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Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA

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Abstract

A model was developed to represent the establishment of a fire-sensitive woody species from seeds and subsequent survival and growth through five size classes. Simulations accurately represent structural changes associated with increased density and cover of the fire-sensitive Ashe juniper (*Juniperus ashei*, Buckholz) and provide substantial evidence for multiple steady states and ecological thresholds. Without fire, Ashe juniper increases and herbaceous biomass decreases at exponential rates until a dense-canopy woodland is formed after approximately 75 years. Maintenance of a grass-dominated community for 150 years requires cool-season fires at a return interval of less than 25 years. When initial cool-season fires are delayed or return intervals are increased, herbaceous biomass (fuel) decreases below a threshold and changes from grassland to woodland become irreversible. With warm-season fires, longer return intervals maintain grass dominance, and under extreme warm-season conditions even nearly closed-canopy stands can be opened with catastrophic wildfires.

Keywords: Fire; Juniper; Succession; Thresholds

1. Introduction

Temperate grasslands and savannas throughout the world have experienced major shifts from grass to woody dominance over the past 100 to 200 years (Johnsen, 1962; Smeins, 1980; Evans, 1988; Archer, 1994). Explanations proposed for these changes include anthropogenic factors such as (1) alteration or elimination of the historical fire regime, (2) alteration of native ungulate grazing strategies and introduction of domestic herbivores, and (3) increase in atmospheric carbon dioxide concentration which may favor C3 species (woody plants) over C4 species (many dominant grasses) (Smeins, 1983; Johnson et al., 1993; Archer, 1994). Once the threshold from grassland to woodland or forest is crossed, an ecologically irreversible new state may be created.

Most analyses of historical vegetation changes in North America and their relationships to native herbivores and fire regimes are based upon anecdotal reports from explorers and early settlers. These assessments are generally limited to changes in the general physiognomy of plant communities and lack resolution about species composition and rates/patterns of change (Smeins, 1980; Forman and Russell, 1983; Weniger, 1985; Branson, 1985; Bahre, 1991; Archer, 1994; Taylor and Smeins, 1994). Relatively

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simple models, parameterized with actual life history and synecological data provide an opportunity to evaluate many of these anecdotal accounts, and test ecological theory.

The objective of this analysis is to describe a simple model that simulates potential increases in a fire-sensitive woody species, and concomitant community changes, when fire is eliminated or fire regimes are altered. The model is parameterized to represent Ashe juniper (*Juniperus ashei*, Buckholz) from the Edwards Plateau of Texas, USA, and results of simulations are compared to actual rates of population increase and temporal patterns of landscape change. Theories of vegetation change including multiple steady states and ecological thresholds are related to the simulations.

2. Background information

The limestone-derived landscapes of the Edwards Plateau of Texas are characterized by highly variable ecological sites, which range from steep canyonlands to high, relatively level divide regions. Soils are generally shallow (10–30 cm) and rocky with frequent limestone outcrops. This topoedaphic diversity generates many different community types that range from closed-canopy forest to nearly open grasslands (Riskind and Diamond, 1988). This study focuses on the semi-arid western divide region of the Plateau. Ashe juniper, the target species, is a non-sprouting evergreen tree or shrub found mainly on the Edwards Plateau of Texas with populations in Oklahoma, Missouri, Arkansas, and the Sierra del Carmen mountains of Mexico (Johnsen and Alexander, 1974).

Before European settlement, fire on the upland divides of the Edwards Plateau is believed to have maintained a grassland or savanna community, with juniper and other woody species limited to stream floodplains and rocky outcrops, or occurring as scattered individuals or mottes within the grassland matrix (Kroll, 1980; Smeins, 1980). Heavy stocking with domestic herbivores lowered fuel loads and hence fire intensity, and decreased competition from herbaceous species. Both factors allowed for increased abundance of woody species, particularly the fire-sensitive Ashe juniper (Smeins, 1980, 1983; Evans, 1988). Over the past 100 years, canopy cover

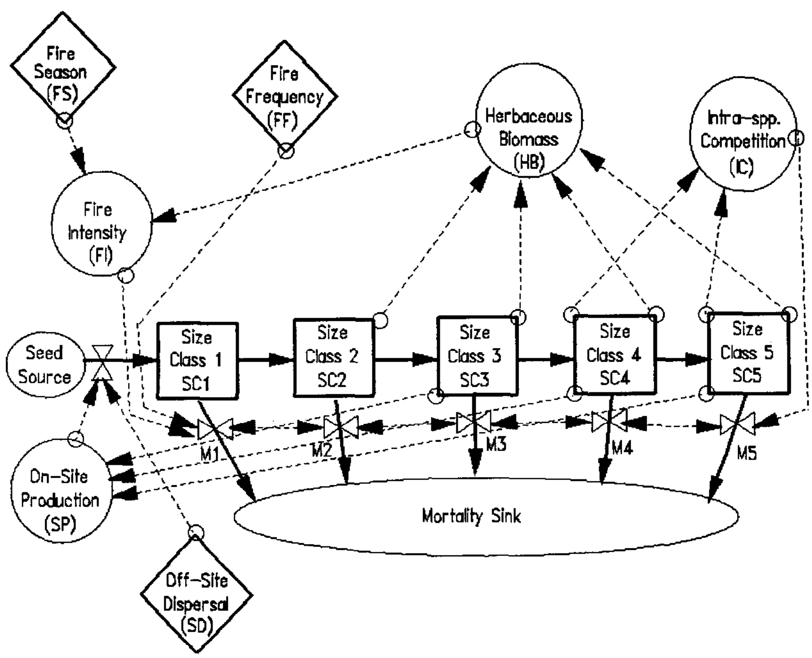

Fig. 1. Conceptual model of establishment and growth of the fire-sensitive woody species, Ashe juniper.

of Ashe juniper has increased which often results in significant changes in plant and animal community composition and structure (Foster, 1917; Smeins and Merrill, 1988; Blomquist, 1990; Fuhlendorf, 1992). Other species of *Juniperus* have been associated with similar phenomena throughout the United States, as well as in other countries (Johnsen, 1962; Miller and Wigand, 1994).

3. Overview of the conceptual model

The model represents the establishment of a fire-sensitive woody species (Ashe juniper) from seeds and subsequent survival and growth through five size classes (Fig. 1). State variables represent density of trees (individuals/ha) in each of the five size classes, with size class 3 representing sexual maturity and size class 5 representing mature trees. Seedling establishment is a function of seed dispersal from off-site sources and on-site seed production. Seed dispersal and establishment from off-site sources is represented as a stochastic event, similar to that expected from dispersal by mammals and birds. On-site seed production depends on density in the three largest size classes. Mortality rates are age-specific and are represented as functions of intra-specific competition and fire frequency and intensity. Mortality due to intra-specific competition, which represents the effect of maximum density and reduced resource availability, occurs as densities in the two largest size classes reaches critical levels. Fire intensity is dependent on amount of herbaceous biomass and season of occurrence (severity of environmental conditions). Herbaceous biomass, which represents availability of fine fuel, decreases as density in the four largest size classes increases. Parameterization and evaluation of the model were based upon data from many life history studies of Ashe juniper and dynamics of communities in which it occurs. The model was formulated as a set of difference equations and simulations were run with a time-step of one year using the program STELLA® (High Performance Systems, Inc., 1994).

4. Quantification of the model

4.1. Size-class distribution and growth rates

The densities (trees/ha) of each of five size classes (SC_i), representing canopy diameters (m) of

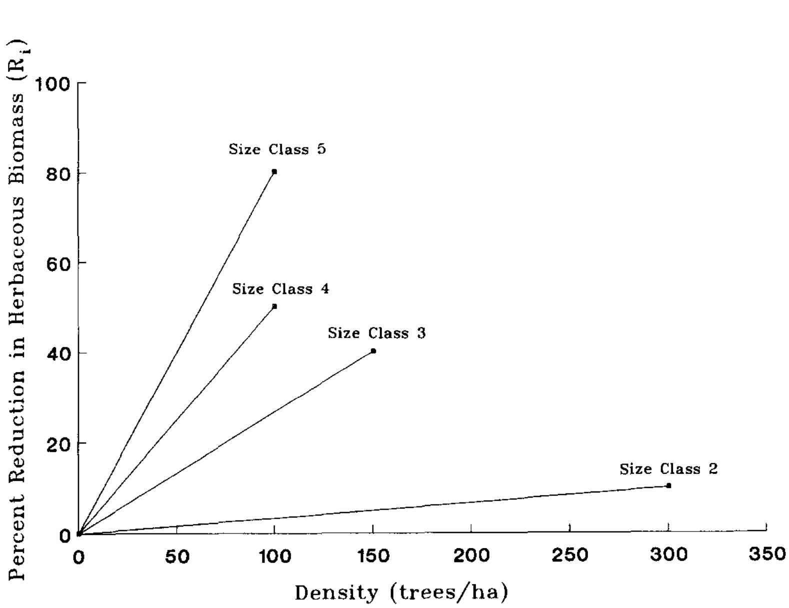

Fig. 2. Percent reduction of herbaceous biomass (R_i) associated with increasing densities of Ashe juniper in the ith size class (Fuhlendorf, 1992).

< 0.75, 0.76–1.50, 1.51–3.00, 3.01–6.0, and > 6.0, were initialized as zero to simulate an open grassland. Growth rate is represented by the number of years a cohort of trees stays in a size class. Trees remain in size classes 1, 2, and 3 for 10 years each, and in size class 4 for 25 years, before accumulating in size class 5 as mature trees (Blomquist, 1990; Fuhlendorf, 1992).

4.2. Seedling establishment

Seed dispersal and establishment from off-site sources (SD) is calculated by drawing a random variable from a uniform distribution on the interval 0 to 1. If the variable is < 0.7 no seeds establish from off-site sources. When the variable is > 0.7, it is multiplied by 30 to determine how many seedlings establish. Thus, on average, seedlings establish 30% of the time with densities ranging from 21 to 30 seeds/ha. Once sexually mature trees (size classes 3, 4, and 5) are established, off-site sources are supplemented by on-site seed production (SP). Additional seedling establishment is based on the density of the three largest size classes and calculated as $(SC_5 * 0.5) + (SC_4 * 0.4) + (SC_3 * 0.2)$. Number of seeds established/ha are conservative estimates based on studies of life history traits and dispersal ecology of Ashe juniper, as well as environmental conditions associated with safe sites and seedling establishment (Blomquist, 1990; Chavez-Ramirez, 1992; Smeins et al., 1994).

4.3. Influences on herbaceous biomass

As density of trees in size classes 2 to 5 increases, the level of associated herbaceous biomass in the community decreases (Fuhlendorf, 1992). The percent reduction in herbaceous biomass, relative to the maximum level attained in the absence of trees, associated with increased density of trees in each size class is shown in Fig. 2. Percent herbaceous biomass remaining (HB) is calculated as: $HB = \prod_{i=2}^{i=5}(1 - R_i)$, where R_i is the percent reduction due to trees in the ith size class.

4.4. Mortality through intra-specific competition

Mortality due to intra-specific competition (IC) does not occur when $(SC_4 * 0.5) + SC_5 < 100$ trees/ha. When IC > 100, the numbers of trees dying each year in the different size classes (M_i) are calculated as: $M_1 = (SC_1 * 0.002 * IC)$, $M_2 = (SC_2 * 0.008 * IC)$, $M_3 = (SC_3 * 0.008 * IC)$, $M_4 = (SC_4 * 0.008 * IC)$, and $M_5 = (SC_5 * 0.008 * IC)$, where $IC = (SC_4 * 0.5) + SC_5$. Competitive relationships of Ashe juniper have not been studied extensively. The values above represent conservative estimates of competitive mortality based on field observations from general ecological studies of Ashe juniper-dominated communities (Smeins et al., 1994). Rates of mortality were determined by identifying values that produced a relatively stable community with the densities of Ashe juniper near an estimate of the maximum for the specific site.

4.5. Mortality through fire intensity and frequency

Primary factors that influence rate of increase in density of fire-sensitive woody plants are fire frequency and intensity (Wink and Wright, 1973; Smeins, 1980, 1983; White, 1980; Bunting, 1983; Ueckert et al., 1994). Fire frequency (FF) is a driving variable which represents number of years between fires and is defined prior to each simulation. Fire intensity (FI) depends on level of fine fuel or herbaceous biomass (HB) and the fire season (FS), where the latter is a driving variable that represents the aggregate effect of factors such as temperature, relative humidity, and wind during either the cool season (FS = 1) or the warm season (FS = 2). Dur-

Table 1
Fire intensities (FI), represented as the proportion of trees dying in a given size class during a year in which a fire occurs, as a function of fire season (FS) and level of herbaceous biomass (HB)

Size class	Fire intensity (FI)		
	Cool-season fire (FS = 1)		Warm-season fire (FS = 2) [a]
	High biomass (HB > 75%)	Low biomass (HB < 75%)	
1	99	40	99
2	90	40	90
3	30	0.1	90
4	0.04	0.03	70
5	0.025	0.015	60

[a] Cool-season fires require fine fuel (HB). Warm-season fires consume the canopies of woody plants (crown fires), therefore HB is not an important factor.

Table 2
Mean (standard deviation, $n = 10$) number of trees/ha in each size class and mean (standard deviation, $n = 10$) percent herbaceous biomass remaining (HB) after 150 years under the indicated fire frequency and season

Fire frequency and season	Size class density (trees/ha)					Herbaceous biomass (%)
	1	2	3	4	5	
No fire	57.0	10.8	8.0	28.4	73.2	32.7
	(38.5)	(3.2)	(5.1)	(11.7)	(10.0)	(3.9)
30 yr, cool	72.7	10.0	7.1	12.9	72.6	37.1
	(56.9)	(8.1)	(4.2)	(4.2)	(4.7)	(3.9)
25 yr, cool	86.7	34.2	11.7	5.8	41.9	58.9
	(42.0)	(33.0)	(18.0)	(5.5)	(27.8)	(20.4)
20 yr, cool	75.3	1.8	1.6	3.9	14.3	82.0
	(23.6)	(1.1)	(1.0)	(0.9)	(2.7)	(2.4)
10 yr, cool	54.7	1.1	1.6	3.3	13.9	83.1
	(33.4)	(0.7)	(1.0)	(1.6)	(3.7)	(3.1)
30 yr, warm	75.2	58.4	62.6	4.1	7.4	70.2
	(37.5)	(38.1)	(26.1)	(2.1)	(1.4)	(5.0)
10 yr, warm	49.8	1.9	1.9	3.6	1.8	93.4
	(16.0)	(0.5)	(0.8)	(1.1)	(0.5)	(0.7)

ing a year when a fire occurs, the number of trees dying in the ith size class (M_i) is calculated as $M_i = \mathrm{FI} * \mathrm{SC}_i$, where FI is chosen from Table 1 depending on the values of FS and HB. Herbaceous biomass is the primary fuel for cool-season fires because it is more easily consumed than woody

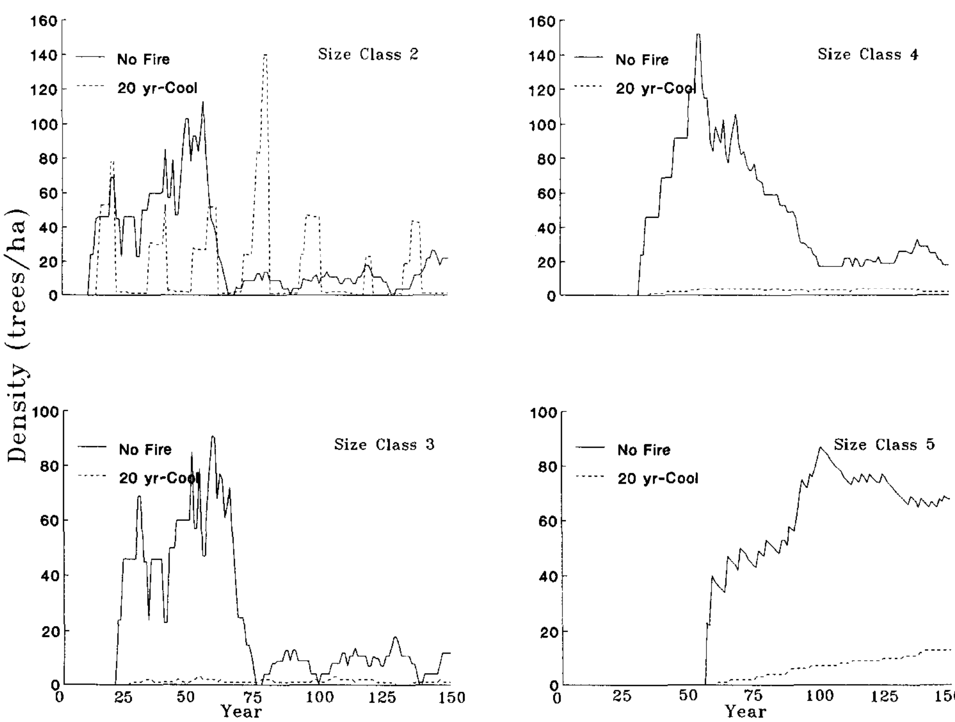

Fig. 3. Density (trees/ha) of Ashe juniper in size classes 2–5 over 150 years from typical simulations with no fire and with a cool-season fire every 20 years.

vegetation. Extreme conditions (warm season) may produce crown fires where the canopies of woody plants actually are consumed by the fire. Therefore, the amount of herbaceous biomass (HB) is not important for catastrophic warm-season fires. There is no mortality due to competition during a year in which fire occurs.

5. Simulated effects of fire on Ashe juniper dynamics

To examine the model's influence on density of Ashe juniper 10 replicate, 150-year simulations of each of 7 different fire regimes were run beginning with an initially open grassland. The simulations were: (1) no fire; cool-season fires occurring every (2) 30, (3) 25, (4) 20, and (5) 10 years; and warm-season fires occurring every (6) 30, and (7) 10 years. Results are summarized in terms of mean density of mature trees, temporal shifts in size-class distribution and total density of trees, and the proportional reduction in herbaceous biomass (Table 2, Figs. 3–5).

Without fire a relatively stable closed-canopy (maximum density for this site) develops from an initially open grassland in less than 150 years (Fig. 3). Canopy cover begins to be dominated by the two largest size classes after about 75 years with all the smaller classes stabilizing at low densities. Prior to reaching maximum densities, dominance is variable among the other size classes.

Response to fire varies with season of the burn and interval between fires. Density of Ashe juniper after 150 years increases with length of the fire interval although the relationship is not linear (Fig. 4). A similar but inverse relationship exists with herbaceous biomass. Simulation results divide into two categories. One depicts a closed-canopy woodland and the other represents a relatively open grassland or savanna. An interval of 10 or 20 years for cool-season fires maintains similar community structure with low densities of large Ashe juniper trees and relatively high herbaceous biomass. A 30-year interval, cool-season fire allows a closed-canopy stand to form, similar to conditions without fire. Cool-season fires with a 25-year interval produce intermediate conditions to the 20- and 30-year intervals. Each simulation, however, can produce either state depending upon random initial seed dispersal during the first 10 years. Random seed dispersal dictates the first year in which seedlings appear and positions this treatment on the threshold between two domains of attraction, as indicated by the large standard deviation (Fig. 4, Table 2). When fires occur during the warm season, maintenance of relatively open grasslands is possible with longer return intervals.

The feedback loop created by the relationship of temporal change in tree density and percent reduction of herbaceous biomass is a good overall measure of model response to treatments (Fig. 5). No fire and a cool-season fires every 30 years responded similarly in that herbaceous biomass decreased rapidly after approximately 40 years. A cool-season fire every 10 or 20 years maintains high levels of

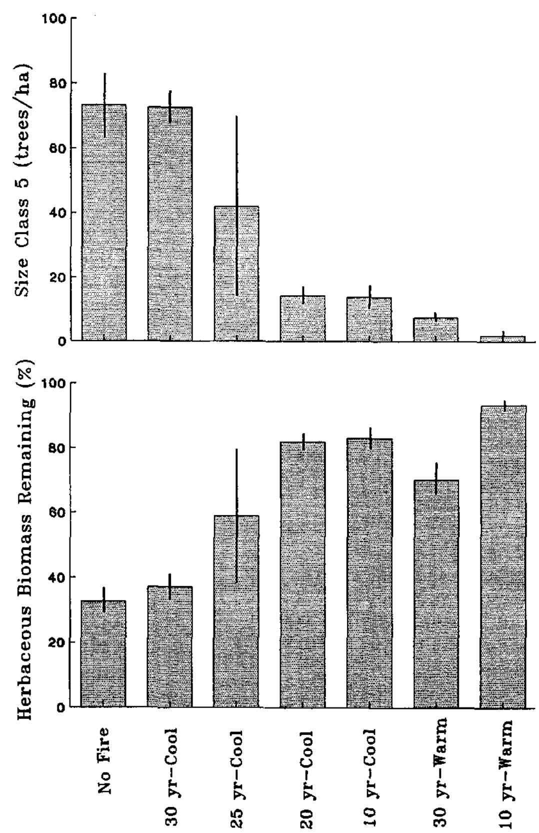

Fig. 4. Mean density (trees/ha) of size class 5 and mean percent herbaceous biomass remaining (HB) after 150 years under the indicated fire frequency and season. Vertical lines represent 1 standard deviation.

herbaceous biomass throughout 150 years. When the interval is extended to 25 years the importance of the random seed dispersal becomes evident again and the two separate domains of attraction emerge. At this interval a relatively open grassland is maintained or a closed-canopy woodland is formed with no intermediate states occurring after 150 years. This sensitivity to variation in the year of first seedling establishment indicates that a threshold is crossed when the fire interval is approximately 25 years.

As return intervals between fires increase, more extreme seasonal variables are required to maintain grasslands. Warm-season fires maintain a relatively open grassland at intervals as high as 30 years (Figs. 3–5). When the temporal scale is extended to 500 years, warm-season burns with a return interval of 10 years formed a stable state with the density of size class 5 at less than 2 trees/ha and little or no reduction of herbaceous biomass.

Timing of the initial fire is as important as fire return interval and further indicates the threshold concept. When the first fire does not occur until 40 years, even a 10-year interval of cool-season fires can not prevent formation of a woodland. However, intense warm-season burns with an interval of 10 years converted a closed-canopy woodland to an open grassland in about 40 years.

The model shows that Ashe juniper on the western Edwards Plateau forms a relatively stable closed-canopy woodland in approximately 75 years with little understory vegetation. Suggestions for management of juniper through fire includes a return interval of 8–10 years (Ueckert et al., 1994). Our model shows fire can maintain a relatively open grassland for 150 years with an interval at less than 25 years. After 20 years, however, there is a sharp reduction of herbaceous biomass. This indicates that a fire interval of 20 years would be sufficient to maintain a low density of Ashe juniper and a high level of herbaceous production if initial density and

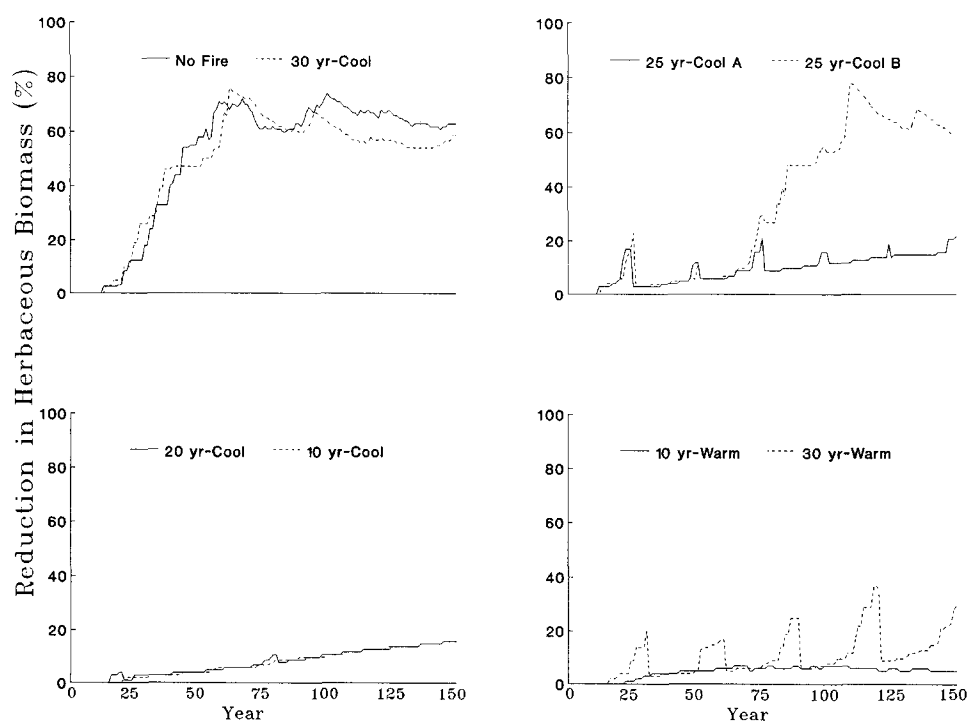

Fig. 5. Percent reduction of herbaceous biomass (100 − HB) over 150 years under the indicated fire frequency and season. Two examples of cool-season fires with a 25-year interval are shown because of the large standard deviation (Fig. 4).

cover is low for Ashe juniper and all fires are successful.

6. Model evaluation

Evaluation of a simulation model on this temporal scale is difficult, but lower-level components of the model, such as initial seed dispersal, growth rates, community relationships, and the influence of fire can be compared to field measurements. The only variable that can not be compared with actual data is intra-specific competition.

Simulations appear to be accurate when compared to historical documentation and field experiments. Field data from a 45-year exclosure on the western Edwards Plateau produced similar results to those simulated (Smeins et al., 1976, 1994; Smeins and Merrill, 1988). Because of an existing seed bank and presence of some seedlings, population increases were slightly more rapid in the field study than in the simulations. For this model, we assumed no existing seed or seedling bank and random initial dispersal.

Smeins (1980) reviewed historical documents that describe extensive open areas in the divide regions of the Edwards Plateau and high frequencies of wildfires. Prior to settlement, fires often occurred during summer dry seasons when dry biomass had accumulated, air temperatures were high, and relative humidities were low. This resulted in intense fires and high mortality to all sizes of fire-sensitive trees (Archer, 1994). Data used to estimate the mortality to Ashe juniper from fire in our model were based on prescribed cool-season, management burns. Simulations indicate that relatively mild fires every 10 to 25 years would maintain a fairly open grassland or savanna for at least 150 years. Some large junipers did exist at the end of this time frame, but periodic severe droughts or intense wildfires would be expected to further limit these survivors. Merrill and Young (1959) found that large Ashe juniper trees suffered higher mortality from drought than did small trees.

Animals, primarily birds (American Robins, Cedar Waxwings), are major dispersal agents of Ashe juniper (Chavez-Ramirez and Slack, 1993, 1994), as well as for other juniper species (Holthuijzen et al., 1987). Establishment would not only be dependent upon dispersal but also proper safe sites and favorable environmental conditions for germination while seeds are viable. Field studies have shown that abundant seedlings are found under and at the edge of mature juniper or other woody species' canopies (Blomquist, 1990). Seed dispersal and existing seedling bank along with increased seed source from large trees and rapid growth of intermediate sized trees are responsible for the model's exponential density curve and these variables agree with field measurements and observations (Archer, 1994; Smeins et al., 1994). Growth rates and time intervals of successive size classes are intermediate to those found by Blomquist (1990) and Fuhlendorf (1992).

Most studies of juniper understory relationships agree that there is an inverse relationship between overstory cover and herbaceous production (Jameson, 1967; Armentrout and Pieper, 1988; McPherson and Wright, 1990). Fuhlendorf (1992) found that the influence of Ashe juniper was limited in small trees but increased as trees became larger with almost complete exclusion of herbaceous growth under mature trees. Simulations of increases in Ashe juniper showed slight decreases in herbaceous biomass until a threshold of densities of trees in the larger size classes was attained, then herbaceous vegetation decreased exponentially.

The influence of fire on Ashe juniper has been extensively studied as a method of control and depends on season and fine fuel load prior to the fire (Arend, 1950; Dalrymple, 1969; Wink and Wright, 1973; White, 1980; Bryant et al., 1983; Ueckert et al., 1994). Herbaceous production on the western Edwards Plateau depends on sites and can range from 800 to 3000 kg/ha. Wink and Wright (1973) found that a relatively continuous cover of fine fuel (herbaceous biomass) at 1000 kg/ha was necessary to carry a fire that would kill 99% of the trees under 1.8 m tall. According to this scenario, high levels of fuel would kill all trees in size classes 1 and 2, as well as some in size class 3. As fuel loads decrease and trees increase in size, only hot fires under severe environmental conditions would produce high mortality (Bunting, 1983; Ueckert et al., 1994). Very intense, catastrophic, crown fires, similar to those reported in many wildfires, would produce high mortality and could open even closed-canopy stands. These extreme conditions were not simulated in this model. In the simulations described here, low mortality of large trees, as well as their influence on herbaceous vegetation is the driving force behind the ecological threshold produced through the simulations.

Competitive relationships of Ashe juniper are not well quantified, so influences in the model are limited to a density-dependent increase in mortality when the community approaches maximum densities. Establishment from seed continues which maintains a seedling bank to fill any future gaps in the canopy. Intermediate size classes decrease in density but some trees continue to exist in all size classes. The densities representing a closed-canopy stable state are conservative estimates of maximum densities associated with the western divide regions of the Edwards Plateau. Higher densities are possible if canopy cover reaches 100% which could occur at some locations, but site heterogeneity and the presence of other woody species would limit complete juniper canopy coverage across the entire landscape. Data are presented as trees/ha but are actually averages across the landscape that include heterogeneity between sites.

7. Discussion

Archer (1994) reviewed historical documentation throughout the western United States and found that changes in grass to woody domination have been (1) rapid, occurring over 50- to 100-years, (2) non-linear and influenced by drought, (3) influenced by topoedaphic factors, and (4) often non-reversible over a management time frame. Even though the current model does not include explicit representation of drought or topoedaphic factors, when parameterized for random initial establishment, growth rates, fire frequency and intensity, intra-specific competition and herbaceous/woody interactions, it accurately simulates community changes associated with ingress of the fire-sensitive Ashe juniper. General theory holds that plant communities, following a disturbance such as fire, move toward a climax community that is relatively stable within the prevailing climate (Clements, 1916). Many alternative theories have been proposed including state and transition models (Westoby et al., 1989; Laycock, 1991) and the concept of ecological thresholds (Archer, 1989; Friedel, 1991). It is argued that frequently more than one stable state is possible for any ecological site. Laycock (1994) discussed several examples where lower successional stable communities persist for decades following the elimination of grazing. Archer and Smeins (1991) stated that up to a certain threshold, a community could be relatively stable and resistant to change from altered grazing or fire regimes. Beyond that threshold, changes to a new state become rapid and potentially irreversible over reasonable time frames.

Simulation of the increase of Ashe juniper on the Edwards Plateau of Texas supports the concept of multiple steady states and ecological thresholds. Two domains of attraction are evident depending upon fire frequency and intensity. Initial changes are slow and can be reversed which maintains relatively open grasslands if fires occur fairly frequently. However, if increases in woody plant abundance continue without fire, eventually herbaceous production is suppressed, which causes a positive feedback where fires are no longer effective. At this threshold, increases in Ashe juniper become more rapid because of the increased seed source, and eventually results in a dense woodland. Any attempt to revert back to a savanna would require intense fires or high input management techniques such as mechanical or herbicide treatments.

High abundances of junipers may be associated with lower diversity of plants and native fauna, and reduction of forage for livestock and wildlife, as well as changes in ecosystem processes, such as nutrient/water cycling, and primary productivity (Archer, 1994). Conversely, their abundance, in association with other hardwood species, may be necessary for some rare species (Kroll, 1980). When fire suppression occurs, due to intentional intervention or as a result of reduced fuel loads due to overgrazing, fire-sensitive woody plants can increase to form dense-canopy woodlands. These changes occur fairly rapidly, but often go unnoticed for many years until the size and growth rates of the trees reach critical levels.

In summary, simulations using the current model, parameterized to represent simple life history characteristics of Ashe juniper, suggest that elimination of fire could be the primary cause of long-term changes in plant communities on the Edwards Plateau of Texas. However, domestic herbivory and climatic variability, which are represented only implicitly via the herbaceous biomass and fire intensity auxiliary variables, respectively, also could be important factors when considering shorter-term fluctuations in local communities. Current emphasis on the predominate influence of fire on simple life history characteristics provides flexibility to reparameterize the model to simulate a variety of other fire-sensitive woody species. But lack of detail in representations of climatic variability and variation in levels of domestic herbivory compromises the model's ability to predict finer-scale fluctuations in local Ashe juniper communities. We currently are gathering additional field data to allow a more detailed representation of herbaceous biomass dynamics in response to different levels of domestic herbivory. This, in turn, will allow a more detailed representation of fire frequency and intensity as a function of level of accumulation of herbaceous biomass.

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