



Cattle, Cutter Ants and Hydrogeomorphic Determinants of Grassland-to-Woodland Transformations

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Grasslands and savannas have transitioned to shrublands and woodlands world wide. These changes in land cover have impacted biogeochemical cycles, land surface-atmosphere interactions and the provision of ecosystem services to pastoral and rural societies whose welfare depends on livestock production. Causes for these dramatic plant lifeform transitions are the topic of active debate. Explanations generally center around changes in climate and disturbance (e.g. grazing, fire) regimes operating against a backdrop of post-industrial atmospheric CO₂ enrichment. A series of studies conducted in the southern Great Plains of North America have revealed how shrub proliferation is the outcome of interactions among livestock, birds, and cutter ants mediated by edaphic/geomorphic properties and how faunal activities, in turn, feed back to influence edaphic/geomorphic properties and shrub encroachment. Results suggest the following scenario for sandy loam uplands: (i) grazing livestock widely disseminate seeds of an arboreal woody plant (mesquite, *Prosopis glandulosa*) while simultaneously reducing grass biomass and eliminating fire. Subsequent to its establishment under these conditions, mesquite (ii) modifies soils and microclimate (island of fertility) and (iii) attracts birds disseminating seeds of numerous other shrub growth forms that preferentially established beneath it. Over time, (iv) shrub clusters organized around mesquite expand in canopy area and coalesce with new shrub clusters. Grasslands are thus transformed into shrublands in this manner. This scenario is supported by land use, historical aerial photography, $\delta^{13}C$, plant growth and modeling data.

In elucidating this scenario, it was discovered that sandy loam uplands were characterized by a well-developed, laterally continuous argillic (Bt) horizon (40 cm depth) with intermittent non-argillic inclusions. Shrubs clusters on the non-argillic inclusions were substantially more abundant and larger (height, canopy area, basal area) than those occurring where the Bt was well-developed. Trenching revealed substantial cutter ant activity at locations lacking the argillic horizon. This generated the hypothesis that as shrub clusters develop, they attract cutter ants, which then disrupt the argillic horizon (faunal mixing), and create hydroedaphic conditions further favoring wood plant establishment and growth and grove formation. To test this hypothesis, clay content was quantified (0-2 m) beneath discrete shrub clusters where the Bt was present and in groves where it had ostensibly been present, but then obliterated by cutter ants. It was reasoned that both patch types should have comparable amounts of clay over the 2 m profile. However, quantitative reconstruction revealed very little clay in the grove sites. This suggests (i) while the argillic horizon was laterally extensive in the sandy loam upland, it failed to form in discrete, spatially discontinuous locations, (ii) that woody plants and cutter ants were preferentially exploiting those areas and (iii) maximum woody cover and shrub community structure on these landscapes will be determined by the pattern and areal extent of the non-argillic inclusions. We are now left trying to explain why an argillic horizon failed to form in isolated, selected locations in the upland.