MECHANISMS OF SHRUBLAND EXPANSION: LAND USE, CLIMATE OR CO_2?

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Abstract. Encroachment of trees and shrubs into grasslands and the 'thicketization' of savannas has occurred worldwide over the past century. These changes in vegetation structure are potentially relevant to climatic change as they may be indicative of historical shifts in climate and as they may influence biophysical aspects of land surface-atmosphere interactions and alter carbon and nitrogen cycles. Traditional explanations offered to account for the historic displacement of grasses by woody plants in many arid and semi-arid ecosystems have centered around changes in climatic, livestock grazing and fire regimes. More recently, it has been suggested that the increase in atmospheric CO_2 since the industrial revolution has been the driving force. In this paper we evaluate the CO_2 enrichment hypotheses and argue that historic, positive correlations between woody plant expansion and atmospheric CO_2 are not cause and effect.

1. Introduction

The density, biomass and stature of trees and shrubs has increased in many ecosystems over the past 200 years in the Southwestern U.S.A. (Branson, 1985; Grover and Musick, 1990; Bahre, 1991) and in other arid and semi-arid ecosystems around the world (see Archer, 1994). Although this phenomenon has been widely recognized, our understanding of mechanisms controlling the rates, dynamics and extent of this vegetation change is limited. Traditional explanations have focused on changes in climate, livestock grazing and fire regimes as causal factors. The possibility that encroachment of woody plants into grass-dominated communities in desert, prairie and savanna ecosystems in recent history has been driven by post-industrial CO_2 fertilization has been proposed as an alternative hypothesis (Mayeux *et al.*, 1991; Polley *et al.*, 1992; Idso, 1992; Johnson *et al.*, 1993). Arguments supporting the hypothesis are based on observations that: (1) Woody plants typically possess the C_3 photosynthetic pathway, whereas the grasses they have replaced in the southwestern U.S.A. and tropical regions are primarily C_4; (2) Historic increases in atmospheric CO_2 have conferred a significant advantage to C_3 species relative to C_4 species with respect to physiological activity, growth and competitive ability; and (3) Invasion of woody plants into C_4 grasslands has been

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accompanied by a 30% increase in atmospheric CO_2 over the past 200 years (from ca. 270 ppm to 350 ppm). The hypothesis is also attractive in that CO_2 enrichment has been a globally widespread phenomenon and, as such, could account for the relatively synchronous occurrence of woody plant invasion and/or encroachment reported from arid land grasslands and savannas around the world. Arguments from modern analogs have also been cited as evidence that Holocene shifts in grass (C_4) – shrub (C_3) abundance in Chihuahuan Desert recorded 7,000–9,000 years ago were the result of changes in atmospheric CO_2 rather than changes in climate or disturbance regimes (Cole and Monger, 1994). An understanding of factors contributing to vegetation lifeform composition shifts thus has implications for interpreting changes in the distant past as well as future vegetation states.

2. Evaluation of the Hypothesis

Despite the apparent plausibility of this hypothesis, there is considerable evidence to suggest factors other than CO_2 enrichment have been the causal mechanism for woody plant invasion or encroachment into arid land grasslands and savannas.

- Under the present atmospheric CO_2 levels of 350 ppm, C_4 species still have quantum yields, photosynthetic rates and water-use efficiencies comparable to or greater than those of coexisting C_3 plants (Ehleringer and Monson, 1993). Thus, there is no ecophysiological basis for presuming a historical shift in competitive interactions that would have promoted replacement of C_4 grasses by C_3 shrubs. Although CO_2 fertilization mimicking historic increases can stimulate growth of C_3 shrub seedlings and reduce requirements for resources needed for early growth and establishment, shrub biomass production was not affected by CO_2 concentration when seedlings were grown with a C_4 grass (Polley *et al.*, 1994).
- Various modeling (Hunt *et al.*, 1991), controlled environment (Riechers and Strain, 1988) and field experimental studies (Owensby *et al.*, 1993) suggest C_4 grasses may be much more responsive to increasing CO_2 than previously assumed (also Poorter, 1993).
- The CO_2 enrichment hypothesis does not help explain the replacement of C_3 grasses by C_3 woody plants which has occurred in temperate zones and cold deserts.
- The hypothesis cannot explain why some sites have experienced woody plant encroachment, while nearby and edaphically similar sites dominated by C_4 grasses have persisted (Figure 1).
- If the CO_2 enrichment hypothesis is correct, widespread shifts from C_4 grasses to C_3 grasses should also have occurred within grasslands during this time frame. Such does not appear to be the case when differences in land use and management have been accounted for.

- The temporal correspondence between CO_2 enrichment and woody plant encroachment is problematic. Although present-day atmospheric CO_2 levels are ca. 30% higher than those 200 YBP, enrichment has been exponential, with a prominent lag phase. In 1903–1925, CO_2 concentrations were ca. 300 ppm (Neftel *et al.*, 1985), only an 11% increase over that of the late 1700s. We question whether this modest increase in CO_2 would have been sufficient to cause the substantial increases in woody plant abundance in grasslands which had been initiated or had already occurred by this time in many areas (Figures 2a, c).
- Paleodata indicates grasses and woody plants have alternated in dominance throughout the Holocene, presumably in response to ecological factors uncorrelated with changes in CO_2 (Van Devender and Spaulding, 1979; Van Devender, 1980).
- The extent to which benefits of increased CO_2 will be manifested in enhanced woody plant growth and competitive ability will be constrained by interactions of other environmental resources, stresses and higher-order ecological interactions (Bazzaz, 1990; Mooney *et al.*, 1991; Morison, 1993). Several studies have failed to demonstrate a significant CO_2 fertilizer effect on woody plant growth over the past century (Graumlich *et al.*, 1989; Graumlich, 1991). For those which have (e.g., La Marche *et al.*, 1984), the response may have been the result of temperature rather than CO_2 (Francey and Hubick, 1988).

In sum, these numerous and significant exceptions limit the utility of the historic atmospheric CO_2 enrichment hypothesis as a robust explanation for the cause of woody plant encroachment into grasslands. The correlation between CO_2 and woody plant invasion may therefore be spurious. The hypothesis that shifts from C_4 (grass) to C_3 (shrub) composition in the Chihuahuan Desert during the Holocene was the result of increases in atmospheric CO_2 from ca. 200 to 280 ppm (Cole and Monger, 1994) are subject to some of these same detractions. While we reject the contention that changes in atmospheric CO_2 in the recent past have directly caused changes in grass and woody plant abundances observed to date, we recognize the possibility that accumulation of CO_2 since the industrial revolution may play an increasingly important role in determining the structure and function of vegetation.

3. Alternative Explanations

Traditional alternative hypotheses attempting to explain woody plant displacement of grasses in arid lands are centered around historic changes in grazing, fire and climatic regimes. For example, Neilson (1986) has hypothesized that the pristine grasslands of the Chihuahuan Desert recorded 100 years ago had established during the cooler, moister climates of the 'little ice age' and were only marginally supported under climatic conditions occurring at the time of settlement. If this

Fig. 1. Fenceline contrast in the Mitchell Grasslands. Queensland. Australia showing stand of *Acacia nilotica* which has developed since the 1940s on one property. but not the other. Local contrasts in physiognomy such as these suggest differences in land management practices as the cause for many of the historic increases in woody plant cover in grasslands and savannas, and not broad-scale factors such as changes in climatic or atmospheric conditions. See Archer (1994) for further discussion. (Photo by S. Archer).

hypothesis is correct, climate-driven succession from mesophytic grasses to more xeromorphic shrubs may have been in progress at the time of settlement and augmented by anthropogenic alteration of grazing and fire regimes. However, after analyzing land use history and changes in woody plant cover on repeat photography in southeastern Arizona, U.S.A., Bahre (1991, p. 105) felt that "probably more time has been spent on massaging the climate change hypothesis than on any other factor of vegetation change, and yet it remains the least convincing." He goes on to argue that the historic displacement of grasses by woody plants in this region has been the result of grazing and fire exclusion (p. 187). Shifts from grass-to-shrub domination have also been well documented at the Jornada Experimental Range in southern New Mexico, U.S.A. (Figure 2c). An analysis of climatic data from 1914–1984 on this site failed to demonstrate any consistent statistical rationale for invoking climate as a causal mechanism in the observed vegetation changes (Conley *et al.*, 1992). Another case study in Utah, U.S.A., also supports these findings (Madany and West, 1983). They used tree ring data to document instances where pine savannas protected from livestock grazing have persisted, whereas nearby edaphically similar sites subjected to cattle grazing changed from savanna to dense woodland soon after the introduction of livestock in the 1860s (Figure 2a). The close proximity of the two sites suggest changes in climate or atmospheric CO_2

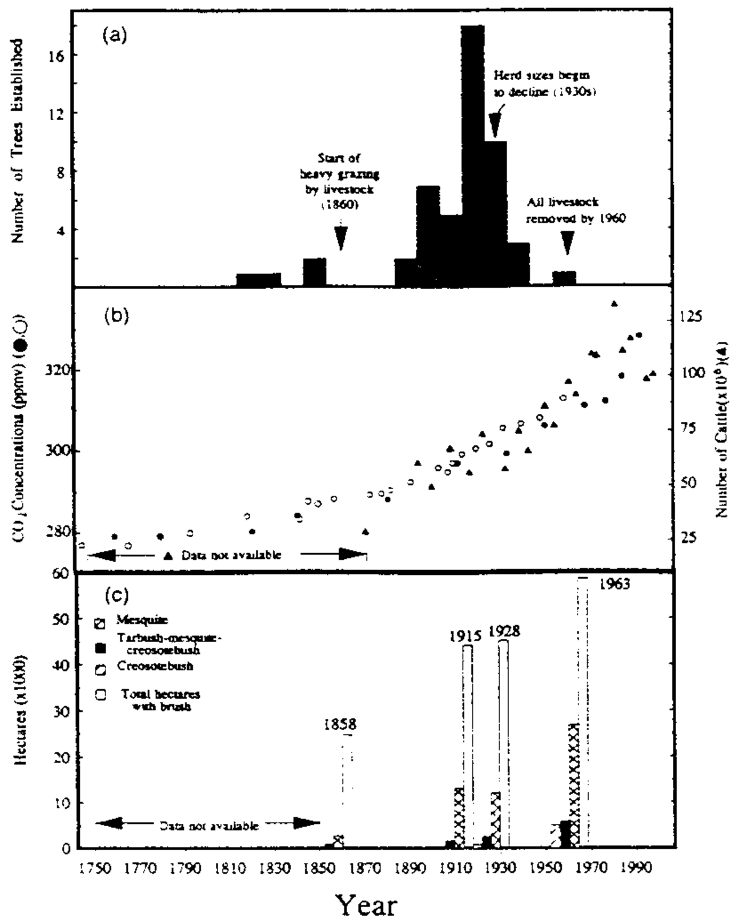

Fig. 2. (a) Temporal patterns of Ponderosa pine (*Pinus ponderosa*) tree recruitment in a semi-arid savanna in Utah, U.S.A. (from Madany and West, 1983); (b) changes in atmospheric CO_2 concentrations (closed circles = Neftel, 1985; open circles = Friedli *et al.*, 1986) and cattle numbers in the United States (closed triangles = USDA, 1989); and (c) changes in woody plant cover on grazed plant communities at the Jornada Experimental Range in the Chihuahuan Desert, New Mexico, U.S.A. (from Buffington and Herbel, 1965). Trends in world cattle numbers (FAO Yearbook of Agriculture) were similar to those shown for U.S.A., but records were less complete.

which may have occurred during this period were not sufficient to invoke changes in vegetation physiognomy in the absence of grazing (see also Figure 1).

Another explanation for the observed shift in vegetation types is the intensification of grazing by livestock.

In North America, uncontrolled utilization of grassland vegetation by domesticated and feral livestock (horses, sheep, cattle, burrows) had so degraded vegetation and soils that federal legislation (the Taylor Grazing Act of 1934) was enacted in an attempt to curtail further deterioration (Stoddart *et al.*, 1975). Scenarios paralleling those of the North American Southwest have also occurred in Africa (Van Vegten, 1983; Skarpe, 1991), Australia (Harrington *et al.*, 1979; Gardener *et al.*, 1990) and South America (Schofield and Bucher, 1986; Bucher, 1987) following introduction of livestock. The widespread invasion of woody plants into grasslands and 'thicketization' of savannas is often coincident with intensification of grazing (Figures 2a, b). Direct and indirect effects of livestock grazing (preferential utilization of grasses, alteration of soil structure and chemistry, woody legume seed dispersal, reductions in fire frequency and/or intensity) significantly influence woody plant population dynamics, generally enhancing woody plant seedling establishment, seed production, plant longevity and stand development (see review by Archer, 1994). Interactions between climate and the direct and indirect effects of grazing have likely influenced the rate and dynamics of woody plant encroachment (Herbel *et al.*, 1972; Archer *et al.*, 1988; Harrington, 1991). For example, climatic events that trigger episodes of woody plant establishment may also enhance grass production and increase the likelihood of fire (Swetnam and Betancourt, 1990) which would subsequently reduce woody plant stature or density and suppress tree and shrub establishment. However, when grazing reduces this fine fuel load and continuity, woody plant encroachment can be rapid (Harrington and Hodgkinson, 1986). For invasive woody plants such as mesquite, which are capable of establishing in dense swards of grasses (Brown and Archer, 1989), post-settlement reductions in fire frequency and intensity associated with fire suppression and livestock grazing (Young and Evans, 1981; Baison and Swetnam, 1990; Savage and Swetnam, 1990) may have been of primary importance. Changes in soil nutrient distribution during and subsequent to establishment of shrubs in grazed systems may constitute a positive feedback and increase the likelihood of additional woody plant encroachment (Schlesinger *et al.*, 1990). As a result, woody plant encroachment may continue to occur even after livestock grazing pressure is reduced (e.g., Smeins and Merrill, 1988; Archer, 1989).

4. Conclusions

Encroachment of woody vegetation into grasslands and savannas reported for many arid and semi-arid systems in recent history have likely involved interactions between climate, atmospheric CO_2 enrichment, fire and grazing. The nature and intensity of these interactions has probably varied over time. As a result, it is difficult to assign primacy to any one factor. However, as spatial and temporal frames of observation are diminished and resolution is increased, edaphic heterogeneity and disturbance assume greater importance in determining vegetation structure (Prentice, 1986). Post-industrial atmospheric CO_2 enrichment and possible climate change may have facilitated shifts from grass to woody plant domination.

However, case studies documenting differences in the rate, pattern and extent of woody plant encroachment (e.g., Madany and West, 1983; Conley *et al.*, 1992; Figure 1) suggest that regional factors such as historic changes in climate or atmospheric CO_2-enrichment were not the proximate factors driving local changes in vegetation. While changes in these broad-scale factors may have occurred, they were apparently insufficient to produce vegetation changes which have occurred at smaller scales. In contrast, numerous case studies have established a strong link between direct and indirect effects of livestock grazing and the encroachment of unpalatable woody plants into arid and semi-arid ecosystems. Differences in livestock species and levels of grazing pressure across landscapes over time would also explain why rates, patterns and dynamics of vegetation change have varied substantially for similar habitats experiencing similar climates and similar levels of post-industrial CO_2 enrichment.

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