Effects of Cattle Grazing on Woodlands in Central Iowa

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Iowa's forests have undergone a dramatic decline in area since settlement by Europeans. Most of the remaining forests have been degraded by an assortment of human impacts, with cattle grazing the most prominent among them. Using a matched pairs study designed to control for environmental differences among plots, I examined the impact of cattle grazing on the forest understory, canopy trees, and tree regeneration. There were distinct groups of understory species associated with ungrazed and grazed plots. Species associated with ungrazed plots were all native and tended to be perennial herbs with fleshy roots. Ungrazed plots also had species preferring moist forests with closed canopies, habitats lacking human disturbance, and with ranges restricted to the eastern United States. In contrast, 30% of species associated with grazed plots were exotic, and the species associated with these sites were more likely to be annuals, have fibrous roots, occur in a wide variety of habitats, and have a cosmopolitan distribution. There were fewer seedlings found in grazed compared to ungrazed woods, and for canopy trees and seedlings, there was evidence for species specific responses to grazing. Woods that have been grazed, but not to the point of canopy loss and sod formation, are representative of the majority of the remaining woods in Iowa; thus, the results of this study are relevant to understanding the dynamics of Iowa forests and to developing plans for their restoration.

INDEX DESCRIPTORS: Iowa forests, plant communities, disturbance, vegetation surveys.

Since European settlement 150 years ago, Iowa's forests have declined dramatically in area and quality. Estimates of Iowa's early forest cover range from 1.8 to 2.7 million ha (out of a total of 14.5 million ha in the state); although this wide range leaves the extent of early forest cover ambiguous, the sharp decline in extent of Iowa's forests, to a low of 0.65 million ha in 1974, is undisputed (Jungst et al. 1998).

Recently, forest cover has rebounded somewhat, but the increase is partially an artifact of how forests are classified in United States Forest Service (USFS) surveys. Two forest cover types, woodland pasture and improved pasture with trees, are not included as timber in forest service surveys because they support active cattle grazing. Between 1974 and 1992, the number of cattle in Iowa declined from 6,674,000 to 3,964,000, a 41% decrease (Jungst et al. 1998). With this decline in the cattle industry and the removal of grazing from forests, many hectares of woodland pasture and improved pasture with trees were subsequently included as forest or timberland in the most recent USFS survey. Consequently, between 1974 and 1990 tabulated forested land in Iowa increased from 0.65 to 0.81 million ha (Jungst et al. 1998).

Cattle grazing has been one of the most widespread and long-lasting factors in Iowa forest decline (Thomson and Hertel 1981). After barbed wire was invented, it was common to fence cattle in woods creating cheap pasture; by 1924, 89% of Iowa's forests were grazed. In 1982, 64% were still grazed (Whitney 1994). A number of studies have addressed the impact of cattle grazing on deciduous forests. Although limited because they lacked replication and often did not include controls, these studies found that cattle grazing may impact soil structure and vegetation due to browsing, trampling, abrasion and soil compaction. Specific changes included an overall decline in species diversity, loss of forest interior species, and an increase in open-site and exotic species (Lutz 1930, DenUyl et al. 1938, Pettit et al. 1995). Species eliminated by grazing may not

return after grazing ceases, especially if sod has developed (Cross 1981, Whitney 1994).

In Iowa, the apparent result of grazing is that a high proportion of Iowa lands now classified as forest consist of only one native layer, the canopy. Understory tree, shrub and herbaceous layers may be absent or highly modified and, if so, are no longer performing natural forest functions of soil protection, wildlife support, and replacement of canopy trees (Farrar, pers. comm.).

This anecdotal evidence of grazing damage suggested a critical need to quantify the effects of grazing on forests in Iowa, particularly to understand both the extent that natural succession and regeneration may restore formerly grazed forests to the diversity and composition of relatively undisturbed forests as well as the extent that an active restoration program is needed.

This study had the specific goals of 1) quantifying the impact of cattle grazing on the understory vegetation of forests in central Iowa by identifying a understory species that may be indicators of both ungrazed and grazed forests; 2) identifying morphological and life history traits that distinguish the two groups of understory species; and 3) examining the impact of cattle grazing on existing canopy trees and their regeneration.

METHODS

Site Selection

The study sites were located in seven central Iowa counties (Fig. 1). The major criterion for selection of sites was the ability to pair otherwise similar grazed and ungrazed areas. I selected a woodland currently or recently grazed (within the past 15 yrs) adjacent to or within 1 km of a woodland that had not been grazed for over 50 yrs. Twenty-five plots were established in the grazed woodland sites; each was then paired with a plot of similar slope, landscape position and aspect in the adjacent or nearby ungrazed woodland site. This resulted in four to eight plots (two to four pairs) at each site, totaling
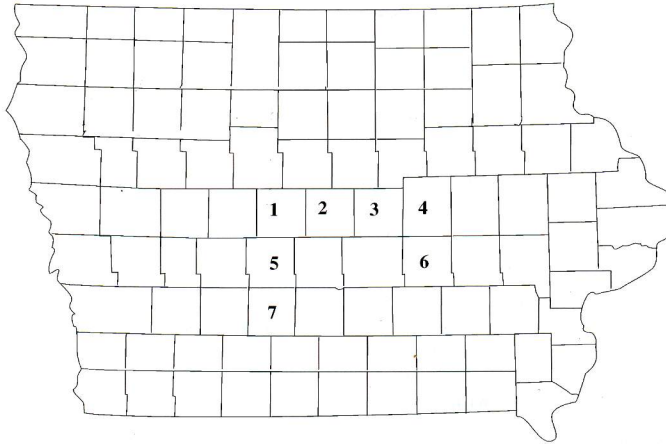
Fig. 1. Study area for the matched pairs study of grazed and ungrazed plots in central Iowa woodlands. Number in parentheses are numbers of pairs in each county. 1 = Boone County (4); 2 = Story County (2); 3 = Marshall County (2); 4 = Tama County (4); 5 = Dallas County (3); 6 = Poweshiek County (2); 7 = Madison County (8).

50 plots (25 pairs). Few woodlands in Iowa are entirely free of past cattle grazing; thus, reference to ungrazed woods throughout this paper refers to areas that have not been grazed within the past 50 yrs.

Plots measured 20 × 20 m and were permanently marked at the SW and NE corners using large screw-style metal anchors. Distance and compass direction of each anchor to a healthy nearby tree was then mapped, and the tree was permanently marked with a small numbered aluminum tag. The tree was then identified and measured (diameter at breast height, dbh, 1.4 m above ground). A map of each plot included the location of trails, streams, fences and useful relocation markers

Plot Inventory Methods

Understory species (herbs, ferns, graminoids, vines, shrubs and subcanopy tree species), were identified to species and assigned one of eight cover classes: 1 = 1–2 individuals or clusters, 2 = few to many individuals, 3 = numerous individuals throughout the plot but with <5% cover, 4 = 5–15% cover, 5 = 16–25% cover, 6 = 26–50% cover, 7 = 51–75% cover, 8 = 76–100% cover. Visual estimates of percent cover were made for each species in the 20 × 20 m plots.

Overstory tree species (i.e., those that contribute to the formation of the upper canopy) were measured in three ways. Diameter at breast height of all trees in the plot with dbh greater than 2.5 cm was measured. Saplings, defined as individuals with stems greater than 1.5 m tall but less than 2.5 cm dbh, were tallied for the whole plot. Seedlings, individuals less than 1.5 m tall, were counted in two 1 × 20 m transects extending the length of the plot from the 5 and 15 m marks. Nomenclature follows Gleason and Cronquist (1991), except for the Poaceae, which follows Barkley (1986).

Environmental factors measured in each plot include slope, aspect and landscape position (upper, mid or lower slope). Aspect (degrees azimuth) was transformed to one of three exposure categories (least exposure to solar radiation, 346–360°, 1–105°; intermediate exposure, 286–345°, 106–165°; most exposure, 166–285°). Topographic position, percent slope, and aspect were combined to create a topographic relative moisture index (TRMI), a composite index that estimates moisture availability (Parker 1982). Plots on upper slopes,

steep slopes or south-facing slopes were scored as most xeric, while mesic plots were on low, relatively level or north-facing slopes.

The canopy density was estimated by 25 densiometer readings. A densiometer provides a fish-eye view of the canopy, and canopy layers at a central point in the middle of the densiometer field may be determined. Three readings were taken along each of five parallel transects placed at the 0, 5, 10, 15, and 20 m marks of each plot. At each reading the canopy was categorized as open, one canopy layer, or two or more canopy layers, and average coverage for each plot was calculated. Total sapling number in each plot was counted as a rough estimate of light levels closer to the forest floor. Three soil samples were taken at 5, 10, and 15 meters along the center transect of each plot; samples were combined and analyzed for total organic matter, nitrogen, phosphorous, potassium and pH.

Data Analysis

Canopy trees, saplings and seedlings, and understory species were analyzed separately. Differences in understory vegetation among plots in recently or currently grazed woods versus those in ungrazed woods were examined by principal components analysis (McCune and Mefford 1999). To control for differences among pairs of plots, each pair of plots was treated as a block in the analysis (for a total of 25 blocks). Understory species were analyzed using percent cover values and again using presence/absence only. Tree species were analyzed using dbh for individuals >2.5 cm dbh and by density (stems per plot) for seedlings and saplings.

To determine understory species that were most strongly associated with grazed vs. ungrazed woods, I compiled a list of the 30 species (approximately the top 20%) most strongly associated with each end of the gradient of grazed to ungrazed plots identified by PCA (Tables 1 and 2). A species was included in the list if it was among the 30 species with the highest PCA axis scores based on the ordination using either the percent cover or presence/absence data; most species qualified on both counts.

Potential functional differences in understory vegetation among grazed and ungrazed sites were examined using the 30 species associated with each end of the gradient. Each species was scored for 12 morphological and life history characters potentially influential in response to disturbance (Mabry and Korsgren 1997, Mabry et al. 2000). These characters were scored from live plants and herbarium specimens and from floristic descriptions (Barkley 1986, Gleason and Cronquist 1991). All characters were categorical; thus the relationship between characters and grazing was analyzed by contingency table analysis.

Differences between grazed and ungrazed plots for mean tree diameter as well as sapling and seedling density (number/plot) were analyzed by ANOVA. Grazing status, species and block (each of the 25 pairs of plots was treated as a block) were the grouping variables, and mean dbh (canopy trees) or density (saplings and seedlings) was the dependent variable.

In addition, tree species were placed in species groups based on habitat affinity. Forests in the study included species that have been divided into three community types, oak-hickory, oak-maple-basswood, and bottomland hardwoods (van der Linden and Farrar 1993). Because I was interested in the effect of grazing on Iowa's dominant oak species, the oak-hickory type was divided into separate groups (white, bur and black oak vs. chinkapin oak, shagbark hickory, white ash and black cherry). A fifth group, composed of introduced or disturbance-related species, was also included. A full list of species included in each group is included in Appendix 1. Contingency tables were used to analyze if the number of individuals in each group of species changed with grazing status. Species groups and

Table 1. Species with the highest loadings on the grazed end of the PCA ordination of plots. A species was included if it was among the 30 species (top 20 percent) with the highest PCA axis scores based on the ordination of plots using either the percent cover or presence/absence data. Frequency is number of grazed plots with each species. Based on cover data = c; presence/absence = p/a; both = b.

Latin Name	Common Name	Family		Frequency
Ambrosia artemisiifolia	common ragweed	Asteraceae	b	3
Arctium minus	burdock	Asteraceae	b	3
Bidens frondosa	devil's beggar's ticks	Asteraceae	b	6
Campanula americana	tall bellflower	Campanulaceae	p/a	15
Carex amphibola	sedge	Cyperaceae	b	20
Carex cephalophora	sedge	Cyperaceae	b	9
Carex normalis	sedge	Cyperaceae	b	4
Chaerophyllum procumbens	spreading chervil	Apiaceae	c	10
Chenopodium sp.	goosefoot	Chenopodiaceae	b	12
Cirsium sp.	thistle	Asteraceae	b	3
Dichanthelium acuminatum	panic grass	Poaceae	b	5
Ellisia nyctelea	water pod	Hydrophyllaceae	b	18
Erigeron annuus	annual fleabane	Asteraceae	b	5
Festuca obtusa	nodding fescue	Poaceae	b	42
Galium aparine	cleavers	Rubiaceae	p/a	44
Galium triflorum	sweet-scented bedstraw	Rubiaceae	c	27
Lobelia inflata	Indian tobacco	Campanulaceae	b	3
Lonicera species[1]	Morrow's honeysuckle	Caprifoliaceae	b	5
Oxalis stricta	common yellow wood sorrel	Oxalidaceae	c	22
Paronychia canadensis	forked chickweed	Caryophyllaceae	p/a	3
Parietaria pensylvanica	pellitory	Urticaceae	b	14
Pilea pumila	clearweed	Urticaceae	b	26
Plantago rugelii	American plantain	Plantaginaceae	b	9
Poa pratensis	bluegrass	Poaceae	b	7
Prunella vulgaris	self heal	Lamiaceae	b	6
Ranunculus abortivus	small-flowered crowfoot	Ranunculaceae	c	44
Ribes sp.	gooseberry	Grossulariaceae	b	48
Rosa multiflora	multiflora rose	Rosaceae	b	31
Taraxacum officinale	common dandelion	Asteraceae	b	17
Triosteum perfoliatum	perfoliate horse gentian	Caprifoliaceae	b	6

[1] Includes *Lonicera maackii, L. morrowii, L. tatarica*

grazing status were the grouping variables and number of individuals was the dependent variable.

Preliminary ordination analyses revealed that currently grazed and recently grazed plots were floristically similar to each other but distinct from ungrazed plots (data not presented). Thus in my analyses in this paper, recently and currently grazed plots were considered together as "grazed" plots.

RESULTS

Understory Species

A total of 187 understory species was tallied in the 50 plots, including 170 native species and 17 (9%) exotic to Iowa. Ordination of sites using understory species revealed a striking gradient from grazed to ungrazed plots (Fig. 2). Species associated with the two types of sites came from almost entirely different ecological and taxonomic groups. Grazed plots were characterized by exotic species and species associated with disturbance. Ungrazed plots were characterized by spring ephemerals and other species often anecdotally associated with rich woods in Iowa (Tables 1 and 2).

Analysis of morphological and life history characters and grazing history revealed similar results. No differences were detected between species associated with grazed and ungrazed plots in fruit type, thorniness, or degree of vegetative spread. However, species differed in mode of diaspore dispersal (P = 0.005), growth form (P = 0.0001), root structure (P = 0.0001), habitat types (P = 0.0001), range (P = 0.017), and in number of native vs. exotic species (P = 0.002) (Table 3). All species associated with ungrazed plots were native, and there were a high number of perennial herbs, and herbs with fleshy roots associated with these plots. They also had more species characteristic of moist forests with closed canopies and habitats with little human disturbance, and with ranges restricted to the eastern United States hardwoods. Conversely, 30% of species associated with grazed plots were exotic. Species associated with grazed sites were also more likely to be annuals, have fibrous roots, occur in a wide variety of habitats, and to have a cosmopolitan distribution (Tables 1 and 2).

Tree Species

Plots included in this study were dominated by a canopy of *Quercus alba, Q. macrocarpa* and *Q.velutina,* but these oaks were not dominant in the regeneration layer. Seedlings of oak species were equally as abundant as seedlings of species in maple-basswood group, and approximately half as abundant as seedlings of floodplain species and the remainder of the oak-hickory species. By the sapling stage, the three dominant oak species were regenerating less abundantly than species in any other group of species (Table 4).

Table 2. Species with the highest loadings on the ungrazed end of the PCA ordination of plots. A species was included if it was among the 30 species (top 20 percent) with the highest PCA axis scores based on the ordination of plots using either the percent cover or presence/absence data. Frequency is number of grazed plots with each species. Based on cover data = c; presence/absence = p/a; both = b.

Latin Name	Common Name	Family		Frequency
Actaea alba	doll's eyes	Ranunculaceae	c	5
Arisaema triphyllum	jack-in-the-pulpit	Araceae	b	29
Asarum canadense	wild ginger	Aristolochiaceae	b	7
Botrychium virginianum	rattlesnake fern	Ophioglossaceae	b	32
Bromus pubescens	brome grass	Poaceae	b	10
Carex rosea	sedge	Cyperaceae	c	36
Claytonia virginica	spring beauty	Portulaccaceae	b	28
Desmodium glutinosum	cluster leaf tick trefoil	Fabaceae	b	36
Dicanthelium latifolium	panic grass	Poaceae	b	3
Dicentra cucullaria	dutchman's breeches	Fumariaceae	c	40
Fragaria sp.	strawberry	Rosaceae	p/a	8
Galium concinnum	shining bedstraw	Rubiaceae	b	38
Geranium maculatum	wild geranium	Geraniaceae	b	20
Helianthus strumosus	rough-leaved sunflower	Asteraceae	b	12
Lonicera sp.[1]	grape or wild honeysuckle	Caprifoliaceae	p/a	9
Osmorhiza claytonii	bland sweet cicely	Apiaceae	c	36
Polygonum virginianum	jumpseed	Polygonaceae	p/a	7
Parthenocissus quinquefolia[2]	Virginia creeper, woodbine	Vitaceae	c	49
Prunus virginiana	choke cherry	Rosaceae	p/a	9
Ranunculus hispidus	hispid buttercup	Ranunculaceae	b	10
Sanguinaria canadensis	bloodroot	Papaveraceae	b	25
Sanicula gregaria	cluster-sanicle	Apiaceae	b	48
Silene stellata	starry campion	Caryophyllaceae	b	10
Smilax ecirrata	carrion flower	Smilacaceae	b	27
Smilacina racemosa	false Solomon's seal	Liliaceae	b	18
Solidago ulmifolia	elm-leaved goldenrod	Asteraceae	b	27
Thalictrum dioicum	purple meadow rue	Ranunculaceae	p/a	7
Toxicodendron radicans	poison ivy	Anacardiaceae	b	40
Uvularia grandiflora	bellwort	Liliaceae	b	17
Viola pubescens	yellow forest violet	Violaceae	p/a	37

[1] either the native *L. dioica* or *L. prolifera*; reproductive structures not present to confirm identification
[2] Includes *P. vitacea*

There was no evidence that mean dbh/plot of overstory trees (i.e., those >2.5 cm dbh) differed between grazed and ungrazed plots, although there was a strong interaction term between grazing status and species, (P ≤ 0.0001), suggesting that mean dbh/plot of some tree species differed with grazing status (Table 5). Species with greater mean dbh in ungrazed plots included *Carya ovata, Fraxinus americana, Quercus macrocarpa* and *Quercus rubra*. Those with greater mean dbh in grazed plots included *Carya cordiformis, Quercus alba, Quercus velutina* and *Ulmus rubra*.

There was not a strong relationship between sapling density and grazing status (Table 5). However, ungrazed plots had more seedlings per plot compared to grazed (mean 49 vs. 41, Table 5, P ≤ 0.0001). There was also an interaction between grazing status and species of seedlings, suggesting that some species were more abundant in grazed vs. ungrazed plots and vice versa (P = 0.013, Table 5). Species with greater number of seedlings per ungrazed plot included *Acer nigrum, Celtis occidentalis, Quercus macrocarpa* and *Ulmus* species, and those more abundant in grazed plots included *Fraxinus americana, Juglans nigra* and *Ostrya virginiana*.

Contingency table analysis of species groups versus grazing status showed no pattern of association for either saplings or seedlings (P = 0.634 and 0.664, respectively). However, there were strong patterns evident for overstory species (Table 6, P ≤ 0.0001). Ungrazed plots had more individuals in the dominant oak and bottomland hardwood groups, while the grazed sites had more individuals in the disturbed site group and the oak-hickory group that excluded the dominant oaks (Table 6).

There were no measurable differences between grazed and ungrazed sites in any of the environmental or soil factors I measured (data not shown).

DISCUSSION

Cattle grazing in natural habitats is widespread globally. The relationship between grazing and grassland ecosystems has been studied extensively (McNaughton 1983, McNaughton et al. 1983). In contrast, data on the effects of grazing on woodlands is sparse, particularly for understory species. Understory species are important components of plant communities, mediating vital ecosystem functions such as water relations, nutrient cycling and interactions with animals such as pollinators and herbivores. To fully restore ecosystem function following anthropogenic disturbance, it is important to understand the dynamics of understory species as well as overstory trees and regeneration.
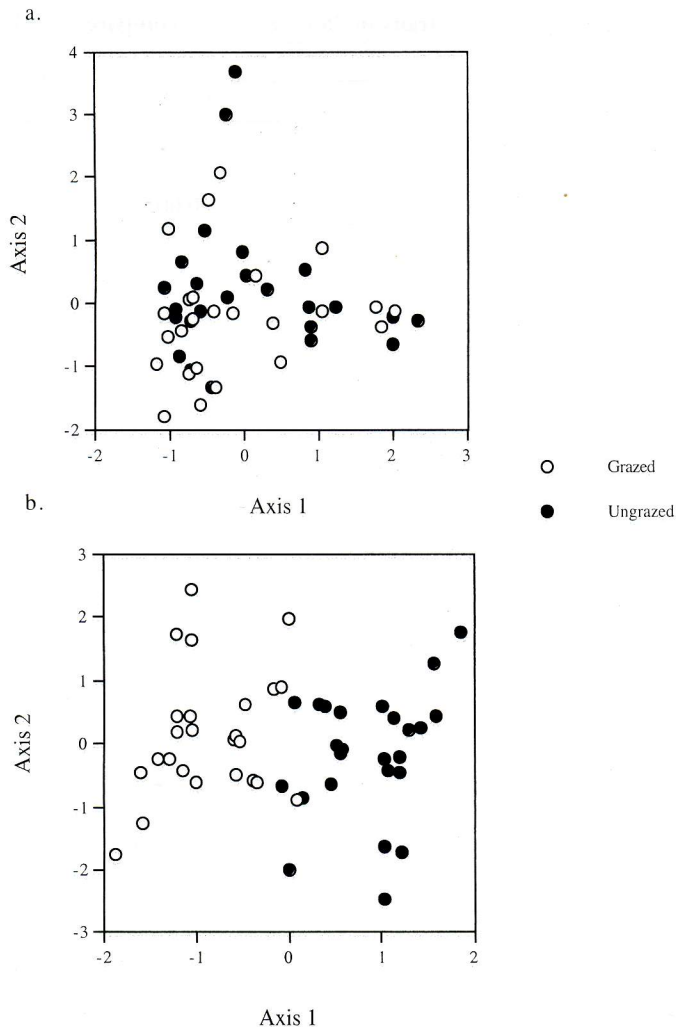
a.

b.

Axis 1

Fig. 2.   a) PCA ordination of 50 plots (25 grazed plots paired with 25 ungrazed plots) based on cover of understory species (non-canopy trees, shrubs, ferns, graminoids and herbaceous species); b) PCA or-dination of the same data set, but with each of the 25 pairs treated as a block. Grazed plots are indicated by open circles and ungrazed as closed circles.

In Iowa, forest studies have fallen into roughly three categories: 1) assessments and descriptions of Iowa's early forest cover and can-opy composition (Pammel 1896, McBride 1926, Davidson 1961, Thomson and Hertel 1981, Thomson 1987, Jungst et al. 1998), 2) description of forest types (Eilers 1974, Nieman and Landers 1974, Johnson-Groh 1985, 1987), and 3) floristic studies (Kucera 1952, Sanders 1967 and 1969, Bach 1982, Raich et al. 1999). Some of these studies have included understory data, but none have included the full spectrum of species replicated across a range of sites. This study is a controlled comparison of grazing history replicated across a wide range of sites throughout central Iowa, and includes data for all canopy layers (i.e., understory species, canopy trees, saplings and seedlings).

Understory Species

Kucera's study (1952) at Ledges State Park and nearby areas in-cluded data on the relationship between grazing and understory spe-cies. Six sites, characterized as open woods and pasture, with the

surface either exposed or "soddy", were compared with eight plots placed in nearby "closed" woods. His list of species occurring only on the disturbed sites included four species and one genus that were also associated with grazed sites in this study (*Taraxacum officinale, Oxalis stricta, Ambrosia artemisiifolia, Arctium minus,* and *Cirsium* sp.). Species Kucera (1952) found only in closed woods sites also over-lapped considerably with species associated with ungrazed woods in this study (*Sanguinaria canadensis, Ranunculus hispidus, Uvularia gran-diflora, Thalictrum dioicum* and *Geranium maculatum*). However, many other species that Kucera (1952) found limited to closed woods had a broad distribution in my study, probably because his data were based on a comparison of 14 plots at one site, whereas the current study compared 50 plots spread across eight sites. Other differences in design between studies that could influence results include plot size, topography and intensity of grazing.

I found only one other study, conducted in forest remnants in Australia, that fully examined the effects of livestock grazing on understory species (Pettit et al. 1995). They found that the most distinct change in the understory flora due to grazing was an increase in exotic species and a decrease in number of perennial native shrubs and herbs, similar to the results found here. Grazed sites in that study also had lower overall species richness (Pettit et al. 1995). No difference in species richness or total cover due to grazing (data not shown) were discovered in this study.

Other non-replicated studies also suggest that grazing can alter understory species composition. An Ohio woodland not grazed for 10 years had 124 species vs. 61 for an adjacent grazed woods (Dam-bach 1944). Sixty-seven of the 124 species occurring in the ungrazed woods did not occur in the grazed woods. In Wisconsin, 38 of 79 species in an undisturbed maple-basswood community, and 32 of 94 in an undisturbed red oak community did not occur in currently or recently grazed woods (Marks 1942). The undisturbed maple-bass-wood site had 79 species compared to 65 for the disturbed sites, but for the red oak there was little difference, with 94 vs. 92 species, respectively (Marks 1942).

Species identified as sensitive to grazing in these studies include *Actaea rubra, Allium tricoccum, Anemone quinquefolia, Arisaema triphyl-lum, Caulophyllum thalictroides, Dicentra cucullaria, Circaea lutetiana, Cardamine concatenata, Geranium maculatum, Helianthus strumosus, Hy-drophyllum virginiana, Panax quinquefolius, Phlox divaricata, Ranunculus* species, *Solidago ulmifolia, Uvularia perfoliata* and *Viola pubescens*. Many of these are the same as species in Iowa that appear to be sensitive to grazing in Iowa (Table 2). Only one study, conducted in Penn-sylvania, contradicted the shift of species found in previous studies and the data presented here. Lutz (1930) found that 26 of 58 species found on a grazed site were not found in an adjoining ungrazed area, but only nine species found in the ungrazed area were absent from the adjacent grazed area. However, as a whole, the previous and current data support the conclusion that there is a suite of understory species sensitive to grazing.

Tree Species

Overall, I found no effect of grazing on mean dbh of trees per plot. In contrast, Lutz (1930) found that grazed woods had only 41% of the basal area of an ungrazed woods. The difference probably lies in my more conservative site selection. This study included grazed woods that had an intact canopy, excluding woods where pasturing had proceeded to the point of tree mortality and conversion of the understory to sod.

Because they more than any group define our woodlands, the re-sponse of oak species to grazing is of particular interest in Iowa. Here the evidence is equivocal. Some oak species had a greater mean dbh in ungrazed woods and others in grazed woods. However, overall

Table 3. Number of occurrences of species categorized by reproductive and vegetative traits in 25 grazed plots compared to 25 matched ungrazed plots. P-values are from contingency table analysis.

	Grazed Plots	Ungrazed Plots	P-Value
Reproductive Characters			
Diaspore Dispersal			
Animal ingested	3	9	0.005
Animal external	5	4	
Ant	0	6	
Passive	19	7	
Wind	3	4	
Fruit Type			
Dry	27	21	0.0528
Fleshy	3	9	
Fruit Type			
Dehiscent	4	8	0.197
Indehiscent	26	22	
Vegetative Characters			
Growth Form			
Annual/biennial	14	0	0.0001
Perennial herb	7	22	
Fern	0	1	
Graminoid	6	3	
Shrub or small tree	3	1	
Vine	0	3	
Vegetative Spread			
Absent or limited	11	12	0.063
Extensive lateral	5	18	
Thorns Present	3	0	0.076
Root Structure			
Woody	3	4	0.0001
Fibrous	27	13	
Fleshy	0	13	
Primary Habitat Type 1			
Moist rich sites	8	22	0.0001
Dry or non-preferential	23	7	
Primary Habitat Type 2			
Shade	8	22	0.0001
Open or non-preferential	26	4	
Anthropogenic Disturbance			
Tolerant	14	1	0.0001
Intolerant	16	29	
Non-native	8	0	0.002
Range			
Cosmopolitan	7	0	0.017
All of U.S., or North America	10	10	
Regional (eastern U.S., midwest)	13	19	

the dominant oaks, *Q. alba, Q. macrocarpa* and *Q. velutina,* had a greater mean frequency of occurrence in ungrazed plots. Oaks, with relatively shallow roots, may be more susceptible to the trampling and soil compaction resulting from grazing (Behre et al. 1929, Lutz 1930, van der Linden and Farrar 1993). This study suggests that the response of oaks to grazing is complex and needs additional study.

There was no evidence that grazing affected the mean number of saplings per plot, but grazing clearly reduced the number of seedlings per plot. Also different seedling species appeared to be associated with grazed and ungrazed sites. Other studies found a similar reduction in seedlings with grazing (Behre et al. 1929, Lutz 1930, Den Uyl et al. 1938, Dambach 1944, Pigott 1983, Edwards and Birks 1986). Lutz (1930) found that regenerating trees were most

susceptible to damage when they were 5–30.5 cm in height. This could explain why there was a reduction in seedling number by grazing but no reduction in number of saplings.

Changes in the physical environment due to grazing may also accompany vegetation change. A New York study found that organic matter and moisture were reduced, the soil compacted, and earthworm activity was lessened in grazed sites compared to ungrazed sites (Chandler 1940). In Iowa, Kucera (1952) measured the quantity of litter and duff, their moisture content, air and soil temperatures, and evaporation rates. He found that open or pastured woods had less litter and duff and lower moisture retention compared to closed woods. Open or pastured woods also had higher air and soil temperatures and higher evaporation rates but lower soil moisture levels compared to the closed stands. Soils in open or pastured woods had

Table 4. Size of canopy trees and abundance of seedlings and saplings in five species groups. Data are averaged over all plots and are mean dbh for canopy trees and mean number of stems per plot for seedlings and saplings.

Community	Canopy Trees	Saplings	Seedlings
Dominant Oaks of the Oak-Hickory*	37.9	1.4	27
Other Oak-Hickory	15.6	3.5	56
Oak-Maple-Basswood	19.7	4.0	29
Bottomland Hardwoods	8.9	9.3	52
Introduced-Disturbed	11.4	1.8	1

*Quercus alba, Q. macrocarpa, Q. velutina

Table 5. Analysis of variance for effect of grazing status (grazed, ungrazed) and tree species on size of overstory trees and numbers of seedlings and saplings. MS is mean square from ANOVA.

	MS	F-Ratio	Probability
Size of overstory trees			
Grazing status	57	0.1	0.767
Species	61,029	94.3	≤ 0.0001
Block	6304	9.7	≤ 0.0001
Species × Status	3300	5.1	≤ 0.0001
Error	647		
Number of saplings			
Grazing status	300	3.5	0.063
Species	212	2.5	0.002
Block	185	2.2	0.003
Species × Status	60	0.7	0.750
Error	85		
Number of seedlings			
Grazing status	221,633	26.7	≤ 0.0001
Species	44,149	5.3	≤ 0.0001
Block	9811	1.2	0.257
Species × Status	15,608	1.9	0.013
Error	8308		

Table 6. Contingency table analysis of forest species groups and grazing status based on number of individuals in each category for canopy trees only ($\chi^2 = 83.7$, df = 4, $P \leq 0.0001$).

	Ungrazed	Grazed
Dominant Oaks of the Oak-Hickory*	98	50
Other Oak-Hickory	97	205
Oak-Maple-Basswood	169	150
Bottomland Hardwoods	343	278
Introduced-Disturbed	2	27

*Quercus alba, Q. macrocarpa, Q. velutina

less volume (more compaction) and slightly higher nitrogen levels, but no differences in organic matter and pH compared to those in closed forests. A study of grazed farmland woods in Indiana also found that soil moisture and light were the most important envi-

ronmental factors differentiating grazed vs. ungrazed woods (DenUyl et al. 1938).

I did not measure microenvironmental differences directly in this study. However, there were no differences in canopy coverage between the paired grazed and ungrazed sites, suggesting that grazed sites were not more open than ungrazed sites. I also found no measurable differences between grazed and ungrazed sites in any of the environmental or soil factors I measured. Pettit et al. (1995) found similar results and concluded that grazing pressure outweighed edaphic factors in determining the floristic composition of plots.

This study included grazed plots in sites with an intact canopy and plots in sites where grazing had been removed for up to approximately 15 years. If I had selected sites where grazing had resulted in loss of canopy trees and formation of sod, the results would have shown a more dramatic impact of grazing on species composition. Despite the conservative study design, I found strong differences in vegetation between plots in currently and recently grazed woods compared to plots in ungrazed woods, particularly for understory species. This study represents a rigorous test of the effects of grazing on the forest understory, while the canopy and other variables are held constant. Woods that have been moderately grazed (but not to the point of canopy loss and sod formation) are representative of the vast majority of the woods remaining in Iowa. Thus the results of this study are directly relevant to understanding the dynamics and restoration of these woodlands.

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Appendix 1.   Species groups of central Iowa forest trees.

Latin Name	Common Name
Dominant oaks of the oak-hickory association	
Quercus alba	white oak
Quercus macrocarpa	bur oak
Quercus velutina	black oak
Other species of the oak-hickory association	
Carya ovata	shagbark hickory
Fraxinus americana	American ash
Prunus serotina	black cherry
Quercus muehlenbergii	yellow oak
Maple-basswood association	
Acer nigrum	black maple
Quercus rubra	red oak
Tilia americana	basswood
Bottomland hardwoods association	
Acer negundo	box elder
Aesculus glabra	Ohio buckeye
Carya cordiformis	bitternut hickory
Celtis occidentalis	hackberry
Fraxinus nigra	black ash
Juglans nigra	black walnut
Morus rubra	red mulberry
Ulmus americana	American elm
Ulmus rubra	slippery elm
Disturbed site-introduced species	
Gleditsia triacanthos	honey locust
Juniperus virginianum	eastern red cedar
Morus alba	white mulberry