). This did come to pass in the Carolina Piedmont, and when the ethnologist Frank Speck (1881-1950) visited the Catawba community in York County in 1913 seeking to learn of their traditional hunting practices, he was forced to conclude that no Catawba then alive had ever hunted any game substantially larger than a rabbit, so thoroughly extirpated were deer from the York County region by that time (Speck 1946). The possibility that large historic deer populations (which Murdock's own source, Logan, described) could have influenced the historic ecology of Schweinitz's sunflowers (for good or ill), represents a conceptual road Murdock did not explore, and it would be nearly two decades before federal reports considered the potential impact of deer on Schweinitz's sunflowers.

3b. Post-Murdock evolution of the Bison and Natural Fire Model

Three years after Murdock's listing statement appeared in the *Federal Register*, the US Fish and Wildlife Service published a "Schweinitz's sunflower Recovery Plan" (Weakley and Houk 1994). The plan did not reference Ward or any archeological sources directly, but the Recovery Plan's authors did take a somewhat different approach from Murdock regarding the historical role of elk and bison. While Weakley and Houk mentioned Murdock's references to elk and bison and acknowledged that such large herbivores "may have played a role" in the historical ecology of Schweinitz's sunflowers, the importance of the extirpation of these herbivores in the decline of this species was not emphasized. Instead, they wrote that "it is almost certain that fire was the primary force that maintained the openness of the prairies and oak savannas found in the Charlotte area in the eighteenth century and earlier" (p.6). This "primary force" is still non-anthropogenic, as they suggested that “the primary ignition source for the fires was probably lightning, striking upland areas during summer and fall droughts.” However, Weakley and Houk were willing here to acknowledge Native Americans as a potential contributing influence, suggesting that “Native Americans living in the area probably used fire as a land management and hunting tool, and they may have significantly augmented the natural fire frequency in the area” (p.6).

Citing personal communication with anthropologist Dan Simpkins as a source, Weakly and Houk also attempted to use Native American history to explain the modern distribution of Schweinitz’s sunflowers. Since “during the mid-eighteenth century, the area around Charlotte became a refuge for remnant tribes decimated by disease and cultural disintegration…any Native American traditional use of fire … may have continued longer in the area of Union and Mecklenburg Counties, North Carolina, and York County, South Carolina, than in most other parts of the Carolina Piedmont” (p.6), thus explaining the concentration of Schweinitz's sunflowers in that particular area. Despite this bold attempt at a historical explanation for a biogeographic puzzle, Weakley and Houk downplayed Simpkins’ suggestion by cautioning that “evidence of Native American use of fire in the Carolinas is, however, largely circumstantial” (p.6). Despite this, the approach of Weakley and Houk represented a significant change from that of Murdock (1991), in that they made some acknowledgement of a Native American presence and granted a possibility for that presence to have been ecologically influential. White-tailed deer, however, remained entirely unmentioned.

The next major step in reinterpreting the historical ecology of the Piedmont prairie came in a 1997 article in the *Natural Areas Journal* by Lawrence Barden, then a professor at the University of North Carolina-Charlotte and a consultant on numerous Schweinitz's sunflower projects. Barden presented a compilation (largely drawn from the work of geographer Erhard Rostlund in the 1950's) of historical sources from the 16th– 19th centuries which all described large open areas in the Carolina Piedmont region, as well as numerous sources describing how Native Americans deliberately set fires which maintained the clearings. Barden reasoned that summertime lighting-caused fires would have played no more than a "minor and infrequent" role, and that Piedmont prairies generally developed "under a regime of primarily dormant season, human-caused fires over a period of thousands of years" (p.152). Barden's conclusion that "these prairies and forests were legacies of Native American culture" (Barden 1997, p.152) agrees fully with the argument of William Denevan that "the Native American landscape...was a humanized landscape almost everywhere...forest composition had been modified, grasslands had been created" (Denevan 1992, p. 369), although Barden does not reference Denevan's work.

Barden also does not cite Ward (1990), but he does consider the claims made for bison in the Carolinas and finds them weak, suggesting (like Ward) that 19th century writers (who were not eyewitnesses) are unreliable, and the pattern in the earlier sources suggests an initial absence of live bison sightings in the 1500's, followed by a few sightings in the early 1700's, a peak in the mid-1700's, and then a rapid decline in "buffaloe" reports. This was interpreted (following

Rostlund 1960) as resulting from a brief period of in-migration by a few wandering western bison into the formerly human-maintained open clearings of the Carolinas following the collapse of hunting pressure from previously high Native American populations.

Overall, Barden's vision of ecological history was practically the opposite of Murdock's, as it portrayed the Piedmont prairie as a fundamentally anthropogenic ecosystem, created by deliberately set fires, and populated with plant species which gradually migrated into the resulting prairie habitats of the Carolina Piedmont from more westerly prairies over thousands of years of aboriginal burning, with bison being only a brief and ecologically insignificant interloper to the Carolina Piedmont.

Following Barden, the only further step possible in this vein is to suggest that the Schweinitz's sunflowers themselves were not merely the indirect beneficiaries of aboriginal burning practices, but that Schweinitz's sunflowers were directly influenced by deliberate Native American actions. This was suggested in 1999 by C. R. Matthews and J. H. Howard, in a genetic diversity analysis (derived from Matthews' 1996 master's thesis work at UNCC) of the species and published in the journal *Castanea*. Using allozyme electrophoresis to investigate the genetic differences between twenty-five Schweinitz's sunflower populations, they found no correlation between the genetic difference and geographic distance. A possible explanation they suggested was that "tribes or groups could have used the tubers of the plant for food and actively cultivated the plant as family groups moved from one area to another" (Matthews and Howard

1996, p.238). Such a practice would have altered gene flow and “erased” any geographic patterns of relatedness. Despite making this suggestion, Matthews and Howard concluded that a formerly large and contiguous population could have more plausibly accomplished the same genetic mixing.

Finally, in 2002, ten years after the initial listing of Schweinitz's sunflower as an endangered species, another paper in *Castanea* presented a synthesis of a decade of work. The lead author, J. Eric Davis Jr., representing the Fish and Wildlife Service, together with two UNCC professors (Barden and J. F. Matthews) and former UNC graduate students as co-authors, flatly stated that “historic Piedmont prairies were maintained primarily by anthropogenic fire” (p.1) and “anthropogenic fire and drainage patterns largely determined Piedmont prairie locations” (p.4). Following Matthews and Howard (1999), they suggested that "the endangered Schweinitz’s sunflower may have served as a food source – the tuberous roots being edible” (oddly, this statement was supported by a reference to “Barden 1997”, although that work contained no discussion of the edibility of sunflower roots) and “trade among tribes in the Piedmont was common and have [sic] contributed to genetic exchange” (Davis et al. 2002, p.5). This claim was further supported by reference to a master's thesis by Estep (2001), another UNCC graduate and co-author, which found no evidence for ecotypic variation between Schweinitz’s sunflower populations, again implying a well-mixed population. The hesitancy of Matthews and Howard (1999) is gone – no alternative hypothesis is presented – Schweinitz’s sunflower tubers are here presented as just another item on the prehistoric inter-tribal commodity market.

3c. Discussion of the first decade (1991-2002)

For anyone interested in the history of science, or in what a "paradigm shift" looks like as it happens in real time, this ten-year sequence will have intrinsic interest. From paper to paper, we see the interpretation of the pre-modern ecology of a species move, step-by-step, from total and unquestioned anthropo-independence to a default assumption that the species was cultivated, transported, traded, and that human actions have determined everything from the species' genes to the construction of its ecosystem.

In the terms of the geographer William Denevan, this is the shift from the paradigm of "the pristine myth" to the paradigm of the "humanized landscape" (Denevan 1992). What is remarkable is how little actual evidence was needed to push this transition. It is true that the original 1991 version of Piedmont prairie historical ecology was ripe for challenge on numerous archaeological, historical, and ecological grounds, but very seldom were these ever made explicit -- the lack of archaeological evidence for Carolina Piedmont bison, certainly a powerful piece of evidence against the bison-natural fire hypothesis, was never cited at any point. No evidence -- historical or archaeological -- was produced showing that any particular Native American tribe ever cultivated, traded, gathered, or used Schweinitz's sunflowers in any way. The original questions regarding the strangely restricted distribution of Schweinitz's sunflower remain unanswered – in fact, they are more mysterious than ever. Under the assumption that sunflower tubers were traded among tribes, wouldn't that suggest a wider distribution, not a narrowly restricted one? If the use of fire for forest clearing was so ancient –

going back thousands of years – and also widespread, being employed by native cultures not only throughout the Carolinas but throughout much of North America, wouldn't that also suggest a wider distribution for Piedmont prairie habitat and thus for Piedmont prairie species, like the Schweinitz's sunflower? If a number of other prairie species from the west (for which no cultivation or trade has been proposed) could follow anthropogenic prairie habitats all the way to the Carolinas, then why couldn't Schweinitz's sunflower manage to spread within the Piedmont a mere 30 km (19 mi) from Charlotte to Gastonia, where suitable habitat appears to exist and other rare Piedmont prairie species are found? The same could be asked of the gap between Rock Hill and Chester, or between Albemarle and Durham? Does this "humanized landscape" interpretation make any testable, falsifiable predictions at all? Or is this, as T. C. Chamberlin (1890) would have put it, simply the trading of one "ruling hypothesis" for another?

4. Review of Hypotheses 2002-2013: The Second Decade

4a. Emerging concerns

Given the productivity of research on Schweinitz's sunflowers during its first decade as a federally endangered species, one might expect continued strong activity in the second ten-year period as well. This did not take place. Five master's theses were produced at UNCC between 1991-2002 which focused on either the Schweinitz's sunflower specifically or the Piedmont prairie ecosystem generally. In the next decade only one related UNCC thesis was produced, a re-analysis of the genetic diversity between Schweinitz's sunflower populations using newer techniques (Savin 2004), and the result simply confirmed Matthews and Howard's earlier (1999) finding that genetic differences do not correlate with geographic distances.

Most of the faculty previously active in Piedmont prairie research (Barden, JF Matthews, Houk) retired during this decade, which accounts for the reduction in new work by graduate students. One master's thesis was completed in this period from the University of North Carolina – Greensboro (Smith 2008) which focused on the more northerly Schweinitz's sunflower populations around Montgomery County rather than on the previously studied southerly populations in York and Mecklenburg Counties. Smith analyzed a number of site variables for Montgomery County populations, and her soil type findings differed substantially from the conventional wisdom of the species' preferences. Earlier writers acknowledged that Schweinitz's sunflowers grew in a wide range of soil types, but a preferential association was often claimed with mafic-rock derived soils (higher in pH, and regionally uncommon) and soils with high clay components (e.g., Weakley and Houk 1994). Smith found many Schweinitz's sunflower sites were in felsic-rock derived soil (lower in pH, and regionally abundant) and in soil textures that were most frequently sandy loams or silty loams – not the high-clay textured soils expected. Documenting Schweinitz's sunflowers in a variety of common soil types only reinforces the difficulty of explaining the species' narrow distribution. Smith also attempted to use GIS data to test for a relationship between sunflower sites and historical features (such as historic trails/archaeological sites) within Montgomery County – a close relationship would seem to be a prediction of the human-cultivated species model suggested by Davis and colleagues (2002). Montgomery County has both a high abundance of archaeological sites and a high abundance of Schweinitz’s sunflower populations essentially scattered throughout. Analysis using these features did find evidence of a non-random relationship between the two, but not evidence of a very close relationship. The analysis also found one present-day feature -- roads -- were very closely correlated with sunflower population locations, an unsurprising conclusion in agreement with decades of unquantified observations about Schweinitz's sunflowers and managed right-of-way areas.

In addition to the decline in graduate theses, only one peer-reviewed article focused on Schweinitz’s sunflowers appeared during the plant's second decade (2002-2013) as an endangered species: a review of its biology by Steven Fields published in the *Journal of the South Carolina Academy of Science* (2007). Fields opened his review with a declaration of his willingness to reject of "the pristine myth" by noting that “no valid discussion of ecology…can exclude humans” (p.27). As is appropriate in a review paper, Fields summarized all elements presented by earlier writers (herbivory by bison and elk, natural fire, and anthropogenic fire) suggesting that natural forces could potentially have acted in combination with anthropogenic forces to maintain Piedmont prairies, writing that "[N]atural forces were no doubt a factor in keeping succession at bay in historic times" (p.28). Fields repeated the hypothesis that Native Americans may have cultivated Schweinitz's sunflowers for its edible tubers, and thus impacted its gene flow, while also acknowledging other hypotheses (a prehistoric region-wide population, or a recent origin through polyploidy speciation) as alternative explanations for the genetic results of Matthews and Howard (1999) and Savin (2004). Fields proposed that by hunting the large herbivores and displacing the Native American fire-starters, Europeans are the likely cause of the Schweinitz's sunflowers' decline, but “ironically” they also created the roadside habitats that have allowed the species to continue to survive. Deer were not mentioned by Fields, and despite over 15 years of federal protection and conservation, he was not optimistic about the trends for the species, and closed with this vague but ominous conclusion:

> “Even with no detailed ecological data it seems clear that without human intervention, extinction will come sooner rather than later for this species” (Fields 2007, p.31).

Fields' review was focused on Schweinitz's sunflowers in the southern extreme of their range, in north-central South Carolina, but negative trends in Schweinitz's sunflower populations were being reported from many parts of its range. Tompkins and colleagues (2010) described a species rich and partially hydric Piedmont prairie discovered in a utility right-of-way in Montgomery County, near Troy in the Uwharrie region of North Carolina. A floristic inventory conducted in 2008 found only five individual Schweinitz's sunflowers remained out of the approximately 100 individuals observed when the site was discovered in 2003. They attributed this "significant" decline to an unspecified "human disturbance" to the site in 2004, and speculated that the decline was worsened with the "recent clear-cut logging of the surrounding area of the site" (Tompkins et al. 2010, p.124). Given that Schweinitz's sunflower has always been described as disturbance dependant and shade intolerant, it is remarkable that logging of a site's surroundings would prove to be such a catastrophic event to the population -- particularly when of the many rare species reported from the Troy site, only the Schweinitz's sunflower was described as having declined. The authors suggested that "a management strategy" be implemented to stabilize the remaining population (now 5 individuals), but they did not say what possible management action might be effective. Extinction did indeed appear to be coming sooner, rather than later, for this population.

In 2010 the US Fish and Wildlife Service (FWS) released what it called a “5-Year Review” (Bibb 2010) for the Schweinitz’s sunflower – the first such comprehensive review since the initial Recovery Plan of 1994 (although state-specific "Status Surveys" for the species had been produced in 2003). This report was seemingly able to point to good news -- in 1991 the known population of Schweinitz's sunflowers had been less than 3,000 stems distributed across six counties, but subsequent discoveries of previously unknown populations (particularly in the Uwharrie region) allowed the FWS to report over 40,000 stems and a known distribution across 15 counties in 2010. Despite this, the species remained in danger because "none of these populations currently show a steadily increasing trend over a period of five years" (Bibb 2010, p.6).

While the FWS here agreed with Fields' recently reported concern for the future of extant Schweinitz's sunflower populations, the FWS review rejected Field's openness to including both anthropogenic and "natural" forces in modeling its historic ecology. The FWS review did not reference Fields' paper and ignored all other research pointing towards an anthropogenic component to historic ecology for Schweinitz’s sunflowers. Instead, the FWS presented the threat to the species in terms drawn directly from the original 1991 listing statement, maintaining that the plant was threatened due to the loss of “natural disturbance (from fire or native grazers)” which are “now largely absent from the present day landscape” (Bibb 2010, p.9). There was no mention of the evidence presented by Barden (1997) that the Piedmont prairie may itself have been anthropogenic in origin and dependant on human-set fire, rather than "natural" fire, and no mention of the evidence that the bison and elk “native herbivores” proposed by Murdock (1991) may never have existed in the Piedmont in ecologically significant numbers. The absence of any mention of possible historical influence from Native Americans, despite their discussion in peer-reviewed publications (e.g., Davis et al. 2002, Matthews and Howard 1999) and even in the original FWS 1994 Recovery Plan (Weakley and Houk 1994), cannot have been accidental, yet no explanation for this omission was given. The anthropogenic hypothesis for Piedmont prairies was not refuted within the 2010 FWS 5-Year Review; rather, the hypothesis, and by extension, all Native American civilization -- was simply treated as invisible. In the words of William Denevan: "the myth persists".

The decision in 2010 to place extirpated “native herbivores” back in the center of Schweinitz's sunflower's ecological model by excluding Native Americans was doubly strange, since the FWS was at the same time acknowledging declines in protected populations, and to explain those declines the 2010 FWS report was willing to reverse the earlier statements that predation was "not applicable" as a threat (Murdock 1991) by acknowledging the possibility that browsing by the sole remaining large native herbivore in the Carolina Piedmont – the white-tailed deer – “may be significantly affecting the survival of transplanted individuals and some native, resident populations” and “may now constitute a significant threat to the species if left unaddressed” (Bibb 2010, p.10).

Although the 2010 FWS 5-Year Review cited only personal communication with a NCDOT employee to support their new position on the possibility of deer damage to Schweinitz's sunflowers, some earlier sources had made incidental acknowledgements of deer browsing on the species. In a master’s thesis Shinn (1996) studied seed germination in Schweinitz’s sunflowers and described a 1994 experiment comparing germination rates in fenced and unfenced plots at Gar Creek prairie in northwest Mecklenburg County, North Carolina. Fencing was not found to affect germination rates (hardly surprising). More interestingly, Shinn described how the idea for the fence/no fence test originated with observations of deer browsing tender Schweinitz’s sunflower sprouts which appeared following a controlled burn conducted at the Gar Creek site in 1993. Shinn claimed this browsing “dramatically reduced” the size of Schweinitz’s sunflowers produced at Gar Creek that year, but no further details were provided (Shinn 1996).

In a later master’s thesis, Estep (2001) sought to assess hypothesized ecotypic variations between Schweinitz’s sunflower populations by performing a reciprocal transplant study. Here browsing was apparently not anticipated (despite Shinn's prior work) and no fencing was used, which resulted in the intended goal of the ecotype study being partially confounded by what Estep called a "substantial" effect on the late-season sunflower height measurements produced by deer browsing. Estep did not quantify this effect, but did note that damaged plants were observed in 44 of 50 plots at one location and 5 of 50 plots at another (Estep 2001). It should be noted that Estep's observations involved his recently transplanted plants, not established plants. It is also worth noting that Estep's heavily browsed location was in the same Gar Creek vicinity where Shinn had previously observed browse damage in 1993.

It is possible the FWS may not have been aware of these earlier deer browsing reports by graduate students, and the students themselves placed very little emphasis on them. The new and tentative concern with deer damage apparently came from a NCDOT source who reported of "80-90%" of transplanted Schweinitz's sunflowers being "consistently" browsed -- a number too large to ignore. By returning to a historical model which posited that the "absence of grazing by large native herbivores" (p.11) was a problem, the FWS placed itself in the awkward position of arguing that *both* the absence *and* the presence of "large native herbivores" constituted "significant threats" to Schweinitz's sunflowers! This conceptual difficulty was not acknowledged within the 5-Year Review, but a reader can hardly escape the implication that regarding large native herbivores, Schweinitz's sunflower purportedly can't live with them, and can't live without them. This seemingly impossible situation agrees with

Fields' earlier conclusion that without human intervention (or if deer browsing was "left unaddressed", as the 5-Year Review puts it (Bibb 2010, p. 10)), extinction was approaching sooner rather than later for Schweinitz's sunflower.

By 2013 more trend data was available for Schweinitz's sunflower populations, and the results were not improving. A "Rare Plant Monitoring Summary" produced for Mecklenburg County (Lampell 2013) described trends from seven Schweinitz's sunflower populations from across that county which had been monitored regularly from 2006-2012. All seven regularly monitored populations declined during that period. In total numbers the combined stem count from these sites dropped from 13,675 in 2006 to 3,509 in 2012 -- a decline of 74%. Two of these populations were on privately owned land, but the other five were on Mecklenburg County-owned properties, and four of these were Mecklenburg County-designated Nature Preserves. The decline cannot be attributed to the lack of protection on privately owned sites, since if the count was restricted to only the four Nature Preserve populations, the 2006-2012 decline would still be 71%. Nor can it be said that 2012 was an unusually bad year -- it actually represents a slight improvement from the 2006-2011 overall decline of 72%. Encroachment by competing vegetation was the only cause proposed in the Summary for the declines at these sites, despite the use of prescribed burns and brush clearing in these preserves by managers specifically intending to maintain sunflower habitat. Herbivore damage was not mentioned in connection with any of the sites under long-term monitoring, but the Monitoring Summary did mention the appearance of "heavy browse pressure from white-tailed deer" at one recently introduced Schweinitz's sunflower site--Dodge City Prairie, a site which will be described in detail in Part I of the experimental portion of this paper.

4b. Discussion of the second decade (2002-2013)

If the first decade of intensive Schweinitz's sunflower research seemed to show movement towards adoption of a Piedmont prairie model inclusive of, or even primarily based on anthropogenic influence, the second decade showed a shift back to Murdock's original non-anthropogenic model based on natural fire and extirpated large herbivores without any reference to Native Americans (e.g., Bibb 2010). The anthropogenic influence model was not refuted by new findings -- it was simply and abruptly ignored.

Overall, the scholarly productivity of the second decade was demonstrably less than the first decade as no significantly new interpretations were offered, and although some new observations were published, they were often presented without making connection to their relevance either for or against any particular hypothesis of historical ecology. While monitoring of many individual populations suggested declines, field work revealed the existence of additional undocumented populations, mostly along roadsides and right-of-ways, and this increased the species' known population and distribution, although still limiting it to the Carolina Piedmont. This marginal expansion of the known distribution of the species may have been what prompted Fields (2007) to write that the "anthropogenic practice [of Native American burning] probably facilitated a large distribution pattern for *H. schweinitzii* and other prairie-adapted species." Fifteen counties in the Carolina Piedmont is certainly more than six, but it should be noted that it is still a highly restricted distribution, far more narrow than any other species found alongside it in these same Piedmont prairies (see Table 1). Of all the species characteristic of Piedmont prairie habitats, Schweinitz's sunflower remains unique as an endemic exclusively found in the North and South Carolina Piedmont (and then in only a portion of the Piedmont, absent from many otherwise extremely rich Piedmont prairie sites). At the end of its second decade as an endangered species, the basic question of why Schweinitz's sunflower has such a restricted distribution remained unanswered, the relationship between the sunflower and native herbivores remained confused and disputed, and the practical interventions needed to address the significant declines reported at many protected populations remained unknown.

5. Applications of Historical Ecology, Predictions, and Testable Hypotheses

Given the swings in scholarly argument and the many enduring mysteries surrounding Schweinitz's sunflower, a practically-minded conservation manager may well ask: what difference does it all make? Why does it matter what we believe about historical ecology? Whether browsing bison or Native American tuber-traders, what does it matter? How does any of this relate to conservation management decisions needed in the present day?

If conservation managers believe the absence of large herbivores is the problem, and that Schweinitz's sunflowers historically needed large herbivores to survive, then there is little reason for them to expect large herbivores in the present day will pose a threat to the species. There would be no reason to fear modern-day moderate levels of browsing if the species is assumed to be adapted to survive under browse intensities from large cervid and bovid ungulates hypothesized to have been powerful enough to have halted forest succession and altered an entire ecosystem's vegetation structure. The management implication from this would be to encourage herbivores at Schweinitz's sunflower sites. Regularly monitoring levels of browse damage would be viewed as unnecessary, and observations of catastrophic levels of browsing (perhaps in the "80-90%" range) may be required before a problem from herbivory is recognized or addressed.

On the other hand, if conservation managers believe Schweinitz's sunflowers have existed for millennia as a cultivated or human-associated species, then there is no reason to expect that heavy herbivory would benefit the species, and no reason to expect Schweinitz's sunflowers should be unusually resistant to browse damage. This would suggest managers should be alert to indications of browse damage, and should support preventative management actions to protect plantings from potentially destructive levels of browse pressure.

Under the presumption of a human-associated past for the species, there are even reasons to expect that Schweinitz's sunflowers could be highly sensitive to herbivores, and could suffer from herbivore damage more readily than other similar wildflower species even when growing side-by-side in the same habitat. A widely noted phenomena in cultivated plants is that they show signs of increased vulnerability to herbivores relative to their wild relatives. A recent meta-analysis of 73 crops across 89 studies found "domestication consistently reduced plant resistance to herbivores" (Whitehead et al. 2017), and that the mechanisms producing this decreased resistance are complex. It is not only fully domesticated cultivars which display this decreased resistance; a study of *Helianthus annuus* (Mayrose et al. 2011) compared cultivated strains of *H. annuus* with strains from wild "natural" habitats and with feral or "weed" strains which grow, unplanted, on human-disturbed sites. They found that both the cultivated and human-commensal "weed" strains displayed increased palatability to insect herbivores and increased susceptibility to fungal infection relative to the "wild" strains from non-anthropogenic habitats.

While the majority of studies on decreased herbivore resistance in cultivated plants have focused on apparent increases in palatability to insect herbivores, studies have also found evidence for domestication producing decreased resistance to mammalian grazing (Waisel 1987). At least 14 species of native sunflower occur in the Piedmont region of North and South Carolina (Weakley 2015); if Schweinitz's sunflowers were found to be uniquely vulnerable to herbivore-induced extinction relative to their congeners, the general phenomena of increased herbivore vulnerability in cultivated or commensal plants could offer a partial explanation.

Native American forest-burning practices would be expected to have increased large herbivore populations at the landscape level, since North America's large herbivores all prefer fragmented forest over unbroken old-growth forest, and historical and archeological evidence supports the view that Native

American burning did indeed produce high deer populations, which they then exploited. Despite the increase in landscape-scale browse pressure expected from a heightened deer population, the immediate areas around Native American villages could have been an exception. These areas would be expected to have experienced concentrated hunting pressure from highly skilled hunters dependant on wild game rather than domesticated livestock to supply their dietary protein -- a phenomenon known as "garden hunting" originally described in the anthropological literature for South America (Linares 1976) which has been more recently applied to Native North American peoples as well (Clinton and Peres 2011). Native Americans in the Carolina Piedmont also kept domesticated dogs (Wilson and Hogue 1995) which may have further contributed to reducing mammalian herbivory in the immediate vicinity of villages. Generations of existence in village-associated habitats kept relatively sheltered from native herbivores by hunters and dogs could have facilitated a loss of herbivore resistance in a Native American commensal or domesticated plant.

Many plant species are highly vulnerable to herbivore damage without having any history in human cultivation, but the possibility of such a human-associated history should give managers reason to take extra precautions in exposing Schweinitz's sunflowers to herbivore pressure -- unless the human-associated hypothesis is rejected in favor of the large-herbivore dependence hypothesis, which would encourage managers do precisely the opposite. Thus a debate in historical ecology retains direct practical relevance to the management of Schweinitz's sunflowers in the present.

A final resolution to this debate may come only from the work of future archaeobotanists or paleoethnobotanists who may recover definitive evidence of Schweinitz's sunflower remains in an archeological context, or establish a clear failure to find such evidence despite many studies capable of detecting such remains, had they been present. At this time techniques capable of detecting a potential root-crop such as Schweinitz's sunflower have not been consistently applied to the Carolina Piedmont. It may be that preservation conditions in the region's archeological record will never allow a definitive answer, but until such investigations are attempted, the possibility remains.

Until then, conservation biologists can indirectly test the present-day implications of the two historical models for Schweinitz's sunflowers by measuring whether mammalian herbivore pressure produces significant negative impacts on Schweinitz's sunflower populations (as the human-associated model would suggest), or whether Schweinitz's sunflowers persist, or potentially increase, under conditions of heavy herbivore pressure (as the ecosystem-altering large-herbivore dependence model would have it). If browsing by native herbivores can be shown to be a key factor in modern Schweinitz's sunflower population declines, then the case for Schweinitz's sunflowers as a historically human-dependant species becomes stronger, and the management actions needed to sustain populations (potentially herbivore exclusion or herbivore population reduction) will become clearer. Answering this question will be the objective of Part II of the experimental section of this thesis.

Part I: Intensive Monitoring at Dodge City Prairie Restoration

METHODS

Site Physical Description

Dodge City Prairie Restoration (Figure 1) is a 3.6 ha (9 ac) Piedmont prairie restoration area located in the northwestern corner of the intersection of York Road (NC Route 49; a four-lane divided highway) and Shopton Road West (State Road 1116; a two-lane paved road), in the southwestern corner of Mecklenburg County, North Carolina, less than 3 km from the South Carolina state line. The site is also the southeastern corner of the 445+ ha (1,100+ ac) McDowell Nature Preserve, a state-registered natural heritage area, which protects the oak-hickory forests which border the prairie to its north. The site is approximately flat, and is irregularly shaped due to a peninsula of forest surrounding a headwater of Porter's Branch, a small stream which enters Lake Wylie and the Catawba River roughly 1.5 km to the northwest. With an elevation of 210 m (700 ft) the site could be considered a local ridgetop, as the adjacent forested land slopes steadily downward to the northwest, dropping over 35 m (120 ft) in elevation before it reaches Lake Wylie.

The site has been mapped as an intersection of three soil types, with Cecil soils in its western half, Davidson soils in its eastern half, and Pacolet soils along the forested border to the north. All three of these soils are described as well-drained, moderately permeable sandy clay loam to clayey soils of medium to strongly acid chemistry (McCachren 1980). Davidson soils are reportedly derived from rocks high in ferromagnesian minerals (i.e., mafic rocks), but they are not described as a basic soil, while both Cecil and Pacolet soils are said to be derived from acidic (i.e., felsic) igneous or metamorphic rocks.

Figure 1: View of Dodge City Prairie. Photo taken 11/7/2017.

Figure 2: Aerial view of Dodge City Prairie, indicating area with Schweinitz's sunflowers in 2013. Image from USDA: https://websoilsurvey.sc.egov.usda.gov/

Site History

Dodge City Prairie is named after a wild-west themed roadside attraction which operated on Shopton Road West during the 1950's. This "Dodge City"-themed park was located roughly 1 km north of the present-day Dodge City Prairie, and the prairie site itself is not known to have ever been developed as anything other than cropland. USGS topographic maps indicate the highway boundaries of the Dodge City Prairie site have been stable at least since the 1940's, with only slight changes as the adjacent roads were first paved, and later widened. These maps also indicate that the northern forest edge of the clearing has also remained largely stable -- a conclusion supported by the mature size of the trees edging the site. Aerial photographs confirm that the core of the site has existed as a continuously open area planted in crops through most of the 20th century -- most recently in corn and wheat (Marshall 2002). Although the surrounding area long remained rural and agricultural, being located almost 20 km from downtown Charlotte, recent expansions of Charlotte's city limits now include land directly adjacent to the site on the east side of Shopton Road West. The site's vicinity today is dominated by suburban residential and light commercial development, and heavy traffic is normal on both roads bordering the site. As an unforested parcel adjacent to an increasingly busy intersection, the site would likely have been sold and developed had it not been acquired as part of McDowell Nature Preserve.

Conservation History

McDowell Nature Preserve's roots go back to 1975 with the creation of McDowell Park, initially concentrated along the immediate shoreline of Lake Wylie. This Mecklenburg County park gradually expanded in size, and its focus evolved from recreation to conservation, reaching nearly its current size and officially becoming "McDowell Nature Preserve" with the adoption of a new master plan in 1997. The "restoration" of the Dodge City Prairie site within McDowell Nature Preserve began in 1999, supported through the USFWS Partners Program, with a planting of a mix of switchgrass, indiangrass, and big and little bluestem on the unforested land left by the former crop fields near the Shopton Road intersection. Prescribed burning was initially avoided due to concerns over the impact of smoke on traffic on adjacent York Road, and periodic "brush-hog" mowing was used to prevent tree encroachment on the clearing. The Dodge City Prairie site is not known to have supported any remnant Schweinitz's sunflowers at the time of its first restoration planting, although the historic presence of the species in the vicinity is supported by the discovery of a very small, but apparently natural population three miles north of Dodge City at Winget Park, another Mecklenburg County-owned property.

History of the Dodge City Schweinitz's Sunflower Population

The first attempt at introducing Schweinitz's sunflowers to Dodge City Prairie came in 2000, with an experimental planting of seeds collected from the McDowell Prairie Restoration site. These seeds did not establish a population. In 2004 over 100 Schweinitz's sunflower plants were relocated to Dodge City

Prairie as mitigation for plants threatened by a construction project on Remount Road near downtown Charlotte. Most of these plants disappeared in 2005, and searches in 2010 for any survivors from this planting failed to locate any.

Following the determination that the first mitigation planting at Dodge City Prairie had failed, a second introduction of mitigation transplants was made in November of 2010, this time using plants displaced from Fort Mill, South Carolina (Lampell 2013). By 2010 the "restoration mix" of warm-season grasses had developed into a dense tall-grass stand across the Dodge City site, leaving very little soil surface exposed and allowing little growth by forbs of any kind. The second mitigation project therefore planted its relocated Schweinitz's sunflowers at intervals along the treeline on the northern edge of the site, where shade from overhanging tree limbs limited the density of the grass. A total of 633 stems with roots and 50 additional roots without stems were planted in clusters along the treeline at close intervals, and these planting sites were marked with small white plastic flags. This essentially linear planting method followed the curving treeline for approximately 100 m (Figure 2). Monitoring in the fall of 2011 found 62 blooming stems, which declined to 30 stems in 2012. Following the 2012 count observers reported that "This population appears to be experiencing heavy browse pressure from white-tailed deer" (Lampell 2013).

Survey Method

During a site visit in early May of 2013 a few very small stem sprouts were observed which resembled the expected appearance of early-season Schweinitz's sunflowers, but species-level identification at this very early growth stage is difficult. No evidence of browse damage was seen on these small sprouts, and quantitative measurements were not taken. Systematic data collection at Dodge City began in mid-June, and was repeated at intervals through the growing season, from late spring to early fall, with the final measurements being taken in October, near the end of the flowering period, but before most plants were senescent (see Table 2).

Table 2. Generalized phenology of Schweinitz's sunflower.

Month	**Schweinitz's sunflower phenological events** *Individual plants may vary from this timetable
April	Earliest shoot emergence.
May-July	Vertical stem growth.
August to Early-September	Proliferative stem branching and flower bud formation.
Early-September to Mid-October	Anthesis.
Mid-October to Mid-November	Seed ripening and leaf senescence.
Late November to April	Death of above-ground stem. Dormancy.

Stem-measurement surveys were conducted on June 18, July 4, July 18, August 2, August 27, and October 8 of 2013. On each of these dates every stem was measured in cm with a meter stick. If the main stem was observed to be browsed/broken, the height to the break was recorded, as well as the height of any axillary stem(s) which appeared to be developing into new leaders. Qualitative observations of insect activity or damage and observations of general plant health were also recorded.

Stems often emerged in close proximity (<~.1 m) to one or more other stems, followed by a larger gap (>~.1 m) to the next nearest stem(s). These groups of close-proximity stems are here referred to as "clusters". This spatial distribution is presumed to be result of the planting method used in 2010 rather than subsequent dispersal, based on the remains of old plastic flags near many of these clusters. Singleton stems are also described as single-stem "clusters" in this study. For this study, stem clusters at Dodge City were marked with small wooden stakes labeled with a unique number identifier written on one side of the stake, positioned so that the referenced cluster would normally be behind the stake when the stake was viewed from the labeled side, allowing reliable identification of indicated stems with the same stake during subsequent surveys.

Stem Data

Stakes marking 87 clusters presumed to be young Schweinitz's sunflowers were installed in mid-June. Two of these clusters were recognized in July as being based on misidentifications of tiny sprouts (<10 cm) of species other than Schweinitz's sunflower, and were removed from the data set, leaving 85 stem-clusters which were tracked through the fall. The 85 clusters contained a total of 168 stems that were identified in the initial June survey. Subsequent surveys discovered an additional 10 stems, which could all be identified with existing clusters by proximity. These late-found stems tended to be either very small, obscured by dense surrounding grass, or both. The majority of these (6 of 10) were discovered on the second survey (Jul 4), with two further additions on the third survey (Jul 18), and two on the fourth survey (Aug 2). No new stems were discovered in the final two surveys (Aug 27 and Oct 8), despite attention during every survey to look for potentially undiscovered stems. The July 4 additions were all smaller than average stems ($\bar{x}$ =13.5 cm, range 6-21 cm SD=6.4 cm vs. $\bar{x}$ =35.6 cm, range=10-135 cm, SD=20.6 cm for the stems detected in June) probably overlooked due to their small-size (or non-emergence) at the time of the initial June 18 survey. The only moderately large (45 cm) stem found late (on Aug 2) was hidden in an especially dense clump of tall grass which prevented its earlier discovery.

Stems tend to become taller and more obvious later in the season, and the lack of further late-season discoveries and the overall asymptotic-approach pattern of stem detections suggests the June 18 count succeeded in detecting the overwhelming majority of stems present (94% of the final tally), and that the final number of stems detected (178) is likely extremely close to, or a precise measurement of, the total number of Schweinitz's sunflower stems which emerged at the Dodge City site during the 2013 season. Because stems discovered after the initial June 18 survey represent such a small percentage (6%) of the total, and since data on these stems is necessarily incomplete (lacking at least one measurement) relative to the other stems, these stems will be set aside from the remainder of the analysis of the data from Dodge City.

Cluster data

The clusters varied in size, containing between 1 and 9 stems each. Although a majority (60%) of the clusters contained only one stem, a majority (70%) of the stems occurred in multi-stem, rather than single-stem clusters (30%). Two-stem clusters were the most frequent (44%) kind of multi-stem cluster, although a narrow majority (51%) of all stems occurred in clusters with more than two stems (see Table 3).

Table 3. Distribution of Schweinitz's sunflower stems in clusters at Dodge City Prairie in 2013.

# of Stems per Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
# of Clusters (85)	51	15	5	7	2	3	1	0	1
% of All Clusters	60	17.7	5.9	8.2	2.4	3.5	1.2	0	1.2
# of Stems (168)	51	30	15	28	10	18	7	0	9
% of All Stems	30.4	17.9	8.9	16.7	6.0	10.7	4.2	0	5.4

*Percentages may not total to 100 due to rounding.

Method of herbivory measurement

A primary objective of this study was measurement of herbivore impacts, particularly claims of "heavy browse pressure from white-tailed deer". The measurement system used involved the recording of the height of every stem known at the site on six dates through the growing season.

Schweinitz's sunflowers normally produce an erect stem which remains unbranched until late in the summer when the upper portion of the stem divides into a proliferation of flower-tipped branches in what has been called a "candelabra" shape. For most of the season the growing stem is tipped with a clearly identifiable apical bud that can be measured to record a stem height, but during the proliferative final flowering stage no apical bud may be determinable, and the height of the tallest flowering branch was recorded as the stem height. If the top of the apical stem was removed (as by browsing) early in the season, the plant usually responded with new growth from latent axillary buds, typically from the closest stem node below the bite. Due to the characteristically opposite leaf and bud arrangement of this plant, two new stems frequently emerged from this node at the same time to replace the lost leader. In the case of a browsed plant, the height of the break in the original main stem was recorded, as well as the height(s) of any axillary replacement leader stem(s). If these replacement leaders were subsequently browsed, the height of these bites and of any tertiary replacement leaders would also have been recorded in the same manner, although no three-time browsing of any stem was observed at Dodge City in 2013.

All herbivory does not necessarily result in the severing of the main stem--leaves or flower buds on the lower branches may be partially consumed without severing the main stem. This study strictly defined a "stem browsing event" as one which resulted in the loss of the apical bud through the severing of the main-stem (or the severing of replacement leader stem, if the original main-stem leader was lost previously) because a main-stem severing browse event leaves a permanent mark on a plant's growth form for the duration of that season, by disturbing the hormonal growth control normally maintained by the apical bud.

The shape of the severed stem stump was used to indicate the species responsible for the browsing (per Vercauteren et al. 2010), with ragged-crushed stems (Figure 3) interpreted as damage by deer, compared with the clean, angle-cut bites (Figure 4) typical of small mammal browsers (i.e., rabbits and rodents, particularly hispid cotton rats). Some browsing was of indeterminate origin. A tender stem may shrivel quickly and die back to a lower node, which can make ascertaining the type of bite difficult even though the fact of a browsing event is clear. Browsing which severed stems near the soil line can leave extremely short stumps which are difficult to detect. Stems which completely and abruptly disappeared were recorded as presumed "browsed" in this study, although it was impossible to determine the browser responsible in such cases unless fragments of the missing stem with distinctive cut surfaces could be found nearly (Figures 5 and 6). Sunflowers can also experience insect herbivory, often evidenced by minute "chewing" damage seen in the appearance of the leaves or even on the apical bud itself, but only insect-damaged stems with a complete loss of the main-stem apical bud were counted as "browsed". Plants sometimes died and wilted while standing in place (and then subsequently disappeared) due to causes other than browsing, and stems which disappeared after wilting were not recorded as browse victims. Observations of all forms of plant death/damage were recorded, in order to place mammalian browse damage into a context of multiple factors potentially impacting sunflower growth at the site.

Figure 3. Example of a "ragged cut" sunflower stem at Dodge City Prairie**.**

Figure 4. Example of an "angle cut" sunflower stem at Dodge City Prairie.

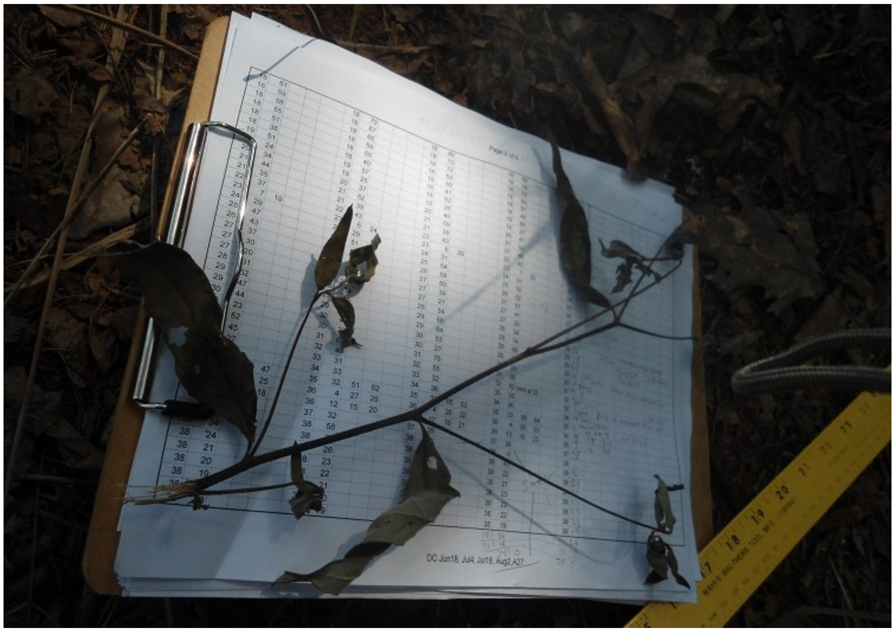

Figure 5. Example of a "ragged" browse fragment at Dodge City Prairie.

Figure 6. Example of an "angled cut" browse fragments at Dodge City Prairie.

Statistical Analysis

Measurement data were recorded in an Excel spreadsheet. Calculations of means, standard deviations, and similar functions were completed using Excel.

RESULTS AND DISCUSSION

Of the 168 stems tracked throughout the season, 10 showed evidence of main-stem browsing at the time of the first survey on June 18, representing 6% of the tracked visible stem population. It is possible that this underestimates the amount of spring browsing, since browsing which removed the entire early-spring stem would not be detectable by an end-spring survey of damage. The height of the spring stem-bites ranged from 5-36 cm above the soil surface ($\bar{x}$= 16.2 cm, SD=9.1 cm). This relatively low browse height is compatible with both deer or rabbit/rodent browsing. The exact dates when these 10 spring browse events occurred cannot be precisely determined, but the fact that several stems had produced 10 cm or more of axillary growth (max. 26 cm) suggests that some of these events may have taken place weeks earlier (i.e., in May), in order to allow time for such regrowth. Other stems displayed minimal amounts of re-growth on June 18, suggesting that some of this browsing was very recent (i.e., in early June). Assuming the first sunflower sprouts appeared in mid-April (as local observations suggest is typical), the total of 10 browsing events by June 18 could reflect an average of 5 browse events (3%) per month over the two months of growth prior to the June 18 measurements.

Overall, the June 18 observations did not suggest heavy browsing had occurred in the spring of 2013, unless it had come in the form of undetected whole-stem disappearances. One of 10 browsed stems was notably "rough-bitten", suggesting deer browsing. At 24 cm, this was the second-highest of the 10 browsed stems observed, and it appeared to be the most freshly bitten, as it was the only browsed stem found without any axillary re-growth at that time. Another stem, bitten at 21 cm and exhibiting only minimal axial regrowth (less than the height of the bite) and apparently also very recent, was cleanly bitten at a sharp angle, suggesting small mammal damage. In the other 8 browsed stems, the type of bite was difficult to determine, due to shriveling of the bite area on the tender spring stems in the greater time elapsed since the bite (as indicated by the substantial axial growth). Over 25% of the clusters were noted for having some form of "chewing" insect damage on leaf blades or petioles. Also observed were several dried stems left from the previous year, including three "stumps" which had been browsed with clean, angled cuts, suggesting small mammals had been active in 2012.

The July 4 survey re-measured all of the plants observed in the June 18 survey and found no additional browse damage. The lack of any whole-plant disappearances (or browse damage of any kind) over a three-week period in late spring/early summer suggests the low browse rate suggested by the June 18 survey was not a underestimation.

The July 18 survey discovered two new browsing events -- one involved the total disappearance of a stem last measured as 58 cm tall, and the apparently recent clipping of only the top of a 28 cm stem, which had not had time to produce any axillary growth when observed. These two events brought the total number of detected main-stem browse events up to 12 (7% of the population). The fact of only two browse events during the five-week period between June 18 and July 18 suggests a reduction in browsing in early summer, as compared to the spring rates, although browse rates in both periods were low (~3% per month in late spring vs. 1% per month in early summer). Meanwhile, three stems (2% of total) with similar heights of ~15 cm were found wilted and standing dead in place in the July 18 survey. The location of these stems close together in heavy shade behind a shrub and the noticeable etiolation of the stems themselves suggests unsuccessful competition for light as the cause of these deaths.

The August 2 survey found four new stems with apical stem damage. One stem previously measured as 52 cm on July 18 had its uppermost portion removed, leaving a 46 cm stem behind. This appeared to be a case of deer browsing, the bitten stem not angle-cut, but appearing crushed flat. The other three stems with apical damage were of a very different sort -- they had previously been measured on July 18 as 20, 20, and 18 cm, and had grown little since their initial June 18 measurements of 18, 18, and 17 cm. On August 2 these stems were measured as 17, 17, and 16 cm, with their apical tips appearing minutely "chewed" off and their appearance noted as defoliated and dying. These were three very slender stems growing together in the same cluster -- the cause of death here appears to be the combination of failure to compete successfully for light in a location farther beneath the tree canopy, with some very small herbivore -- presumably a chewing-mouthed insect such as a coleopteran, orthopteran, hymenopteran or lepidopteran larva -- administering the *coup de grâce* by nibbling the stunted apical bud and skeletonizing the few leaves produced by these depauperate plants, which were already failing to produce upward growth and were incapable of recovery from this (normally minor) loss of tissue. Although apparently not the victims of mammalian browsing, these three stems are counted as "browsed" here because the tip of their apical stem was removed (Figure 7).

Figure 7. Stems with leaves chewed and apical buds removed at Dodge City Prairie.

Three additional stems also appeared to be in the process of dying (heights 28 cm, 13 cm, and 27 cm). As with the insect-browsed stems described above, these small stems were located in denser shade and had experienced insect leaf damage, although not apical bud removal. Some degree of leaf damage from insects was noted on the majority of the stems at the site, with another half-dozen, mostly shorter stems growing under the overhanging tree canopy, being nearly defoliated, although surviving. While leaf damage was also observed on taller stems in sunnier situations, taller stems had many more total leaves and the limited amount of leaf damage relative to their total leaf area made insect leaf damage on larger plants much less conspicuous.

Among the taller stems in sunnier situations, three were observed to be bent but not broken or browsed (original heights 78, 75 and 62 cm). This may be the result of trampling by large animals, such as deer, which commonly produce trails of bent and crushed grass stems along their favorite paths as they run or jump through the grassy prairie.

Overall, at the beginning of August, 16 of the 168 tracked stems (10%) had experienced apical bud removal of some kind, three from insects (2%), two from deer (1%), one from a small mammal (1%), and 10 from indeterminate mammalian herbivores (6%), while 6 stems (4%) had died (or were near death) without having experienced apical browsing.

The August 27 survey found more browsing took place between Aug 2-27 (3.5 weeks) than in the entire year up to that point, with 26 new browsing events documented. Of these, eight events were whole-stem "disappearances" leaving no visible stump. However, in five of these eight cases sunflower stem and leaf fragments were identified in material left behind, with the stem fragments' ends cut with the distinctive clean-cut angled edge of small mammal herbivores, allowing identification of the browser despite the lack of a visible stump. Of the 18 events where a stump was visible, 17 stumps displayed a clean, angled cut and often additional angled-cut stem and leaf fragments. In only one case was the stem stump found cut in a rough, deer-like manner. This single roughly-bitten event was also unique for the August 27 survey in that the location of the bite was much higher above the ground (65 cm) while the highest of the angled-bitten stumps was 26 cm ($\bar{x}$=11 cm, SD=5.3 cm for angled-bite events leaving visible stumps, n=17; if angled-bitten events identified from stem fragments are included as stump heights of 0 cm, then $\bar{x}$=9 cm, SD=6.7 cm, range=0-26 cm, n=22). This roughly-bitten case also differed in that the upper portion above the bite was found left behind as a large, complete fragment, rather than having been chopped into numerous short fragments as were the angled-bitten remainders. The height loss from the single roughly-bitten event was 26 cm (a loss of 29% of the pre-browse stem height). By contrast, the angled-bite events were typically more damaging both in the absolute quantity of stem removed ($\bar{x}$=37 cm, SD=18.3, range 20-98 cm, n=22) and as a percentage of the stem lost ($\bar{x}$=81%, SD=15%, range 57-100%, n=22).

All together from August 2-27 there were 22 browsing events associated with angled-bites, one with a rough-bite, and three events were indeterminate due to no fragments or stump being recovered. Assessing the cumulative damage at the end of August, 42 separate browsing events were detected, and 40 of the 168 tracked stems (24%) experienced apical tip removal of some kind (with two stems being browsed on two separate occasions), including three by insects (2%), three by deer (2%), 23 by small mammals (14%), and 13 by indeterminate mammalian herbivores (8%), with eight additional stems (4%) dying without having experienced apical browsing, and three stems dying (2%) after having experienced apical insect browsing.

The final survey at Dodge City took place on October 8, near the end of the flowering period. Despite the long interval (6 weeks) between this and the previous survey, only 17 new browse events were found to have occurred since August 27, indicating a decline in the average daily browse rate from the peak rate of browsing observed in August. Of the post-August 27 browse events, 13 were angled-cut small mammal bites, while four were roughly-cut deer bites. Stumps were located for all browse events in the period, thus there were no whole-stem "disappearances" to identify from fragments alone. Also, four additional plants had side branches with some flower buds roughly bitten off, but without damage to the highest main-stem flowers, which excludes these from the count of main-stem browse events. The angled-cut events during this period were again distinct from the roughly-cut bites in height: angled-cut stump heights averaged 12 cm (SD=3.6 cm, range 5-18 cm, n=13) while roughly-bitten stumps averaged 62 cm, (SD=26.7, range 25-89 cm, n=4), creating no overlap in height between the two categories. The roughly-bitten stems typically had little more than their upper-most stem tips removed. Stem height losses on roughly-bitten stems during this period averaged only 2 cm (SD=1.4 cm, range=1-4 cm, n=4) compared against the August 27 heights, while the angled-cut stems lost much larger amounts of biomass per plant, with an average height loss of 30 cm (SD=20.0, range=7-68 cm, n=13). Measured as a percentage loss, small mammal damage produced an average loss of 65% of the stem (SD=18.2%, range 33-83%, n=13), while deer browsing produced an average loss of only 5% (SD=6%, range 1-14%, n=4). Fall small mammal main-stem browsing at this site thus appears more than three times more common than fall main-stem browsing by deer, and small mammal browsing produced stem height losses that averaged over ten-times greater than stem height losses from the deer browsing in the same period.

Assessing the cumulative damage at the end of the growing season (Figure 8), 59 separate browsing events were detected, and 54 of the 168 tracked stems (32%) experienced apical tip removal of some kind (five stems were browsed twice), including three apical-browse events produced by insects (2%), seven by deer (4%), 36 from small mammals (21%), and 13 by indeterminate mammalian herbivores (7%). Twelve additional stems (7%) died completely without having experienced apical browsing, and three stems died (2%) after having experienced apical insect browsing. Only one stem at this site which experienced sub-total mammalian browsing was observed to die completely following the browsing, although some stems browsed late in the season did not produce regrowth and ended the season as leafless stumps. Nine stems (5%) were wholly "disappeared" in 2013, with five of these cases showing fragmentary evidence (but no stump) suggesting small mammal browsers, while in the other four cases there was no fragmentary evidence, leaving their browsing agents indeterminate. The quantity of stem tissue removed by browsers varied from 1 cm to nearly 1 m (98 cm), with the greatest losses being associated with small mammal browsing, not deer browsing. No stem that experienced small mammal browse damage at any time in the year succeeded in producing flowers in October, although one stem with late, light browsing by deer and one stem with early spring indeterminate browsing recovered to produce limited numbers of blooms (four and two blooms respectively). Only 15% of the stems at this site produced any blooms in 2013, and bloom numbers per flowering stem were generally low ($\bar{x}$=6 blooms/stem, SD=5.7, range 1-21, n=25).

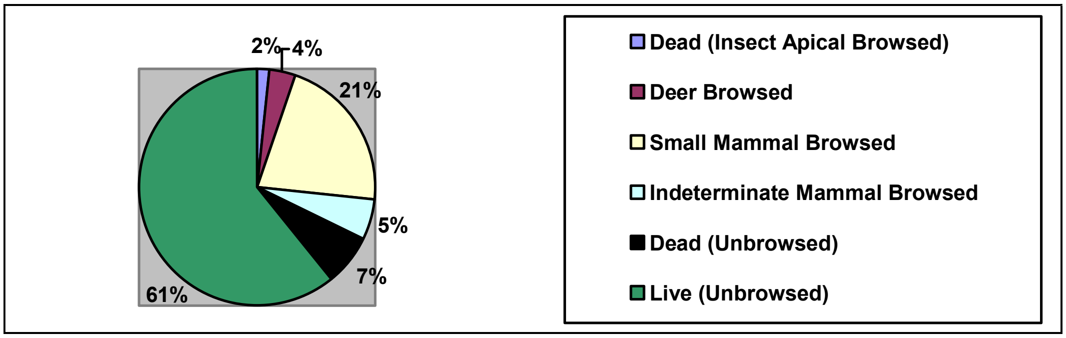

Figure 8. Status of sunflower stems at Dodge City Prairie in Oct 2013 (n=168) (note: twice-browsed stems are listed under their most-damaging event).

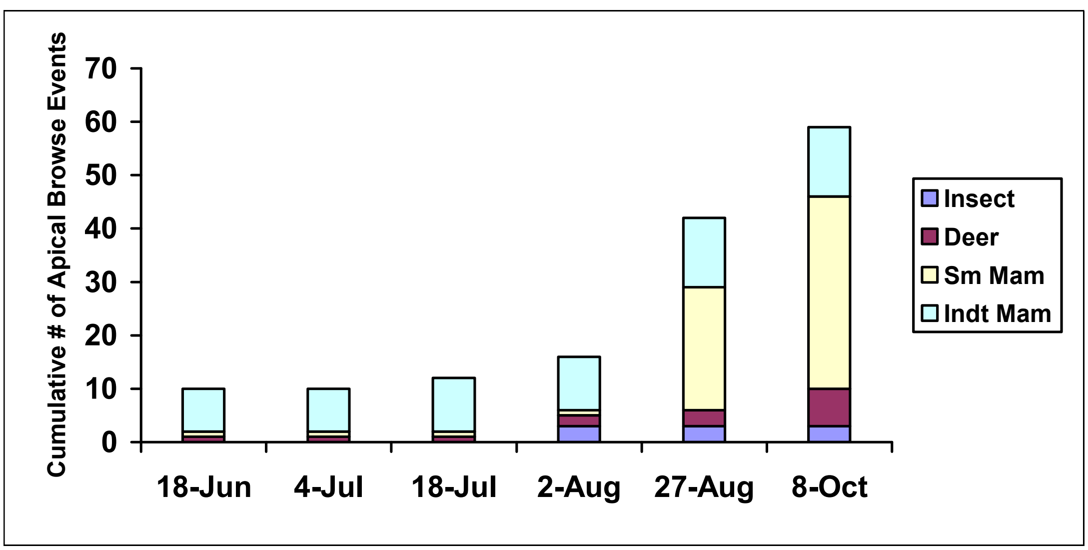

Figure 9. Seasonal distribution of browse events by type at Dodge City in 2013.

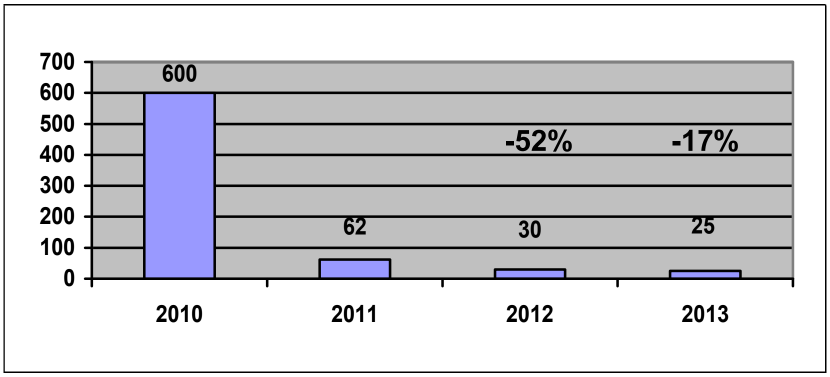

Figure 10. Number of flowering* stems at Dodge City Prairie in 2010-2013 (numbers from Lampell (2013) with 2013 data measured by this study; *includes 600 stems planted in 2010 -- not necessarily flowering that year).

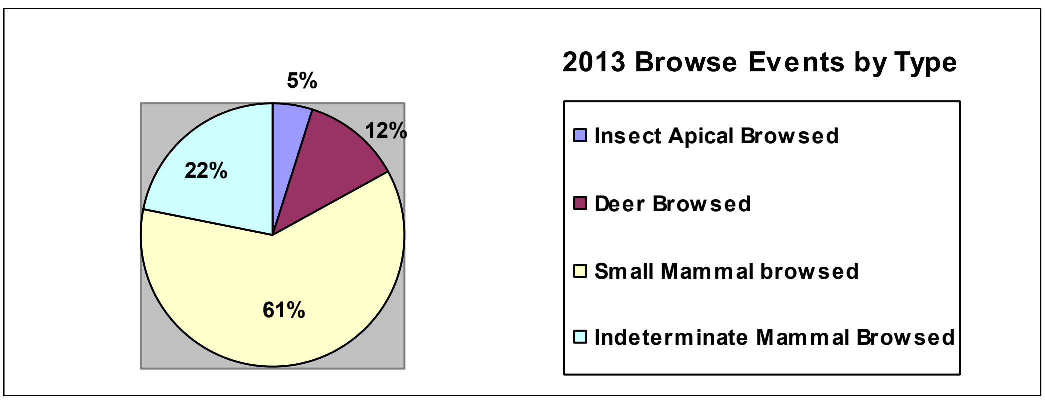

Figure 11. Stem browse events at Dodge City in 2013 by type (n=59).

Evaluation of Hypotheses

Hypothesis 1**:** That browsing of Schweinitz's sunflowers at Dodge City Prairie is occurring.

Hypothesis 1 was confirmed -- browsing damage was observed at Dodge City Prairie in 2013. There were 59 individual browse events detected, involving 54 stems (5 stems being browsed on two separate occasions) or 32% of the stem population (n=168). Apical browse damage was observed matching patterns associated with deer, small mammals, and very rarely, chewing insects.

Hypothesis 2**:** That white-tailed deer are the primary agent of browsing on Schweinitz's sunflowers at Dodge City Prairie.

Hypothesis 2 must, surprisingly, be rejected. Nothing in the abundant literature on Schweinitz's sunflowers suggested non-deer herbivores were active on this species, but this study found small-mammal type damage comprised 61% of all browse events observed: a proportion over five times greater than the percentage of deer-type browse damage at the Dodge City site (Figure 8). Only seven out of 59 apical browsing events were ragged bites clearly identifiable as deer-browsing, a total far less than the 36 browsed stems with cleanly-angled bites typical of small mammal browsers. Even if all 13 cases of "indeterminate mammalian browsing" were also attributed to deer, small mammal browsing would still be the majority damage type seen in 2013. Observations of old stem stumps displaying clean, angled bites left from the 2012 season at this site are additional evidence that small mammal browsing has been on-going and overlooked (or misidentified) as deer damage in previous years.

In addition to being over five times more frequent than deer-type browsing, small mammal-type browsing was also associated with the greatest losses of plant tissue. This was true both during the survey period covering flower bud production (Aug 2-Aug 27) and the period including anthesis (Aug 27-Oct 8), the two periods when identifiable mammal damage was frequent enough to make a comparison most meaningful. Stem tissue losses on stems browsed by small mammals during these two periods averaged 81% (SD=15%, range 57-100%, n=22) and 65% (SD=18.2%, range 33-83%, n=13) of stem height, respectively, while stem tissue losses from the few deer browse events observed resulted in a loss of 29% in the case of the single August event, and a mean loss of 5% for the Aug 27-Oct 8 events (SD=6%, range 1-14%, n=4). Thus deer browsing here produced limited losses of stem tissue, never exceeding 30% of the stem's height, while small mammals usually removed more than half the height of any stem they attacked. Because most leaves and all flower buds occur on the upper half of the stem in the proliferative and flowering seasons, removing a stem's upper half during this time eliminated their reproductive potential for the year and greatly reduced their leaf area available for photosynthesis before dormancy.

Small mammal-type browsing was notable for its seasonal distribution (Figure 9), as both small-mammal and deer-type browsing were observed at equally low levels in late spring (although the number of indeterminate events was higher), followed by a period from June 18 to August 2 when not a single small mammal-type browse event and only one deer-type event was observed (plus two indeterminate events). Small mammal browsing then surged dramatically in August, with 22 small-mammal type events observed between August 2 and August 27, while deer-type and indeterminate events continued at rates consistent with the early season (with one deer-type and three indeterminate events observed in August). The surge in small mammal browsing in August after a period of over six week without any small mammal browse events implies that either small mammals (but not deer) abruptly changed their dietary habits to prefer Schweinitz's sunflowers in mid-August, or the number of small mammals at Dodge City Prairie increased dramatically during this time.

The striking increase in small-mammal browsing at Dodge City in August may have been the unintended result of conservation measures being taken specifically for the benefit of Schweinitz's sunflowers at the larger McDowell Prairie restoration site located ~1.6 km (1 mi) north of Dodge City Prairie (monitoring at McDowell Prairie is further described under Part II of this study). Hundreds of acres of McDowell Prairie were brush-hogged in mid-August to prevent tree encroachment on that site, just before the surge in small-mammal browsing was observed at Dodge City Prairie. Large-scale mowing would displace the high populations of rabbits and hispid cotton rats which were previously observed to live in McDowell Prairie in the early summer of 2013 (see Figure 14) and some fraction of these animals may have found their way to the unmowed, but much smaller, Dodge City Prairie site, and temporarily concentrated their feeding there. Shopton Road West connects these two sites, and the grassy roadside would offer one of several routes between them. Deer would not be expected to be displaced in the same manner by the McDowell

Prairie mowing, since they could continue to utilize the forest-field interface around McDowell Prairie regardless of field mowing, as they are not specifically dependant on the grassland habitat itself. Small mammals specializing in tallgrass/herbaceous fields (such hispid cotton rats) are well-known for their avoidance of forested habitats with dense grass/herbaceous ground structure (Mengak and Guynn 2003, although cotton rats will disperse through forest, Bowne et al. 1999) and would be expected to relocate their populations in any remaining grassy/herbaceous habitat they can reach. That they would concentrate themselves (and their herbivory) in the next-nearest prairie restoration site (and next-nearest population of endangered sunflowers) would seem to be a case of the law of unintended consequences. Failing to mow McDowell Prairie would lead to trees eventually shading out that Schweinitz's sunflower population, but the mowing could have be done in winter without producing this kind of highly-damaging "rodent tsunami" effect on Dodge City.

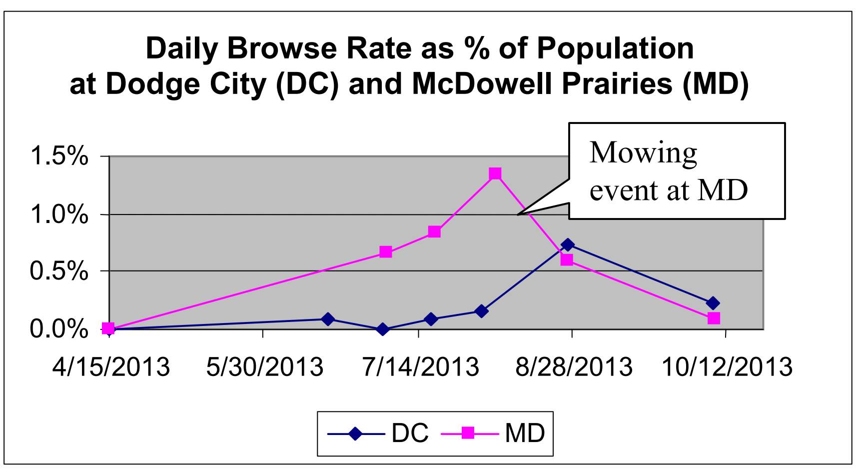

Figure 12. Daily Browse Rates at Dodge City and McDowell Prairies in 2013. Note: dates on x-axis are for reference only -- not identical to survey dates.

Figure 12 illustrates how the daily browse rate (shown with all damage types combined, but predominately small-mammal and deer browsing) was much higher at McDowell Prairie through June and July than was observed at Dodge City Prairie at any time, rising to a peak at McDowell Prairie in early August just prior to the mowing event. This agrees with constant observations of small-mammals at that site during that period, and data from McDowell Prairie confirms that small mammals were not averse to browsing Schweinitz's sunflowers there during mid-summer season. The simultaneity of the decline in browsing (heavily inclusive of small mammal browsing) at McDowell Prairie with the surge specifically in small-mammal browsing at Dodge City, both immediately following the McDowell mowing that destroyed a large area of dense grass and shrub small mammal habitat, compellingly suggests a displacement of browsing mammals from McDowell to Dodge City resulting from the mowing. The very low browse rate at Dodge City relative to McDowell prior to the mowing may reveal that Dodge City Prairie, at 3.6 hectares (9 ac), is intrinsically too small to support a permanent dense population of field-dwelling small mammals, and that its small mammal population is a sink that is regularly refreshed by migrants from the much larger McDowell Prairie, with its 53 ha (130 ac) of restoration grassland, plus an adjacent 16 ha (40 ac) in a powerline right-of-way clearing running from McDowell Prairie south to Tryon Road, just west of Dodge City Prairie. This 1.9 km (1.2 mi) powerline corridor has potential to be favored as a dispersal path through the otherwise forested center of McDowell Nature Preserve, then leaving only a 0.8 km (0.5 mi) grassy forest-edge roadside to bring migrant field mammals to Dodge City Prairie. The straight-line distance between these two prairie restorations would be ~1.6 km (1 mi) for animals cutting directly through forest, and studies have found that while hispid cotton rats prefer to disperse along grass/shrub corridors, they do frequently and successfully disperse through forested land as well (Bowne et al. 1999), suggesting multiple routes for displaced small mammals would be possible (Figure 13).

It must be noted that the distance involved here is surprisingly long for a mass dispersal of small mammals. Bowne and colleagues' (1999) radiotelemetry study demonstrated that individual cotton rats are capable of dispersing up to 1400 m (0.8 mi) in <10 days, but only 19 (20%) of their 96 displaced rats traveled "long-distance" (>250 m) in that time. Long-term monitoring of the northward range expansion of hispid cotton rats in the Great Plains has found an annual rate of 8 to 11 km (5 to 7 mi) per year (Genoways and Schlitter 1966), but the mechanisms involved in this movement are unclear.

If only a small percentage of cotton rats are inclined toward "long-distance" dispersal, the probability of suddenly populating Dodge City Prairie with rats in August through induced dispersal would come down to the densities involved. Seasonal population densities of hispid cotton rats can exceed 100/ha (sometimes up to 120+/ha) in temperate habitats (as in SE Virginia, in Rose and Salamone 2017). For the 53 ha McDowell Prairie, 100 rats/ha could mean 5,300 hispid cotton rats present at the site in late summer prior to mowing. Raising 3.6 ha Dodge City Prairie to a similar density would require only 360 rats -- the equivalent of <7% of the hypothetical McDowell Prairie population. Because the daily browse rate at Dodge City Prairie peaked (after the McDowell mowing) at ~50% of the daily browse rate peak observed at McDowell Prairie before it was mowed, the small mammal densities at Dodge City likely never equaled the pre-mowing small mammal density at McDowell Prairie. To raise 3.6 ha Dodge City Prairie to 50% of the hypothetical 100 rats/ha maximum density at McDowell Prairie would require a mere 180 rats to make the journey -- the equivalent of 3% of the hypothetical pre-mowing McDowell Prairie population. Given Bowne and colleagues' (1999) finding that 20% of their tracked cotton rats dispersed "long-distance" (>250m) in <10 days, 3% appears to be a plausible fraction for what could be called a "very long-distance" (but demonstrably possible) dispersal of 1600m over a period of several weeks. It should be noted that McDowell Prairie was mostly but not completely mowed, and small-mammal browsing continued to be observed in the small unmowed patches, demonstrating that some fraction of the pre-mowing small mammal population did not disperse, which agrees with the reported proclivity for most individual cotton rats to spend their life within a small home territory, if possible. Could 3% of a dense population of small field mammals disperse 1.6 km (1.0 mi) through forest (or slightly farther when following roadside and powerline corridors) in three weeks to colonize a new habitat after a mass displacement event? This study suggests they could, and such an event is the most likely explanation for the abrupt August surge in small mammal browsing seen at Dodge City in 2013.

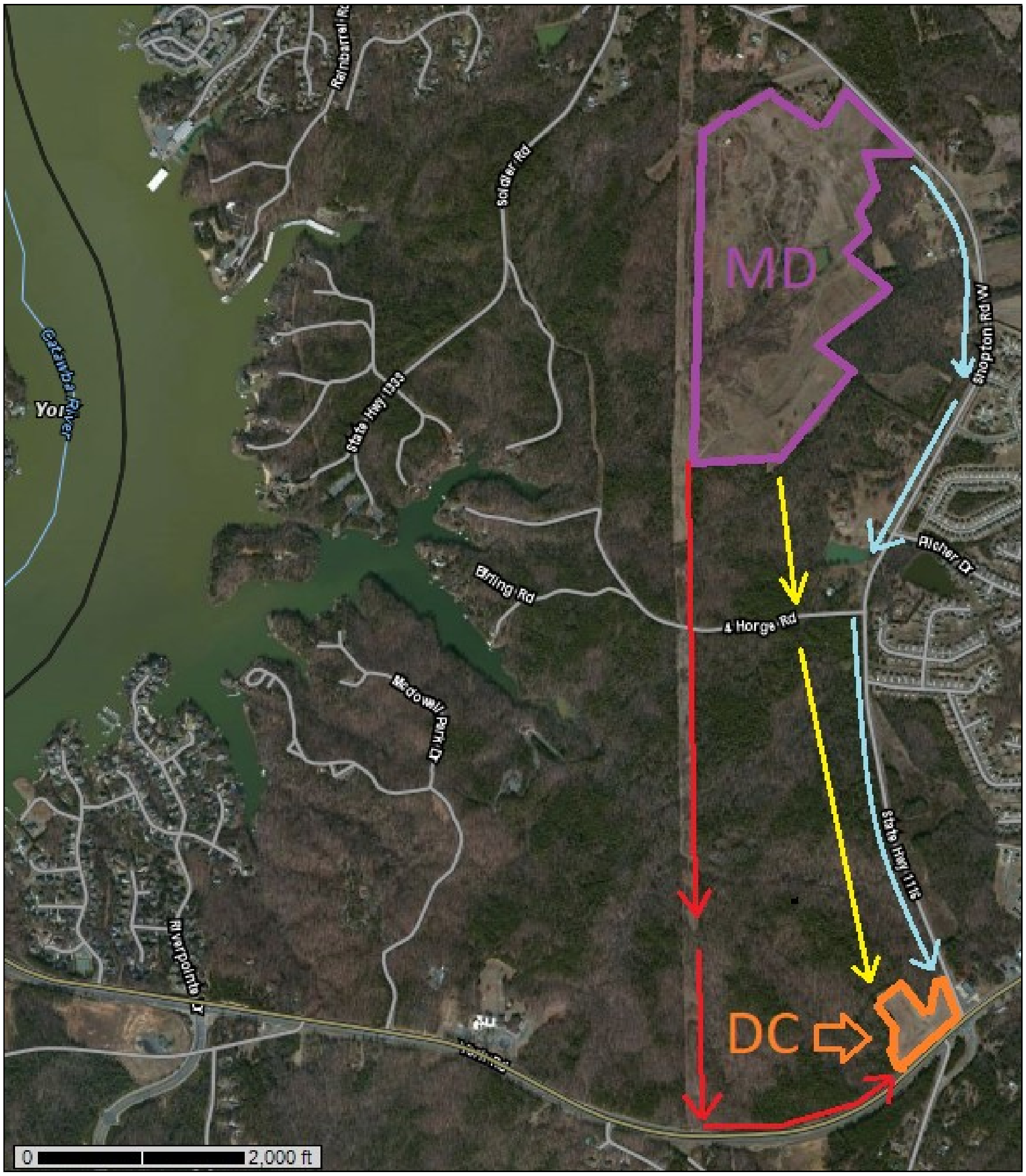

Figure 13. Potential small mammal routes from McDowell (MD) to Dodge City Prairie (DC): Powerline corridor to York Road roadside (red), Shopton Road West roadside (light blue), and direct route through forest (yellow). Image source: websoilsurvey.sc.egov.usda.gov

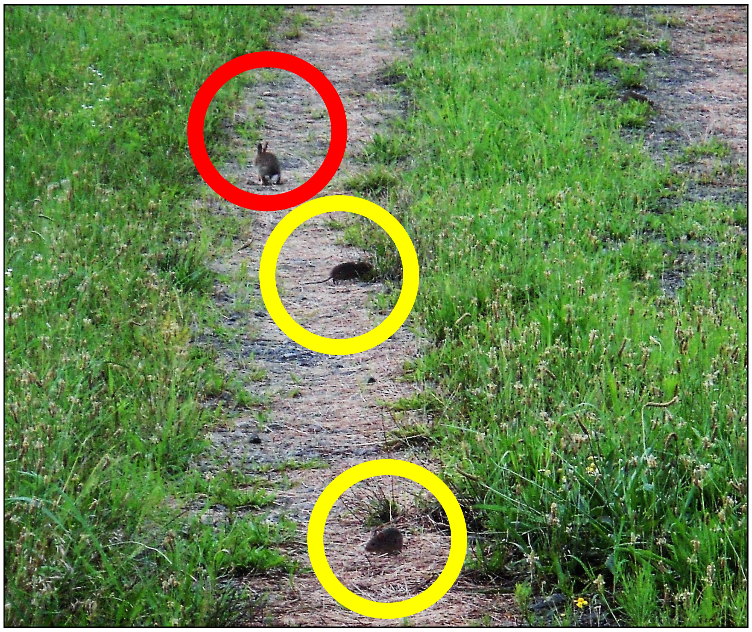

Figure 14. Typical small mammal activity at McDowell Prairie in mid-June of 2013, pre-mowing (note circled rats (yellow) and cottontail rabbit in rear (red)).

Hypothesis 3**:** That browsing of Schweinitz's sunflowers at Dodge City Prairie is "heavy" (defined here as >50% of stems experiencing apical browsing during a season, cf. terminology in Pierson and deCalesta 2015).

Hypothesis 3 must be rejected -- the total frequency of apical browsing was 32% of all stems at the site, which does not meet the pre-determined threshold for "heavy" browsing. It is possible that some early-season browsing which removed whole stems may have escaped detection, but there is no evidence to suggest this actually occurred. The 32% figure does not include non-apical stem browsing, but even if side-branch browse events were included, they were not frequent enough to bring the total browse frequency to the 50% threshold.

That the browse rate was not "heavy" (by one definition) does not equate to "unimportant". Any browse rate which reduces a population's net reproduction rate from positive to negative will destroy the population if sustained over time. If the net reproductive rate for Schweinitz's sunflowers is typically low (as is generally believed), even a small depression in net reproduction resulting from browsing could seal the fate of a population under sustained browsing.

Figure 10 shows the trend for flowering stems counted at Dodge City Prairie. Can the browse rate measured in 2013 explain this trend? Let us begin with the assumption that a perennial sunflower plant strong enough to flower in a given year ought to be, other things being equal, strong enough to flower again in the following year. Therefore, since there were 30 flowering stems counted in 2012, we would expect 30 flowering stems in 2013, other things being equal. Instead we find only 25 flowering stems in 2013, a decrease of 5. Can the browse damage observed in 2013 plausibly explain this decline, or must we look to other factors? A counterfactual thought-experiment may be helpful here.

From the Dodge City data in 2013 we find that 100% (n=14) of the stems which ended the season with a height of 80 cm or greater produced flowers. Of the 16 unbrowsed stems with a final stem height between 50-80 cm, 69% flowered (n=16), and of the unbrowsed stems with final heights less than 50 cm, 0% produced flowers (n=84).

Stem height data from 2013 shows four stems achieved a height of at least 80 cm by the middle of the 2013 growing season before being attacked by browsers in the late season, and then subsequently failed to bloom. From the

100% bloom rate observed in stems of this height at Dodge City which survived unbrowsed through the fall, we can reasonably predict that all four of these 80+ cm stems would have bloomed in 2013 had they not been browsed. We observed no example of an 80+ cm stem dying spontaneously in late summer at Dodge City to suggest otherwise.

Monitoring data also shows that 11 stems achieved heights between 50-80 cm in the summer of 2013 before experiencing browsing, and then did not bloom post-browse. From the 69% bloom rate observed in unbrowsed stems of this height range, we could expect approximately eight of these 11 stems would have been likely to bloom had they not been browsed. Adding the four potentially blooming stems from the 80+ cm height class to the eight potential blooming stems from the 50-80 cm height class would suggest that the total number of blooming stems at Dodge City in 2013 could have easily been 12 blooming stems higher than the 25 blooms actually observed (for a potential total of 37), had late-season browsing not occurred (Table 4).

Table 4: Number of flowering stems at Dodge City Prairie Restoration for 2011-2012 as reported by Lampell (2013), compared with numbers projected and measured by this study for 2013.

Year	2011	2012	2013 Projected from summer stem heights, if no fall browsing	2013 As observed, with browsing
# of flowering stems	62	30	37	25
Year-to-year change in flowering stems		-32	+7	-5
Percent change		-52%	+23%	-17%

Therefore, the amount of late-season browsing observed in 2013 was plausibly responsible for pushing the number of flowering stems down from a potential high of 37 (a 23% increase over 2012) to the actually observed 25 (-17% from 2012). Such a counterfactual can never be demonstrated with certainty -- it remains possible that the stems which were already over 80 cm by the summer could have been prevented from blooming by some other factor if late-season browsing had been excluded (struck by lightning, perhaps). The benefit of modeling this counterfactual is to demonstrate how easily even a "non-heavy" browse frequency could alter the year-to-year trend measured for a population.

Other factors at Dodge City: Switchgrass and Browser Synergy?

Given that all the mammalian herbivores potentially implicated as browsers at Dodge City are considered native to the Carolina Piedmont, the vulnerability of Schweinitz's sunflowers to population decline and failure as result of herbivore impacts may be surprising. However, there is evidence that Piedmont prairie "restorations" such as Dodge City differ significantly from the historic Piedmont prairies. Switchgrass (*Panicum virgatum*) is a major component of many prairie restorations (including Dodge City), where it often forms dense stands, but there is evidence that switchgrass and Schweinitz's sunflowers did not historically occur together. Davis and colleagues (2002) surveyed the vascular floras of six "prairie remnant" sites in south-central North Carolina, including several with Schweinitz's sunflowers. They produced a list of 277 plant species which they considered to have either a "strong" or "weak" association with Piedmont prairies. Switchgrass was not found in any of these "prairie remnants", and was not listed as even as a "weak" prairie associate. Restoration managers have been aware that switchgrass was not found in any of Piedmont prairie remnant sites in Davis and colleagues' study, but because switchgrass seed was more available than other native grass seeds, it was considered useful for Piedmont prairie restoration and it has been "generally considered a Piedmont prairie species" (Fogo 2005, p.69). The frequent inclusion of switchgrass in Piedmont prairie "restorations" may be another case of unintended consequences, where the effort to plant "restoration" sites with a common "native" grass (native to the Carolina Piedmont generally but not necessarily native to Piedmont prairie habitats with Schweinitz's sunflowers specifically) has arguably created environments where Schweinitz's sunflowers and other herbaceous dicots struggle to compete.

Switchgrass is capable of very dense growth and it is known to be a stiff competitor against forbs; one study found recruitment of prairie thistle (*Cirsium canescens*) seedlings to be 16 times higher when sown away from proximity to switchgrass (Louda et al. 1990). Established Schweinitz's sunflower plants with large root stores are demonstrably capable of achieving much greater heights than switchgrass (compare the ~4 m Schweinitz's sunflower towering over all neighboring grasses in Figure 22 with the typical .5 to 1.5 m height listed for switchgrass (Radford et al. 1968)), but the impact of low-cutting browsers represents an Achilles' heel to this strategy because small mammals, unlike deer, attack stems from below the grass layer and can instantly reduce a tall sunflower stem to a subordinate position under the grass layer's shade. In a sparsely vegetated environment new shoots from a low-cut stump may still be able to collect sunlight, but in a dense environment regrowth from a stem cut near the ground in the later season will capture very little light.

The potential for selective herbivory to alter the competitive balance between plant species has long been expected at the theoretical level, and while few studies have documented it directly (see review in Louda et al. 1990), some examples have been investigated which found selective rodent browsing altering the competitive balances between prairie forbs and grasses (Howe 2008). The rapid decline of Schweinitz's sunflowers at Dodge City may be the unexpected result of a particularly pernicious synergy between the destructiveness of small-mammal herbivores and the competitive vigor of switchgrass.

Finally, the planted switchgrass at both Dodge City and McDowell Prairies may be responsible for increasing small mammal populations beyond the levels otherwise expected, particularly hispid cotton rats. Hispid cotton rats are well-known to prefer dense, lush herbaceous vegetation, often with a switchgrass component (Rehmeier 2005), and recent studies have found that planting switchgrass in forest-dominated landscapes specifically increases hispid cotton rat abundances (King et al. 2014). More rats would be expected to produce more browse damage. The results presented in the present study suggest the links between switchgrass, small mammals (especially hispid cotton rats), and rare forbs including Schweinitz's sunflowers merit additional research to help conservation managers untangle these potentially destructive relationships.

Part II: Monitoring of Seven Southern Schweinitz's Sunflower Populations

METHODS

Part I of this study described, in detail, the occurrence of browsing on Schweinitz's sunflower at Dodge City Prairie, but findings from one site should not be uncritically generalized without further data. To address this, six additional Schweinitz's sunflower sites in Mecklenburg and York Counties were also monitored during the summer of 2013 to record browsing and growth patterns that could place Dodge City in a larger context. The sites were selected to reflect, as fully as possible, the variety of habitats in which Schweinitz's sunflowers occur in the York-Mecklenburg vicinity. Sites were also selected to include locations where both increasing and decreasing population trends were previously reported. Unlike Dodge City Prairie, no specific reports of browsing or the absence of browsing have appeared in print regarding any of these additional sites.

A map indicating the relative locations of these study sites is provided below (Figure 15) together with a key to the abbreviations used to represent these sites throughout this document. Additional details about the locations and characteristics of these seven sites (including Dodge City) are presented in Tables 5 and 6.

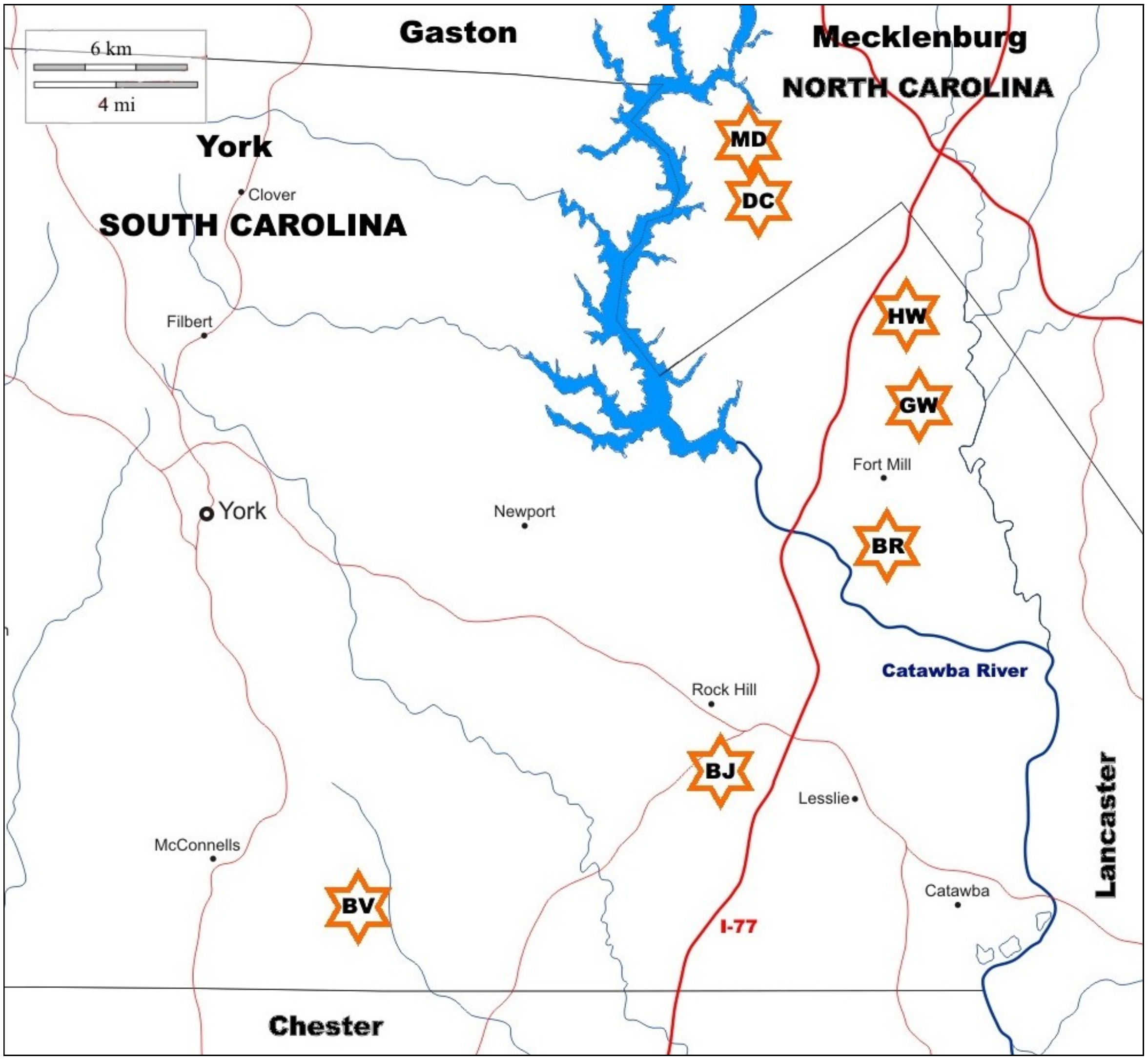

Figure 15. Map of Schweinitz's sunflower study site locations.

Key	Site Name
MD	McDowell Prairie Restoration
DC	Dodge City Prairie Restoration
HW	Highway 21 Bypass
GW	Anne Springs Close Greenway
BR	Banks Road
BJ	Rock Hill Blackjacks Heritage Preserve / Wildlife Management Area
BV	Historic Brattonsville

Map modified from York County Map, source: http://d-maps.com/carte.php?num_car=61767&lang=en

Table 5. Schweinitz's sunflower study site locations

Site Name (abbreviation)	Site Type (area of "prairie")	County	Nearest City/ Township	Surroundings (woodland always present)	Total Est. Population Size	Sample Method (~100-200 stems from each site)
McDowell Prairie (MD)	Prairie Restoration (55 ha)	Mecklenburg	Charlotte	Suburban/ Residential	low <500	Partial, stem clusters marked
Dodge City Prairie (DC)	Prairie Restoration (3 ha)	Mecklenburg	Charlotte	Suburban/ Residential	low <500	Comprehensive, stem clusters marked
Hwy 21 Byp (HW)	Roadside (0.5 ha)	York	Fort Mill	Suburban/ Residential	low <500	Almost comprehensive*, stem clusters marked
ASC Greenway (GW)	Prairie Restoration (2 ha)	York	Fort Mill	Suburban/ Residential	med <1,000	Comprehensive within sampling sub-area, stem clusters marked
Banks Road (BR)	Powerline Right-of-Way (1 ha)	York	Fort Mill	Urban/ Industrial	med <1,000	Transect
Blackjacks HP (BJ)	Remnant/ Right-of-Way (5 ha)	York	Rock Hill	Urban/ Industrial	very large 1,000+	Transect
Brattonsville (BV)	Prairie Restoration (4 ha)	York	McConnells	Rural	very large 1,000+	Transect

*One small area (~1 square meter) with 130+ small seedlings tightly packed was excluded, due to practical considerations.

Table 6. Schweinitz's sunflower study site descriptions

Site Name (abbreviation)	Population Source	Population Trend (in Bibb 2010)	Distance to nearest Woodland	Site Soils: Mafic or Basic Soils in *Italics* (USDA Data)	Latitude (*N)	Stems tracked in this study
McDowell Prairie (MD)	Introduced	Declining	Highly variable, range 15-120 m	*Mecklenburg, Iredell*	35.11	103
Dodge City Prairie (DC)	Introduced	Declining (in Lampell 2013)	All <10 m	*Davidson*, Pacolet, Cecil	35.09	168
Hwy 21 Byp (HW)	Natural	Stable?	All <10 m	Pacolet	35.07	170
ASC Greenway (GW)	Introduced	Decreasing	20 m - 50 m	Cecil	35.03	229
Banks Road (BR)	Natural/ Augmented	Increasing	All 25 m	Pacolet	34.98	96
Blackjacks HP (BJ)	Natural	Increasing	10 m - 20 m	*Brewback*	34.90	181
Brattonsville (BV)	Introduced	Increasing	15 m - 30 m	Cecil	34.87	105

Site Descriptions and Monitoring

The monitoring procedure for recording stem heights and browse damage for all of these sites was generally the same as that described for Dodge City, with some modifications made logistically necessary due to site differences. While the population at Dodge City was small enough to track comprehensively, at sites with much larger populations sampling methods were used. For densely-populated sites a tape transect was laid through the population and the numbered marks on the tape were used to identify individual stems, eliminating the need for numbered stakes to mark stem clusters. For sites which were not dense enough to allow the use of a transect tape, but where the total number of dispersed stems would make comprehensive monitoring with numbered stakes impractical, a sub-area of the site was targeted and all stems within that sub-area were flagged and monitored. The number of surveys each site received also varied slightly, due to scheduling limitations and events which occurred at the sites during the season. For consistency, all sites received their first survey no later than July and their last survey in October (except GW).

Schweinitz's sunflowers may be listed as a federally endangered species, but this does not always protect them from destruction by mowers operating during the growing season. When a small percentage of the monitored sunflowers were destroyed by mowing at certain sites which are discussed below (MD, HW), the affected plants were retroactively excluded from the sample. When a significant percentage of the sunflowers at one site (GW) were mowed in late September, the monitoring season for that site was cut short, making that site the only one with a September end-date. As described for Dodge City in Part I, when stems were found within the sampling area after the initial survey, these "late discovered" stems were tracked at all subsequent survey dates, but they were excluded from the overall data set. Across all sites, the mean number of late discovered stems was fewer than 10 per site ($\bar{x}$= 7% of each site's gross sample, range 1%-22%). Some of these stems were certainly present but overlooked at the time of the first survey, but at one site (BV) there was an unusual abundance (n=18) of very small late discovered stems which were found during the third and fourth surveys (Aug 8 and Aug 29) that could have been genuinely late-emerging stems. None of these stems attained more than 22 cm in height. The reason for these late emergences at that site is unknown, but some may have been a response to stem browsing events, as they appeared in proximity to stems browsed a few weeks earlier.

Individual Site Descriptions

McDowell Prairie (MD) is a former agricultural field managed as a Piedmont Prairie Restoration in Mecklenburg County, North Carolina, just south of the city of Charlotte. Schweinitz's sunflowers were introduced to the site in several plantings from 1994-1998, and nursery-propagated plants from seeds collected on-site were introduced annually from 2003-2006. With this support the population peaked in 2006 at 5,650 stems, only to decline by 97% to a mere 159 stems in 2012. With 55 ha (134 ac) of maintained early successional habitat, it was the largest "prairie" area included in this study, although only a tiny fraction of that area actually supported Schweinitz's sunflowers. The site was burned in 2011, and much of the site was mowed in August of 2013. This mow attempted to avoid areas with sunflowers, but some stem clusters were still destroyed. Stem clusters at McDowell Prairie were marked by numbered wooden stakes (Figure 16), as at Dodge City, but the larger size of the site and widely scattered occurrence of Schweinitz's sunflowers across McDowell Prairie made the monitoring of all sunflower clusters at this site impractical due to the difficulty of locating all extant sunflowers when stems were still small at the beginning of the growing season. A sample intended to contain a number of stems roughly equal to the number being tracked at Dodge City was initially selected, but some of these stem clusters were destroyed by mowing during the growing season. These stems were then retroactively excluded from the sample, leaving McDowell Prairie with a somewhat smaller total number of tracked stems than Dodge City (103 stems tracked at McDowell vs. 168 tracked at Dodge City).

Figure 16. Schweinitz's sunflowers bloom at McDowell Prairie, 10/11/2013.

Dodge City Prairie (DC) is a small 3.6 ha (9 ac), formerly agricultural Piedmont Prairie Restoration site located 2.5 km (1.5 mi) south of McDowell Prairie, within the 450 ha (1,100 ac) McDowell Nature Preserve property owned and managed by Mecklenburg County. Attempts to introduce Schweinitz's sunflowers in 2000 and 2004 both failed, and a third attempt was made in 2010. The 2010 planting introduced over 600 sunflower plants along the edge of the prairie restoration in the ecotone between the tall grasses of the prairie restoration area and the overhanging canopy of the adjacent hardwood forest. Much of the tall grass now seen is switchgrass (*Panicum virgatum*) that was introduced as part of the initial restoration project (background of Figure 17). Counts of flowering stems dropped from 69 stems in 2011 to 30 stems in 2012. "Heavy deer browse" was reported at this site in 2012. As described in Part I of this study, stem clusters at Dodge City were marked with numbered wooden stakes, and the entire population at the site was small enough to make comprehensive monitoring of the this site's population possible.

Figure 17. Schweinitz's sunflowers bloom at Dodge City Prairie, 10/8/2013.

The Highway 21 Bypass (HW) site is a roadside just north of Fort Mill, South Carolina, 7 km (4.4 mi) southeast of Dodge City. For 450 m (1,480 ft) the west side of the highway is a slumping roadcut into a forested hillside, where a spontaneous population of Schweinitz's sunflowers occurs along the face of the cut and on the road shoulder below, although frequent SCDOT mowing during the growing season inhibits the establishment of sunflowers on the lower shoulder. On the opposite side of the highway is an apartment development. Individual Schweinitz's sunflowers can be found on other road margins in nearby neighborhoods. The growing population in the north Fort Mill vicinity produces volumes of fast-moving traffic on Highway 21 Bypass, particularly at rush hour.

At this site numbered orange flags were used to mark stem clusters instead of wooden stakes (Figure 18). Some flags were found already at the site which appeared to have been placed to mark many of Schweinitz's sunflower clusters present, although a few of these flags were found next to plants which appeared to be *Helianthus microcephalus,* rather than *Helianthus schweinitzii. H. microcephalus* is a common species on dry roadbanks in the Carolina Piedmont (Weakley 2015) that has been noted to often occur with Schweinitz's sunflowers (Weakley and Houk 1994), and confusion of these two species has a long history. All Schweinitz's sunflower clusters present at this site were monitored for the growing season, with the exception of some stunted plants and seedlings on the lower road shoulder which experienced summer mowing by the SCDOT and therefore could not be flagged (attempted flags were mowed) and which had no opportunity to attain a normal height.

Figure 18. Schweinitz's sunflower post-bloom at Highway 21 Bypass, 10/22/2013.

Anne Springs Close Greenway (GW) is an 850 ha (2,100 ac) privately owned and managed nature preserve in Fort Mill, South Carolina, 4.6 km (2.85 mi) to the southeast of the Highway 21 Bypass site. Opened to the public in 1995, the Greenway includes a 2 ha (5 ac) prairie restoration area along a hiking/biking path, surrounded by forest and pasture fields. Schweinitz's sunflowers were introduced here in 1997 as part of the prairie restoration. A prescribed burn was conducted in 2012 to prevent shrub invasion and maintain the site's grassy open-woodland character (Figure 19). As at the Highway 21 Bypass site, numbered flags were used here to mark sunflower cluster locations. The goal at this site was to mark and monitor all sunflowers to the south of a hiking/biking trail which divided the prairie restoration area. While the sunflowers at this site were scattered irregularly, they proved to be more abundant than initially expected, and comprehensive monitoring of the south prairie section ultimately resulted in a sample of 229 stems, the largest tracked sample from any site in this project. Many of these stems were found along grassy edges of the prairie area adjacent to the hiking/biking trails. In late September a heavy mower was used to maintain the short grass growing on these trails, and also widened the trail shoulders by mowing into the adjacent prairie, with the result that many flagged sunflowers which had been growing in trail-adjacent locations were destroyed just prior to the onset of bloom production. Due to this event, monitoring at this site concluded in September, rather than in October as at all other monitored locations, and it was not possible to obtain a count of stems blooming at the site.

Figure 19. Schweinitz's sunflower area at Anne Springs Close Greenway, 9/16/2013.

Banks Road (BR) Schweinitz's sunflower site is 5.9 km (3.7 mi) south of the Greenway site, located in the middle of a large power transmission line right-of-way just south of Fort Mill, South Carolina. The Duke Power (now Progress Energy) right-of-way is 140 m (450 ft) wide, and extends at this width for over 5 km (3 mi) to the east, with forested land and industrial facilities bordering it to the north and south. Although sunny grass and shrub habitat is largely continuous through this corridor, this study focused on a dense Schweinitz's sunflower population just west of Banks Road which appeared localized in a small area of approximately 1 ha (2.5 ac). The sunflower population here has been described as partially spontaneous with some additional plants introduced to augment the population. Due to the density of sunflowers at this site a transect line was used here to sample the population and identify plants for tracking purposes. A surveyor's tape marked with decimal feet was laid out for approximately 33 m (110 feet) from the base of the closest powerline pylon (Figure 20). All Schweinitz's sunflowers within 1 m to the left and right of the transect tape were measured and identified with their position relative to the tape (e.g., "sunflower at tape 27.3', on right side"). This method eliminated the need to install numbered flags or stakes to identify sunflower stems. This method produced a sample of 96 stems. Effort was made to lay the transect through the population in an impartial manner, oriented to prominent landmarks (pylons), rather than by aiming the transect to hit or avoid the areas densest with Schweinitz's sunflowers. While a larger sample size could likely have been obtained by a "guided" transect placement, the original lay was used to preserve the impartiality of the sample.

Figure 20. Schweinitz's sunflower area at Banks Road, 9/4/2013.

Rock Hill Blackjacks Heritage Preserve/Wildlife Management Area (BJ) is located 6.8 km (10.8 mi) to the southwest of Banks Road, in the city of Rock Hill, South Carolina. The 117 ha (291 ac) property is owned and managed by the SC Department of Natural Resources (see Schmidt and Barnwell 2002 for floristic details and site history). The majority of the property is forested, leaving approximately 5 ha (12.5 ac) maintained as early successional "prairie", including rights-of-way maintained for cable and water lines. The Schweinitz's sunflower population here is primarily spontaneous, with some transplants having been added to augment the population. The population was also notably dense, with sunflowers concentrated in the rights-of-way and seemingly present in only a fraction of the adjacent managed early successional areas. Like Banks Road, Blackjacks Preserve is surrounded by a mix of industrial development and forested land, but unlike Banks Road and the other spontaneous sites in this study, this site is southwest of the Catawba River. As at Banks Road, the density of sunflower stems present at this site made it practical to use a transect tape to sample the population, which was otherwise far too large and dense to sample comprehensively (Figure 21). The transect line was oriented by a prominent telephone pole visible at the site, extended for 12 m (40 ft) in a north/south line, and was used to sample stems within 1 m to the left or right of the transect tape. The higher density of stems at Blackjacks produced a sample of 181 stems by this method (the second highest sample of any site) while using less than half the length of tape used at Banks Road. The tallest Schweinitz's sunflower from any site in 2013 was found here (Figure 22), although not within the transect sample.

Figure 21. Schweinitz's sunflowers bloom at Blackjacks Heritage Preserve, 10/1/2013.

Figure 22. Unusually tall (~4 m) Schweinitz's sunflower at Blackjacks Preserve, 10/1/2013.

Historic Brattonsville (BV) is a 314 ha (775 ac) acre property operated by the Culture and Heritage Museums of York County. The Brattonsville site is located 14.3 km (8.9 mi) to the southwest of Blackjacks Heritage Preserve, near the town of McConnells in York County, South Carolina. Schweinitz's sunflowers were introduced into former agricultural fields at the site within a 4 ha (10 ac) conservation easement which is managed to maintain "prairie" habitat. Schweinitz's sunflowers were initially introduced to Brattonsville in 2000 and 2002, and have since spread throughout the easement area. The majority of the Brattonsville property is forest, and the surrounding properties are a mix of rural agricultural and forest. This site is unique in this study for its location outside (by a few kilometers) the known distribution of spontaneous Schweinitz's sunflower populations, which reach their southern and western limits in South Carolina in the vicinity of Rock Hill. While prescribed burns have been used at Brattonsville, mowing has been the primary method to maintain early successional conditions. The sunflower-supporting fields are mowed annually in late fall, after all flowering and seed-drop is complete. Adjacent fields without sunflowers are mowed earlier, in October (Figure 23), but care is taken to completely avoid mowing the conservation areas where sunflowers are still blooming and setting their seeds at that time. Grasses in the sunflower area are abundant but noticeably shorter here that at other sites, with broomsedge grass (*Andropogon virginicus*) being common and switchgrass (*Panicum virgatum*) apparently absent.

This site was notable among the sites in this study for supporting what appeared to be the largest total population of Schweinitz's sunflower stems, and the largest area actually occupied by Schweinitz's sunflowers. Due to the extremely large number of stems present at this site, a 30 m (100 ft) transect line was used to sample the site, with the line oriented between a pre-existing metal survey pole and a large tree (Figure 24). With the site's high density of stems it was necessary to narrow the transect sample to include just 0.15 m on both sides of the transect tape. This produced a sample size of 105 stems, closely comparable to the sample size from Banks Road for a transect of similar length, but obtained here while using one-sixth as much width, making Brattonsville by far the densest Schweinitz's sunflower population site included in this study.

Figure 23. Schweinitz's sunflowers post-bloom at Historic Brattonsville, 10/23/2013.

Figure 24. Schweinitz's sunflower area at Historic Brattonsville, 8/29/2013.

RESULTS AND DISCUSSION

Data collected revealed that some Schweinitz's sunflowers at all seven sites experienced main-stem browse damage in 2013, although the frequency of such damage varied greatly between sites.

Table 7. Browse rates observed across study sites

Site Name (abbreviation)	Survey Start/End Dates	# Surveys	# Stems Tracked	# of Browsed Stems	% of Stems Browsed	Total # of Browse Events	Mean Bites per Stem	Mean Bites per Browsed Stem	Max Bites per Stem
McDowell Prairie (MD)	July5-Oct9	5	103	65	63%	108	1.05	1.66	6
Dodge City Prairie (DC)	June18-Oct8	6	168	54	32%	59	0.35	1.09	2
Hyw 21 Byp (HW)	July17-Oct19	5	170	17	10%	17	0.10	1.00	1
ASC Greenway (GW)	July12-Sept16	4	229	172	75%	396	1.73	2.30	7
Banks Road (BR)	July13-Oct17	5	96	31	32%	46	0.48	1.48	4
Blackjacks HP (BJ)	July31-Oct5	3	181	49	27%	56	0.31	1.14	4
Brattonsville (BV)	July9-Oct15	5	105	12	11%	12	0.11	1.00	1
Total		33	1052	400	38%	694			
Average		4.71	150.29	57.14	35.88%	99.14	0.59	1.38	

Across all seven sites, 1,052 stems were tracked, with an average of 4.7 observations recorded for each stem during the growing season. Of these 1,052 stems, 38% experienced main-stem browsing of some kind, and many stems experienced more than one browse event. Browsing rates varied from as low as 10% to as high as 75% of the stems at a site experiencing browsing (Table 7).

Of primary interest to this study was the possibility of a relationship between sites with higher browsing rates and sites with previously-reported declining populations. Three sites monitored had previously reported declining populations, three had increasing populations, and one site (HW) which was previously reported as "Stable?". Observations by the author over several years confirm that the Highway 21 Bypass (HW) population, which occurs on the bank of a roadcut, is approximately stable in size. The plants higher on the bank regularly produce large numbers of seeds which usually fall lower on the road shoulder, where DOT mowing keeps most of the resulting seedlings stunted and non-flowering. This prevents the population from expanding, despite the vigor of many plants rooted in the upper portion of the roadcut. As a stable population which shows no sign of decline, the Highway 21 Bypass population is included with the "increasing" populations for the purposes of this analysis.

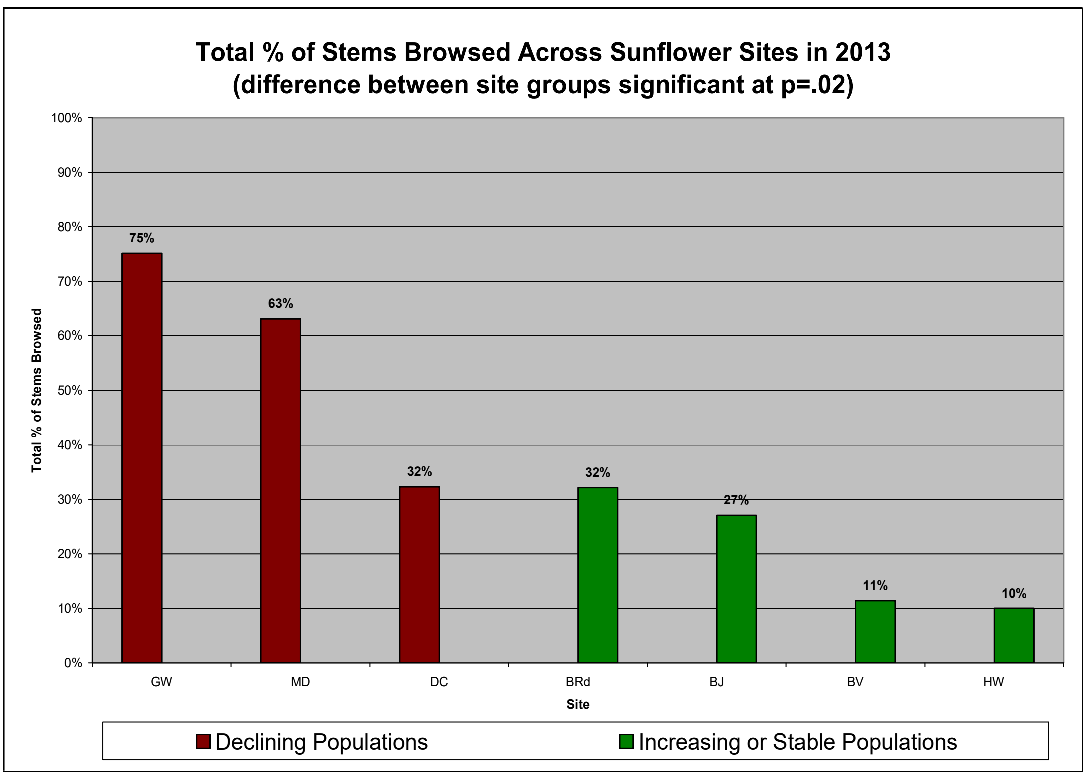

Figure 22. Percentage of stems browsed at Schweinitz's sunflower sites in 2013.

As seen in Figure 22, all sites with populations previously classified as "increasing" (or stable) had browse rates of 32% or less, while all sites with populations previously classified as "declining" had browse rates equal or greater than 32%. Using a one-tailed t-test, this pattern was found to be a statistically significant difference, and the mean browse frequency for declining populations was over twice that of the non-declining populations (stem-browse frequency at declining-population sites $\bar{x}$=57%, SD=22%, n=3; at non-declining sites $\bar{x}$=20%, SD=11%, n=4; t(5)=2.89, p=.017 (one-tailed)). As the browse rate values were percentages, all were arcsine square root transformed before t-testing for groups with equal variance using EXCEL, after an F-test confirmed variance in the data was acceptably equal (see Appendix 1).

Given this relationship, it should be possible to predict a site's population trend with some confidence if the overall browse-rate were known, unless the browse rate fell around 32%, where there was a slight overlap in the ranges of the two groups.

However, looking only at the whole-season browse rate could obscure differences in the seasonal timing of browsing in these groups. When seasonal fluctuations in the daily browse rate are displayed for all sites (Figure 23), a pattern appears where declining populations all experienced much higher (>0.5%) daily browse rates specifically in the late summer (August) than do non-declining populations, which uniformly experienced low (<0.5%) browse rates in August. Daily browse rates early in the season (June-July) do not differ clearly between the two groups. Daily stem-browse rates >0.5% in August were found at all sites with declining populations (mean 1.1%, n=3), while all stable/increasing populations displayed daily August stem-browse rates <0.5% (mean 0.2%, n=4).

Might the browse rate in August be particularly important to determining population trajectories? Possibly. August is the time when Schweinitz's sunflowers set their flower buds, and browsing events in this period usually destroyed the reproductive potential of the affected plant for the year. Plants browsed earlier in the growing season (in spring or early summer) have time to produce new growth. Early-browsed stems recovered and bloomed in the fall at many sites, showing the resiliency of these sunflowers to early season browsing. Perhaps most seriously, an unrecoverable loss of stem tissue (and associated leaves) to browsing in the late summer may compromise a plant's ability to restore its underground carbohydrate reserves that it will use in the following spring, potentially impacting individual plant survival as well as reproduction.

The possibility that stem loss in late summer could be more damaging than stem loss in the early season was suggested by the report of Barden (1994) which described the results of top-killing prescribed burns conducted in different seasons on two Schweinitz's sunflower populations. A top-killing burn is similar to a severe browsing event in that the upper stem is effectively removed and in both events Schweinitz's sunflowers may respond with new growth from the stem base or root crown. In both Barden's report and in the present study stem-removal in the early season was sometimes followed by new growth and flowering in the fall of that year, while late summer stem-removal resulted in minimal regrowth and never in flowering in the same year. More importantly, Barden reported that an early season top-killing burn was followed by increased stem heights and stem numbers in the year after the burn, while a late summer (August) top-killing burn was followed by a decline in both stem heights and in stem numbers in the following year. This suggests underground reserves were indeed compromised by August stem-removal, with lasting consequences.

Despite the suggestive nature of these observations, the fact remains that Barden's report was based on just two sites, and while the present study monitored seven populations, only two (Dodge City and Banks Road) had comparable overall browse rates distinguished by different seasonal timing. A larger sample of sites would be needed to test how significant the timing of browse events is to their effect on a sunflower population. While this study demonstrated a statistically significant relationship between a site's overall browse rate and its population trend, the significance of the seasonal timing of browsing to population trends requires additional research.

This question has implications beyond browser management, as stem-loss from mowing and summer burning occurs at many Schweinitz's sunflower sites, and this timing may not be optimal. The choice to use summer for prescribed burns (or mowing, as a burn substitute) is sometimes justified by the desire to simulate "natural" fire, often associated with summer heat and lightning. Historical sources (Barden 1997) described Piedmont prairie fires as occurring in the winter: the traditional time for Native American burning. Evidence for maladaptation to late summer stem loss would be compatible with the hypothesis of a close historic relationship between Schweinitz's sunflowers and humans.

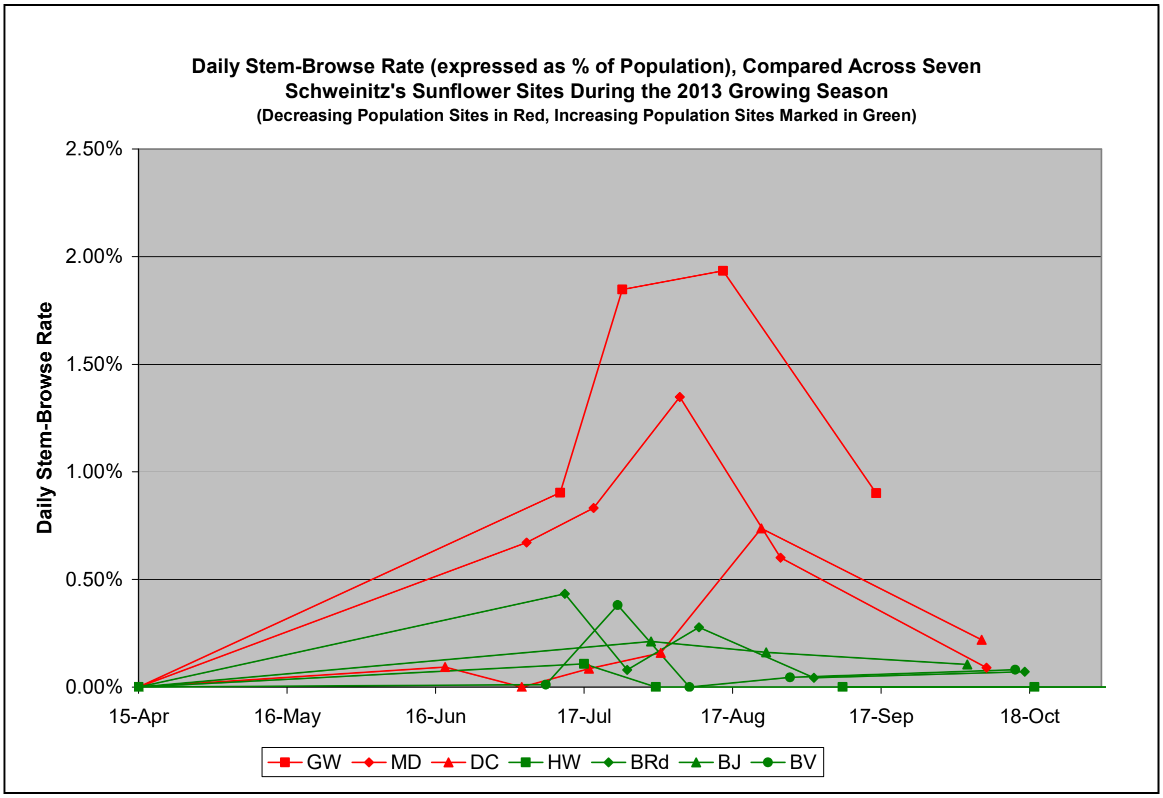

Figure 23: Daily stem-browse rates (expressed as % of each population) from seven Schweinitz's sunflower sites.

Noteworthy observations from individual sites, and follow-up observations from 2017.

Browse damage at McDowell Prairie (MD) involved a balanced combination of deer-type damage and small mammal-type damage, and the overall browse rate of 63% was the second-highest of any site monitored. As of 2017, this population is still extant, but many of the stem clusters tracked in 2013 were found to have since disappeared, supporting the view that the declining trend at the site, already evident in 2012, has continued. Management actions at this site since 2013 have included prescribed burns (including summer burns) and brush-hogging to prevent shrub-encroachment, but the site's Schweinitz's sunflower population does not appear to have stabilized.

Browse damage at Dodge City Prairie (DC) in 2013 was described in detail in Part I. Follow up observations in 2017 found no trace of any Schweinitz's sunflowers surviving at the site, despite increased management efforts after 2013, including brush-hogging of the dense switchgrass and even a controlled burn in 2015, made in the hope of altering the site's conditions to save the declining population. Direct herbivore exclusion was not attempted.

Browsing at the Anne Springs Close Greenway (GW) Schweinitz's sunflower site in 2013 was overwhelmingly deer-type browsing, with only 4 browse events out of 396 (1%) being angled-cut small mammal-type bites. Interestingly, despite having the largest sample size of any site (n=229), not a single case of a whole-stem "disappearance" was seen here -- possibly connected with overwhelming predominance of deer browsing and lack of small mammal browsing at this site.

Deer typically attack stems from above, limiting the impact of each individual bite event, but the cumulative effect of the deer damage seen here was severe. This site experienced the highest overall browse frequency of any site, with 75% of all stems experiencing apical browsing, and 55% of all stems experiencing apical browsing more than once. Sunflower stems experiencing browse damage here usually attempted regrowth, but deer frequently returned to browse the same plant again and again each time new tender shoots would appear, with some individual plants experiencing apical removal six or even seven times. This repeated browsing appeared to exhaust the regrowth potential of many stems attacked in this way.

The overall impression here was of pyric herbivory (herbivory increased after fire). The mechanism would seem to be that the 2012 burn cleared away brier and shrub tangles which previously impeded deer access and simultaneously stimulated herbaceous growth within the small "restoration" area. Easy access and an abundance of palatable new growth would attract high numbers of browsing deer from the surrounding forest to the burn area, raising the browse frequency to levels higher than those measured at any other site. Follow up observations of this site in the fall of 2017 located only a small number of Schweinitz's sunflower stems (nearly all of which showed fresh deer-type damage), far less than the several hundred stems seen in 2013. This was disappointing, since many other prairie-associated herbaceous species were doing well at the Greenway in 2017, reinforcing the impression that Schweinitz's sunflowers are a particularly browse-sensitive species, for which the shade-reducing benefits of burning must be weighed against the cost of pyric herbivory.

The Highway 21 Bypass (HW) site was notable for the near-absence of browsing in 2013, with only 17 bitten stems observed out of 170 stems monitored (10%) -- the lowest rate for any site in this study. All 17 of these bites took place in the spring, and were observed as old scars already present on stems when monitoring began at this site in July. Because the bites were not fresh, the mammal responsible is indeterminate. A deer jawbone was found at the site -- likely a casualty from the traffic on the adjacent highway. The highway itself may thus be acting as a "predator" on any deer which attempt to visit this site, offering the site a form of protection. The sunflowers recovered well from what little browsing they did experience, and flower production was high, despite most of the site being partially shaded by tall trees. Large numbers of small seedlings present did not show any evidence of mammalian browsing, but periodic mowing of the road shoulder during the summer by the DOT keeps many of them stunted. The population of adult plants is not large, but follow-up observations in 2017 confirmed that their numbers appear to remain stable. Unlike the Greenway, Dodge City, and McDowell populations, the Highway 21 Bypass population is a spontaneous occurrence rather than a deliberate introduction -- apparently this roadcut is congenial as a nearly browser-free refugium microhabitat, "naturally" preserving a remnant of the species amidst the suburban development of the north Fort Mill area.

The overall browse frequency at the Banks Road (BR) Schweinitz's sunflower site in 2013 was 32% -- the same as the overall browse frequency at Dodge City, and the highest of any site with a previously reported "increasing" population trend. Two major differences may make the browsing at Banks Road less damaging than the similar frequency of damage at Dodge City.

First, while the majority of the damage at Dodge City was small mammal-type damage, at Banks Road the damage was overwhelmingly deer-type or indeterminate damage -- not a single case of angled-cut small mammal-type damage was seen within the stem sample (n=96). Angled-cut damage was found on some plants in the vicinity, suggesting that small mammals do exist at the site, but at a low density. There was only a single case of a whole-stem "disappearance" at Banks Road -- without recovery of fragments it must be classified here as an "indeterminate mammalian" browse event. As seen elsewhere, deer damage at Banks Road frequently struck the uppermost tops of stems, resulting in limited quantities of tissue lost per event compared to the low-cutting small mammal attacks seen at some sites (particularly at Dodge City).

Secondly, the majority of the browse damage at Banks Road occurred before mid-summer (of the 31 stems browsed, only 2 (6%) were first browsed after July 13), rather than in late summer as seen at Dodge City, which allowed a greater opportunity for browsed stems to regrow.

Observations of the Banks Road population in 2017 suggest that it spread slightly during the 2013-2017 period, and the contrast between the apparent slow growth at Banks Road with the rapid decline and total extirpation of the Dodge

City population highlights how differences in the timing and type of browse damage could be important in determining how much browse damage (in terms of the absolute frequency of stem browsing) a population can sustain and still maintain itself.

The browse rate at Rock Hill Blackjacks Heritage Preserve/Wildlife Management Area (BJ) in 2013 was measured to be 27%, and as at Banks Road, the type of damage observed was predominately deer-damage. Out of 56 browse events detected, only one event (2%) displayed an angled-cut surface characteristic of small mammal damage. Overall the population in 2013 appeared to be flourishing, in agreement with the "increasing" trend previously reported for the site's population. The transect sample of 181 stems only captured a small fraction of the total sunflowers present, with some sunflowers near the transect being conspicuous for their exceptional size.

Remembering the condition of the Blackjack Preserve population in 2013 makes the follow-up observations in 2017 particularly surprising: in the fall of 2017 there were very few Schweinitz's sunflowers blooming at the site -- in places where many tall blooming stems once stood, in 2017 primarily short, stunted stems were found showing evidence of repeated rounds of browsing and re-browsing. The type of damage seen at Blackjack in 2017 strongly resembled the heavy, repeated deer damage previously seen only at the Greenway site in 2013. Although the trend previously reported for Blackjacks Preserve was "increasing", at some point, presumably after 2013, this clearly turned into a decreasing trend. The surrounding habitat has remained open and prairie-like, and both prescribed burns and mowing were used in the years after 2013 to maintain that state, but the sunflower population, at least of blooming stems, was obviously down by >90%. Despite the decline in Schweinitz's sunflowers, other herbaceous plants still appeared lush at Blackjacks in 2017. Given the absence of any other visible cause for the decline except the simultaneous increase in the browse frequency, a relationship is strongly suggested. This raises the question of why the browse frequency would have increased. An increase in the local deer population would increase browsing--but why should the local deer population have increased at this particular site?

A hypothesis could be developed from observations made in 2013 of hunter-associated litter items (including an empty box of rifle cartridges) suggesting that hunting with guns was taking place at Blackjacks during that year. While Blackjacks is a Wildlife Management Area, it is closed to gun hunting for deer due to safety concerns, and is classified as an "Archery Only" zone due to its location within the city of Rock Hill. The site was opened to archery hunting in 2000 with the justification that hunting could maintain the (then low) deer population before they could grow numerous enough to threaten the many rare plants at the site. However, archery hunters are a tiny group compared to gun hunters in South Carolina (only 8% of deer harvested in SC are taken with archery weapons) and archers have a hunter success rate less than half that of rifle hunters (Ruth and Cantrell 2017). My observations suggest that poaching (hunting outside of regulations, in this case, with guns) was taking place in 2013. If poaching by gun hunters was formerly a factor keeping the local deer population in check, then a decrease in the hunting effort at Blackjacks after 2013 could have released the deer population to rapid growth, resulting in the decline in Schweinitz's sunflowers observed.

Another contributing factor may have been the clear-cut logging which took place after 2013 on a previously forested property adjacent to Blackjacks Heritage Preserve. This clear-cutting was far enough removed from the Schweinitz's sunflower site that no direct impacts would seem possible, but if this event outside the Preserve displaced deer into the remaining forest within Blackjacks then this could have also contributed to the increase in deer browsing observed. Schweinitz's sunflowers may need disturbance, but the potential for disturbances to alter herbivore patterns with negative consequences should be considered.

These possibilities serve to illustrate the complex web of factors -- including human behaviors -- that could be influencing local browse rates and Schweinitz's sunflower population trajectories. The post-2013 decline at Blackjacks Preserve demonstrates how even a well-established, legally protected site with a positive population trend can be vulnerable to rapid population decline, particularly if conditions around the site change.

The browsing rate at Historic Brattonsville (BV) in 2013 was very low, only 11%, which was the lowest of any site not immediately adjacent to a highway. Browsing damage there in 2013 was most often indeterminate, with both deer and small mammal-type browsing seen at very low frequencies. Obvious deer bites to side branches (and therefore not counted with main-stem browse events) also occurred. Follow-up visits in 2017 found the sunflower population at Brattonsville remained just as large, if not even larger than it was in 2013. This may be the largest single population of Schweinitz's sunflowers currently existing in South Carolina. The reasons for the low browse rate at this site are not immediately clear. It may be that in this rural and predominately agricultural setting, the local deer hunting practices around Historic Brattonsville still keep deer populations and feeding behaviors in check in a way that does not occur in suburban or urban nature preserve settings where hunting is banned or greatly limited. Suburban development is usually thought of as a threat to plants due to the possibility of direct habitat destruction, but alterations in hunter-herbivore relationships can also come with development. The potential for suburban deer densities to exceed rural deer densities should be considered when planning locations for conservation projects, but this benefit to rural sites may only last as long as rural hunting traditions are preserved.

CONCLUSIONS

"Many cases are on record showing how complex and unexpected are the checks and relations between organic beings, which have to struggle together in the same country." Darwin (1859)

First, browse damage is ubiquitous on Schweinitz's sunflowers, being observed in every population where this study monitored for it, including five populations in South Carolina, a state where browse damage on Schweinitz's sunflowers has never been previously reported.

Second, browse damage is a multi-agent phenomenon, with white-tailed deer, small mammals, and, rarely, insects being observed to defoliate and terminate growth in individual Schweinitz's sunflower stems, despite no previous report attributing browse damage on this species to any agent other than deer.

Third, the frequency of browse damage shows a statistically significant relationship with population trends in Schweinitz's sunflower populations.

Finally, although the hypothesis that Schweinitz's sunflower is suffering from a lack of intense grazing by large mammalian herbivores has been promoted for decades, all observations suggest the opposite -- Schweinitz's sunflowers do not thrive as browse intensities increase -- they decline. When we examine a Schweinitz's sunflower population that is stable or increasing, we find the measurable rate of browsing to be lower, not higher. It is time to accept that treating Schweinitz's sunflowers as a browse-sensitive species is the best working hypothesis we have, and to manage the species accordingly.

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Appendix 1: Statistical output from EXCEL.

t-Test: Two-Sample Assuming Equal Variances		
	Decreasing	*Increasing*
Mean	0.8564231	0.454551
Variance	0.0524994	0.020235
Observations	3	4
Pooled Variance	0.0331408	
Hypothesized Mean Difference	0	
df	5	
t Stat	2.8903352	
P(T<=t) one-tail	0.0170867	
t Critical one-tail	2.0150492	
P(T<=t) two-tail	0.0341734	
t Critical two-tail	2.5705776	

F-Test Two-Sample for Variances		
	Decreasing	*Increasing*
Mean	0.8564231	0.454551
Variance	0.0524994	0.020235
Observations	3	4
df	2	3
F	2.5944825	
P(F<=f) one-tail	0.2217371	
F Critical one-tail	9.5520818	

Appendix 2: Recommendations for managers of Schweinitz's sunflowers

1) Implement regular population monitoring, and remain alert to changing trends.

2) Regularly assess plants for herbivore damage, with careful attention to the types of damage and the agents potentially involved.

3) Consider how any action (burning, mowing, hunting, etc.) taken both in and around a sunflower population could affect the local intensity of herbivory (either by increasing herbivore numbers, displacing herbivore populations, or allowing herbivores greater feeding access to the sunflowers).

4) Consider a site's potential herbivores when choosing locations to introduce relocated populations.

5) Fencing can be used to protect plants from browsers -- protecting a fraction of a population is still better than allowing a total population failure.

6) Proactive introduction of protective fencing is better than fencing a few stunted survivors left behind after a sudden surge in browsing has taken place.

7) Management which acknowledges multiple working hypotheses can avoid the pitfalls of a management strategy based on a single ruling hypothesis, particularly if that hypothesis is historical and speculative in nature.

8) Experiment (carefully).

9) Communicate outcomes and observations, even negative results or results counter to accepted theory, for the benefit of the larger conservation community.

10) Do not accidentally mow your sunflowers in the middle of the growing season.

11) Do not give up. If creating a stable, successful population was easy, this would not be an endangered species. Success may be rare, but it is possible.