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TREE-GRASS INTERACTIONS IN SAVANNAS[1]

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ABSTRACT

Savannas occur where trees and grasses interact to create a biome that is neither grassland nor forest. Woody and gramineous plants interact by many mechanisms, some negative (competition) and some positive (facilitation). The strength and sign of the interaction varies in both time and space, allowing a rich array of possible outcomes but no universal predictive model. Simple models of coexistence of trees and grasses, based on separation in rooting depth, are theoretically and experimentally inadequate. Explanation of the widely observed increase in tree biomass following introduction of commercial ranching into savannas requires inclusion of interactions among browsers, grazers, and fires, and their effects on tree recruitment. Prediction of the consequences of manipulating tree biomass through clearing further requires an understanding of how trees modify light, water, and nutrient environments of grasses. Understanding the nature of coexistence between trees and grass, which under other circumstances are mutually exclusive or unequal partners, yields theoretical insights and has practical implications.

INTRODUCTION

The term savanna has been widely used and variously defined. The prevailing ecological usage denotes communities or landscapes with a continuous grass layer and scattered trees. This mixture of contrasting life-forms, coupled with

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strong alternation of wet and dry seasons in tropical and subtropical regions, distinguishes savanna structure and function from that of forest, grassland, and desert biomes (35, 80, 148, 160). Savannas are among the most striking vegetation types where contrasting plant life forms co-dominate. They are geographically extensive and socioeconomically important in tropical (177, 208) and temperate (4, 40, 105) regions. Tropical savannas cover about 1600 M ha (147), an eighth of the global land surface; they cover over half the area of Africa and Australia, 45% of South America, and 10% of India and Southeast Asia (196). Temperate savannas in North America occupy over 50 M ha (105). More importantly, savannas contain a large and rapidly growing proportion of the world's human population and a majority of its rangelands and livestock.

Savannas have been broadly subdivided based on the stature, canopy cover, and arrangement of woody elements (40, 49, 88, 137). "Savanna grasslands" contain widely scattered trees or shrubs, and these may grade into "tree savanna," "shrub savanna," or "savanna woodland." "Savanna parkland" is a two-phase mosaic landscape in which circular clumps, groves, or "mottes" of woody plants (discrete phase) are dispersed throughout a grassy matrix (continuous phase) (13, 111, 136, 203). In some regions, the wooded patches in these two-phase mosaics occur as linear bands arrayed parallel to slope contour lines (114, 176, 202). The phrase "savanna landscape" denotes areas where savanna vegetation is dominant but may be interspersed with riparian or gallery forest, or patches of woodland, swamps, or marshes.

The origin, age, nature, and dynamics of savannas are not well understood. The spatial pattern and relative abundance of grasses and woody plants in savannas are dictated by complex and dynamic interactions among climate, topography, soils, geomorphology, herbivory, and fire (15, 186). These interactions may be synergistic or antagonistic and may reflect stochastic variation or positive feedbacks. In addition, some savanna vegetation has undoubtedly been derived and maintained by prehistoric, historic, or recent human activities. In many areas, "natural" and anthropogenic factors interact, making it difficult to identify, isolate, or quantify the key determinants of savanna structure.

In this review we focus on the ecological processes that regulate the balance between woody plants and herbaceous vegetation. Postulated mechanisms and conceptual models of life-form interactions are evaluated using field observations and experimental evidence. We use "savanna" to refer to mixed tree-grass communities on well-drained soils; and we exclude treeless or nearly treeless grasslands, marshes, bogs, and sites with seasonally flooded soils. The word "tree" is used as shorthand for the more general phrase "woody plant," which includes arborescents, fruticose shrubs, and long-lived lignified forbs. "Grass" includes both the true grasses (Poaceae) and the sedges (Cyperaceae). In both cases the terms are used to describe life-forms rather than species.

HUMANS IN SAVANNAS

Much of the rich history of hominoid evolution has occurred in savannas (72), and activities of humans have influenced the structure and function of savanna ecosystems. Deliberate use of fire by hominids (by 2.5 MYA) likely increased the fire frequency in African savannas (38). Aboriginal fires in Australia began at least 40,000–60,000 years BP, and perhaps as long as 140,000 years BP (16). Fire was undoubtedly used extensively by prehistoric humans in North and South America as well (162). Current patterns of vegetation distribution across savanna landscapes may still reflect activities of prehistoric inhabitants. For example, the distinct communities dominated by *Acacia tortilis* that occur within *Burkea africana* savannas of South Africa appear to have developed on Iron Age settlement sites (32). In Kenya, past distributions of temporary corrals used by nomadic pastoralists markedly influence patterns of *A. tortilis* distribution and recruitment (131).

Human population growth and widespread Anglo-European expansion and settlement in the eighteenth and nineteenth centuries have influenced tree-grass mixtures worldwide. Extensive clearing of trees for fuel, lumber, and cropland have fragmented forests and produced anthropogenic or degraded savannas (63, 154, 177, 208). In other areas, fire suppression, overhunting or eradication of indigenous savanna animals, and the introduction of livestock and exotic trees have caused herbaceous degradation and a progressive increase in woody plant density, known as bush or brush encroachment (1, 8, 65, 113, 119). As a result, areas that were once forest may now be savanna-like, while areas that were once grassland or open savanna may now be shrublands or woodlands with little grass biomass. Documentation of historical changes has been facilitated by spatially explicit reconstructions from ground and aerial photographs, analysis of stable isotopes of soil carbon, dendrochronology, and biogenic opals (11).

STUDIES OF WOODY PLANT-GRASS INTERACTIONS

The Effect of Woody Plants on Grasses

The presence of woody plants can alter the composition, spatial distribution, and productivity of grasses in savannas. The effects of trees on grasses ranges from positive to neutral to negative, and these may depend on (*a*) the ecophysiological or specific characteristics of the tree and grass growthforms (canopy architecture, rooting patterns), photosynthetic pathway (C_3, C_4, CAM), photosynthetic habit (evergreen, deciduous), and resource requirements (light, water, nutrients); (*b*) availability of resources as influenced by interannual variability in the amount and seasonality of precipitation and topoedaphic properties; (*c*) extent of selective grazing, browsing, or granivory; and (*d*) frequency, intensity, and extent of disturbances such as fire. Though not well quantified, the nature of tree-grass interactions can change with time. At decadal time scales, tree aging and factors that influence tree size and density must be considered.

EFFECTS OF ISOLATED TREES ON HERBACEOUS SPECIES COMPOSITION At the scale of the tree, the species composition of the herbaceous layer may change along gradients extending from the bole to the canopy drip-line and into the adjoining inter-tree zone. In subtropical or temperate systems, C_3 grasses and herbaceous dicots may occur primarily beneath tree canopies, with C_4 grasses dominating patches beyond the canopy (61, 75, 127, 151). Herbaceous species respond individualistically to tree influences. Some grasses may be ubiquitously distributed beneath and between tree canopies, whereas others may congregate at the drip-line or have clear affinities for one microhabitat or another (10, 75, 94, 100, 195). Differences in species composition under and away from savanna trees are more distinct in low than in high rainfall zones (25, 27), suggesting that environmental gradients are stronger in habitats where effects of the radiant energy regime or root competition have a greater influence on species interactions. Grazing and browsing pressure may also alter patterning of herbaceous vegetation in savannas. In heavily grazed savannas, few differences between tree-crown and grassland zones may occur (28). Conversely, browsing of trees with low, dense, evergreen canopies can enhance morning and afternoon light levels, facilitate establishment of unique grasses, and increase total herbaceous biomass beneath the tree canopy (61). In other cases, browsing may stimulate tree growth and thus suppress grasses (164).

EFFECTS OF ISOLATED TREES ON HERBACEOUS PRODUCTION Savanna trees affect herbaceous phenology, production, and biomass allocation (root/shoot and leaf/stem) as well as species composition. Trees have historically been viewed as competitors with grasses, especially in temperate zones, and are widely regarded as having a negative impact on herbaceous production, particularly where livestock production is a primary land use. However, well-documented exceptions to this generalization indicate that assessments should be made on a case-by-case basis. The productivity of areas under tree canopies may be enhanced by improved water and nutrient status but be suppressed by low irradiance and competition between trees and grasses for belowground resources. Thus, at the scale of the individual tree, the net effect on grass production can be negative, neutral, or positive and can change with tree age or size and density. As with species composition, the relationship is influenced by a variety of factors including grazing, browsing, and rainfall.

Experimental evidence for positive interactions, or facilitation, among plants has increased markedly during the past 10 years, and many of the examples involve trees, shrubs, and herbaceous vegetation (45). The beneficial effects of trees on grasses can occur via amelioration of harsh environmental conditions, alteration of substrate characteristics, or increased resource availability (26,45). For example, increased herbaceous production beneath tree canopies in a Kenyan savanna was associated with lower soil temperatures, lower plant water stress, and greater soil organic matter concentrations, mineralizable N, and microbial biomass compared to those of adjacent grassland away from tree canopies (25, 195). Experimental manipulations suggest that factors related to soil fertility (23) and amelioration of radiant energy regimes (124) variously interact to influence herbaceous production. The magnitude of tree enhancement of grass growth varies with annual rainfall. In oak (*Quercus douglasii*) savannas in the western United States, herbaceous production is enhanced under tree canopies in drier regions but is reduced under tree canopies where annual rainfall exceeds 500 mm (104). In drier regions of Kenya (450 mm annual rainfall), tree species (*Acacia tortilis* and *Adansonia digitata*) had a similar and positive influence on herbaceous production (95% higher under trees than in the open). However, on a more mesic site (750 mm annual rainfall), tree canopy enhancement of herbaceous productivity was substantially diminished and differed with tree species (52% higher under *A. tortilis* canopies than in the open, but only 18% higher under *A. digitata*) (27). While these results support the hypothesis that facilitation is most likely to occur in stressful environments (45), a comparison of 10 studies showed that enhancement or suppression of grass production by tree canopies was unrelated to annual rainfall (117).

Tree roots may extend well beyond their canopies, the extent depending upon tree species, tree age/size, soil type, and annual rainfall. Soil moisture depletion (42) and trenching studies (5,6) indicate that shallow, lateral roots can be important in water uptake and maintenance of leaf area and transpiration, even in trees widely regarded as phreatophytic. It is thus possible that elevated herbaceous production beneath tree canopies is partially the result of reductions in herbaceous growth resulting from root competition beyond the canopy, where the benefits of enriched soil nutrients and amelioration of the radiant energy are minimal. In southern Texas savanna parklands, herbaceous biomass was reduced within tree clusters but did not vary with distance from canopy edge nor with size of cluster, suggesting that tree effects did not extend beyond the canopy zone. The evergreen arborescent *Juniperus virginiana* also suppresses herbage biomass markedly beneath its canopy but has little impact on biomass away from its canopy over tree heights ranging from 2 to 6 m (57). In contrast, removal of *J. pinchotii* plants elicited a significant herbaceous response up to 6 m from canopy margins in shallow, rocky soils, but such removal had little influence on herbaceous production beyond the canopied zone on deeper soils (56). Tree-root exclusion on a *Burkea africana* site in South Africa resulted in increased grass height and basal area over a two-year period (93), and *Acacia karroo* trees suppressed grass growth up to 9 m from their canopies (164). Tree root effects on herbaceous production may also be mediated by rainfall amount. Trenching experiments in a Kenyan savanna, where tree roots extended up to 9 m beyond crowns, failed to demonstrate a statistically significant release in herbaceous production under or away from tree canopies at a low rainfall site (23). However, trenching of the same tree species at a high rainfall site stimulated herbaceous production 16–36%.

TREE SIZE AND HERBACEOUS PRODUCTION The magnitude of differences in herbaceous production under, versus away from, savanna trees can also vary with tree age, size, and density. Time of tree occupation will influence soil properties, and microclimate can change as the tree canopy develops (10). The positive effects noted above may therefore not occur until many years after tree establishment. In some cases, the negative effects of trees on grasses may not be apparent until plants reach a critical age/size (46, 57, 61, 108, 164). In other cases suppression of herbaceous production may be comparable over a wide range of tree sizes (5–70 m^2 canopy area) (73), despite significant differences in microclimate and rainfall interception (74). Thus, tree effects can be overridden by other site or environmental effects. When trees are young and small, facilitation may be more important than competition, and grass production is enhanced; as trees and shrubs become larger, competition may overshadow facilitation and adversely affect herbaceous production (2, 10). At the landscape level of resolution, grass composition and production are also affected by tree density as well as tree size/age. As described in the subsequent paragraphs, there is often a strong, negative correlation between tree density or cover and grass cover or biomass. Because of the potentially positive effects of trees on grasses, herbaceous diversity and production may be greater where there are a few trees than where there are no trees, but the trend is reversed at high tree densities (46, 151, 165).

TREE DENSITY AND HERBACEOUS PRODUCTION Encroachment of trees and shrubs into what were formerly sparsely treed grasslands has resulted from commercial livestock grazing over the past two centuries in semi-arid savanna regions (8, 10, 12, 119). As woody plant cover or density increases, grass production typically declines dramatically. Encroachment of trees may further intensify grazing pressure, as landholders seldom destock in response to decreases in grass production associated with increases in tree density. Because bush encroachment may lead to failure of commercial ranching systems, landowners commonly engage in extensive bush clearing. The bush encroachment problem has thus been the main impetus for research into tree-grass interactions in savannas. Herbaceous production generally increases after the removal of trees, except in some low rainfall zones (20) or where grazing or past land use has limited the availability of perennial grass propagules or favors exotic weeds and shrubs (24). Factors affecting herbage response to tree-clearing include initial tree size or age-class distribution, density, method of tree removal, condition and composition of understory vegetation at the time of treatment, and posttreatment climate, grazing, and browsing (71, 149).

The negative effect of trees on grasses may result from rainfall interception, litter accumulation, shading, root competition, or a combination of these factors; and the effect depends on the leaf area, canopy architecture, and rooting patterns of the tree. Where trees were removed, the typical relationship between grass production and tree biomass, cover, or basal area was a negative exponential, with the steepest decline in grass production resulting from the initial increments of tree cover (41, 129, 190). Similar relationships between grass growth and tree cover were found in response to naturally occurring variations in tree density (33, 85, 115, 127, 151).

The degree of curvature in the relationship between grass growth and tree biomass is mediated by environmental conditions, resource availability, and the understory composition. For example, the relationship can be nearly linear on highly productive sites (or in wet years on less productive sites), becoming progressively more concave on marginal sites and in drier years (141, 191). The relationship may also be linear on ungrazed sites, shifting to nonlinear when preferential grazing shifts the balance in favor of woody plants by reducing grass competition and fire frequency (110). The functional form of the relationship may also differ for C_3 vs. C_4 grasses (positive vs. negative correlation—127) and for grass, forb, shrub, or total understory production (linear vs. nonlinear negative correlation—181). Inconsistencies in overstory-understory relationships may therefore be explained when growth-form, site, and environmental factors are considered (106).

The response of grasses to tree removal is typically greatest by those growing on patches with physicochemical properties that are enhanced by trees (170, 171). Grass growth after clearing may be further augmented by nutrients released from decomposing tree residues. As a result, the magnitude of "release" of herbaceous production after tree removal may be greatest on landscapes with high cover of mature, large woody plants. Relative to those not influenced by trees, soils enriched by trees have the potential to sustain higher levels of grass production long (>13 yr) after tree removal (173, 174). However, this potential may not be realized because trees and shrubs may rapidly (within 3 to 10 years) recolonize the site and depress herbaceous production to pre-clearing levels (71, 75). For sprouting woody plants, stem densities may increase above pretreatment levels and cause a shift in tree composition to species less desirable for livestock and wildlife (62). In other cases, bush clearing has successfully enhanced wildlife diversity (29) and fostered co-existence of livestock and wildlife (150). Past bush clearing activities have too often ignored impacts on nontarget plants, noncommercial or nontarget herbivores, and system-level properties and processes.

The Effect of Grasses on Woody Plants

WOODY PLANT ESTABLISHMENT For woody plants with potentially long lifespans and low post-establishment mortality rates, seedling recruitment is a critical life-history stage. The effects of herbaceous vegetation on woody plant recruitment is variable, and multiple mechanisms can operate in complex ways to influence emergence and establishment (53, 54). Grasses may regulate woody plant recruitment directly (competition for light, water, nutrients) or indirectly (as fine fuel loads influence fire frequency and intensity). There is much evidence for a strong negative effect of grasses on trees still small enough to be within the grass layer or the flame zone of grass-layer fires. However, in the absence of grazing, browsing, and fire, changes from open- to closed-bush savanna can occur rapidly (135). Thus, while grasses may reduce emergence, growth, and survival of woody seedlings, the competitive reduction may not be large enough to cause high mortality or complete exclusion. For example, although survival of an evergreen tree (*Juniperus virginiana*) was highest in grazed pastures (57%), survival of seedlings in pastures that had not been grazed for >50 years was still 40% (145). In South African savannas, reductions in grass competition did little to affect seedling establishment of *Acacia karroo* (120). Results from field experiments indicate that in the absence of fire, woody plant encroachment in savannas can be high across a wide range of herbaceous composition and biomass (9). Tree recruitment may occur during periods of moisture availability, when competition from grasses is minimal. However, the fine fuels which accumulate during these periods of high moisture may also dispose the system to fire (166) and thereby limit tree recruitment (70). Where grazers consume grass and remove fine fuels, fire frequency declines (17, 138) and woody plant abundance increases (98). As woody plant abundance increases and further suppresses grass production, a positive feedback develops, making fire increasingly unlikely. Thus, while grass biomass may interact negatively with woody stand development in savannas, it may be a determinant to tree density and stature primarily as it influences the fire regime.

Many savanna trees are well-adapted to fire and readily regenerate vegetatively or from seed. For some species, tolerance to fire can be observed in very young (2–3 years of age—204) or small plants. In these cases, fire may suppress but not necessarily eliminate trees from savannas (77, 179). Many apparently treeless or sparsely tree-covered grasslands may contain many woody plants concealed among the grasses and these may be decades old with well-developed root systems (67, 69, 112). Reduction in browsing pressure (21) or suppression of grass growth and fires for a number of years, for instance by grazing and drought, allows suppressed trees to quickly escape the grass layer and achieve vertical dominance (36, 180).

GROWTH AND REPRODUCTION OF ADULT TREES Few experiments have assessed the impact of grasses on the growth and reproduction of mature trees. Analysis by Hoffman et al (78) of a 17-year record of grass and shrub basal cover suggests that increased summer rain would increase grass cover and that increased grass cover would decrease shrub cover. In Patagonian steppe, removal of shrubs did not alter grass production, but removal of grasses increased deep soil water, shrub leaf water potential, and shrub production (133). At Nylsvley, South Africa, an experiment was done in two adjacent savannas with soils differing in nutrient content and water-holding capacity (93). The nutrient-rich savanna with fertile, fine-textured soil was dominated by widely spaced *Acacia tortilis* trees; the coarse-textured, nutrient-poor site was a savanna woodland dominated by *Burkea africana.* Grass removal had no significant effect on *Burkea* growth but led to increased *Acacia* trunk radial growth and twig extension. The lack of *Burkea* response suggests that on coarse-textured sites, soil moisture recharge to deeper portions of the soil profile being used by tree roots occurs whether or not grasses are present. Conversely, grasses were capable of limiting water recharge of deeper soils on the fine-textured site, thus reducing *Acacia* growth. Stuart-Hill et al (164), working on a heavier clay soil, noted an even stronger response in *Acacia karroo* tree growth to grass clearing (40–166% increase). Together, these studies suggest that the outcome of the interaction of tree and grass life-forms with contrasting rooting patterns is regulated by the interaction of rainfall amount, seasonality, soil texture, and grass cover. The fact that tree sizes and densities on savanna landscapes are often highest in intermittent drainages characterized by fine-textured soils seems contradictory to the trend for greater sizes and densities on coarse-textured uplands. However, in cases of intermittent drainage, the additional moisture and nutrients received as run-off from upland portions of the landscape apparently override soil texture constraints.

Grass species differ greatly in their capabilities for resource use and extraction. As a result, the intensity of grass effects on trees will relax or intensify as grass composition changes in response to climatic fluctuation, succession, or grazing. Where grasses are heavily grazed, woody plant longevity (197), resource acquisition (44) and growth, time to reproductive maturity, and seed output may increase relative to lightly grazed sites (9, 109). In addition, the inverse relationship between grass production and tree canopy cover may shift from linear to a negative exponential, as the capacity for grasses to sequester resources is diminished by grazing (110).

Tree-Tree Interactions

If competition within life-forms is stronger than between life-forms, coexistence of grasses and trees is theoretically possible. Tree-tree interactions likely determine density and pattern of woody plant distribution across savanna landscapes and, hence, patterns of grass biomass and distribution. Even so, there have been surprisingly few experimental studies investigating the mechanisms that influence how woody plants interact with each other in savannas.

Competition between trees in savannas has generally been inferred from field studies of the spacing and size of trees (68, 126, 158, 159). The sum of the size of neighboring savanna trees is generally positively correlated with the distance between them, suggesting a competitive interaction. Self-thinning in *Prosopis glandulosa* stands has been inferred from comparison of different-aged stands on similar soils. Young stands (median stem age is 27 years) were characterized by high densities of small plants, whereas older stands (median stem age is 42 yr) were characterized by low densities of large plants (194). Thinning may reflect competition among lateral roots, as has been observed in desert shrublands (99), or it may start as belowground competition for soil resources in high density patches and give way to competition for light, which leads to a regular pattern of dominant surviving trees (91).

Savanna tree distribution can be over-dispersed (a quasi-regular spacing, suggesting competition), clumped (suggesting facilitation), or random. Within a single savanna plot, some species may be over-dispersed while others are clumped, and there may be statistically significant associations or disassociations between species. Clumped tree dispersal also occurs in response to localized variation in topography (e.g. termite mounds), soil depth (10, 134, 136), and fire patchiness (77). Competition between trees can occur in most open savannas but is influenced by topoedaphic factors and is often counterbalanced by elements of facilitation, especially during the phase in which tree seedlings are established. Experimental investigations of tree-tree interactions are required if we are to increase our understanding of mechanisms influencing or controlling patterns of tree spacing and density in savannas.

Is the Tree-Grass Mix in Savannas Stable or Unstable?

The widespread and persistent occurrence of savannas suggests some form of stability. The phenomenon of bush-encroachment suggests meta-stability. The asymmetry of the competitive effect of trees on grass in relation to the effect of grass on trees implies instability.

These viewpoints are not necessarily incompatible because they are based on observations at different scales in space and time (157). Competition experiments are typically conducted on a few individual plants at a scale where the competitive interaction may be unstable, with favoring of mature trees over grasses, but grasses over immature trees. In a community patch a few hectares in extent, weakening the suppressive effect of the grass layer on young trees for a few years can lead to open savannas being converted to tree-dominated thickets. Once established, the thicket may take decades to revert to an open savanna, if it ever does. At the scale of a whole landscape, savannas can persist over periods of millennia, since the landscape consists of many patches in different states of transition between a grassy dominance and a tree dominance.

MODIFICATION OF THE ENVIRONMENT BY WOODY PLANTS

Environmental modifications caused by trees and shrubs have been widely investigated in arid and semiarid systems (74). These modifications take many forms, some of which have positive effects (facilitative) and others negative (competitive). Where the net outcome is positive, the overall interaction is said to be facilitation; where it is negative, the interaction is competitive. Since the strength of the modifications decrease with distance from the plant, a mixed tree-grass community consists of a spatial patchwork of different degrees of competition and facilitation (56, 183). Furthermore, the nature of the interaction may vary with time and climatic fluctuation (93, 198) or fire-herbivore interactions (55). Environmental conditions may favor trees in some years, grasses in other years. Trees may have a net facilitative effect on grasses some years and a net competitive effect in other years.

Water

All savannas are water-limited for at least part of the year. It has therefore been widely assumed that competition in savannas is for water. However, some grasses are better adapted to subcanopy environments than to environments away from trees (3). The input of rainfall to the subcanopy habitat via stemflow and throughfall will depend on the size and intensity of rainfall events and the size, bark characteristics, canopy architecture, and leaf area of the tree (74). Interception losses on the order of 5% to >50% of gross annual rainfall have been reported (94, 118, 169), but stemflow can concentrate significant amounts of moisture near the base of trees (128, 169). As a result, measurements of soil moisture on transects from the stem outward into the between-canopy zone generally show peaks of wetness close to the stem (due to stemflow) and at the canopy perimeter (due to edge drip), with a drier area beneath the main canopy (163, 165).

Proliferation of fine feeder roots may enable woody plants to monopolize near-surface soil moisture concentrated via stemflow (207). Deep percolation of stemflow water, facilitated by large root channels and low bulk densities associated with subcanopy soils, could also favor deeply rooted woody plants. Duff or litter layers accumulating under trees can reduce the amount of moisture reaching mineral soil and, in conjunction with reduced light levels, limit herbaceous production. In other cases, modest reductions in radiant energy associated with tree shading can lower soil temperatures, reduce evaporative demand and water stress on understory plants, and enhance subcanopy soil moisture storage, availability, and plant water-use efficiency (3, 25, 87, 94, 117). Through the process of hydraulic lift, deeply rooted trees and shrubs may increase soil moisture to shallow-rooted understory species (43, 52).

The interspersion of grasses and woody plants also alters the hydrology of the savanna at a landscape scale by influencing horizontal patterns of water distribution (86). On loamy and silty soils, infiltration of rainwater into the soil is sensitive to surface conditions. Soil surface exposed to direct raindrop impacts becomes sealed and sheds a large fraction of the rain. A dense grass cover improves infiltration (101), the extent depending upon the growth-form (92), but this cover is vulnerable to fire, drought, and grazing. In some cases, the presence of trees helps to maintain ground cover, since tree cover is less variable between years and less easily removed by herbivores or fire, and tree leaf litter is more persistent than grass litter. However, in cases where trees significantly depress herbaceous production, bare ground may increase, making sites more susceptible to losses of water and nutrients via surface flow. The trees and grasses in some savanna landscapes on gentle slopes and loamy soils segregate into alternating bands or patches known as tiger bush in Africa (202), mulga bands in Australia (97), or vegetation arcs in Mexico (114) and the Middle East (201). The bare or sparsely grass-covered strips shed water, which is captured in soils associated with the up-slope portion of tree-covered strips. Enhanced woody plant recruitment on the up-slope portion of the tree strip relative to the down-slope portion (102) may cause these bands to slowly move up the landscape.

Nutrient Accumulation Below Woody Plants

In addition to altering soil moisture and structure, both evergreen (18, 122, 143, 209) and deciduous trees typically enhance pools of soil nutrients (C, N, P, and cations) and their fluxes beneath their canopies (25, 47, 59, 60, 66, 82, 83, 90, 116, 170, 171, 172, 184, 195). Nutrient enrichment of soils may vary with species (19), and patches with leguminous trees may contain more soil nitrogen than patches with nonleguminous trees (31, 130, 185). In other cases, nitrogen pools or mineralization rates are comparable between legume and nonlegume tree patches (27, 64) and between deciduous and evergreen shrub patches (103). The higher carbon and nitrogen densities in subcanopy soils may reflect differences in abiotic conditions under and away from trees and the fact that trees have foliage with higher nutrient content, higher litter inputs, and/or lower decomposition rates than the plants in the herbaceous layer.

Nutrient enrichment occurs across a broad array of tree and shrub growth-forms and species inhabiting diverse climatic zones. Three mechanisms have been proposed to account for this phenomenon (184). Trees may act as nutrient pumps, drawing nutrients from deep horizons and laterally from areas beyond the canopy, depositing them mainly beneath the canopy via litterfall and canopy leaching (90, 146). The supporting evidence for this mechanism is circumstantial. As noted earlier, savanna tree roots may extend outward many times the canopy radius and penetrate more deeply into the soil than do grass roots. The second mechanism is that the tall, aerodynamically rough tree canopy acts as an effective trap for atmospheric dust (30, 58, 167). The dust contains nutrients, which wash off the leaves during rainstorms and drip into the subcanopy area. Though not well quantified, a third mechanism may be of importance where trees are sparse and may serve as focal points attracting roosting birds and mammals seeking shade or cover. Herbivores that take refuge in the shade of trees may enhance the local nutrient cycle (66). Perching birds may enrich soil nutrients (23) and deposit seeds of other trees and shrubs whose germination and establishment may be favored in the subcanopy environment (10).

While the "island of fertility" phenomenon has been widely recognized, little is known of the rates of nutrient enrichment in tree-dominated patches. Bernhard-Reversat (30) found good correlations between total C and N in soil under *Acacia senegal* and *Balanites aegyptiaca* tree canopies and tree girth ($R^2 = 0.62$ and 0.71, respectively), suggesting that soil nutrients change with time of woody plant occupancy of a patch. Barth (18) found significant correlations between piñon pine age and various soil properties. In savanna parklands of southern Texas, soil carbon storage increased linearly with tree stem age, ranging from 19 $g\ C\ m^{-2}\ y^{-1}$ in uplands to 70 $g\ C\ m^{-2}\ y^{-1}$ in moister lowlands (TW Boutton, SR Archer, unpublished information); rates of N storage ranged from 1.7 $g\ N\ m^{-2}\ y^{-1}$ (uplands) to 6 $g\ N\ m^{-2}\ y^{-1}$ (lowlands).

A consequence of the accumulation of nutrients in the subcanopy area may be impoverishment beyond the canopy zone (but see 47). The contrast in soil nutrients under vs. away from tree canopies may be further magnified by concurrent losses from herbaceous patches resulting from heavy grazing. This mechanism has been held responsible for the overall decrease in animal production in desert shrublands in the United States when shrubs invade grasslands (144). In Africa and Australia, nutrient accumulation in patches in the landscape is generally looked on favorably, since it raises the nutrient content of at least some of the grass above the critical threshold for digestion by ruminants (146).

Shading and Microclimate Modification

The tree leaf area index (LAI) in savannas is low compared to that of forests or grasslands (148). The LAI in the subcanopy zone may be two to six times higher than the average for the savanna as a whole (0.5 to 1.0 is typical for dry savannas), since the tree leaves typically are concentrated into a tree cover fraction of 15–50%. The savanna tree canopy reduces direct and indirect solar radiation reaching the shaded area by 25–90% (25, 66, 83, 94, 172). Since the semi-arid tropics where savannas predominate are among the sunniest places in the world, the amount of radiation reaching grasses below the tree canopy may still be sufficient for a relatively high rate of photosynthesis (117). The total energy budget in the subcanopy area is less attenuated than the photosynthetically active radiation because a large part of the energy is advected from the surrounding intercanopy areas in the form of heated air. Transpiration and leaf temperatures may therefore remain high in the subcanopy zone despite shading and reductions in soil temperature. The latter may be important for seed germination and seedling establishment.

HERBIVORES AND FIRE

Low-growing, thorny trees may provide a refuge in which palatable grasses can persist in heavily grazed environments (121, 193). Trees dispersed to and capable of establishing in grass-dominated zones can provide vertical structure attractive to perching birds that disseminate seeds of other woody species (13). Small mammals and insects attracted to trees or bush clumps may subsequently influence patch dynamics via granivory, burrowing, and seedling predation. Seedlings and small trees are particularly vulnerable to herbivory from insects (107), browsers, or by grazing herbivores, which trample them or consume them along with grass (34, 81). In some cases the tree seedlings associated with clumps of unpalatable grass may escape herbivory during this critical stage of their life cycle. In North America, the widespread eradication of prairie dogs in the early 1900s may have contributed to the release of trees and shrubs recorded in many Great Plains grasslands in recent history (194).

High grass biomass can affect tree biomass by fueling fires (89); grazing reduces the fuel load and hence affects fire frequency, intensity, or continuity of spread (17, 138). Browsing, on the other hand, helps to keep woody plants within the flame zone (and conversely, fires keep woody plants browsable). Thus, a strong grazer-browser-fire interaction influences tree-grass mixtures. For example, control of the rinderpest virus led to increases in Serengeti wildebeest populations; the resultant intensification of grazing pressure reduced fire and grass competition and released small trees (153). The increased small tree production allowed giraffe numbers to increase, while giraffe browsing limited tree growth. Woodland decline and grassland expansion in the Serengeti-Mara woodlands since the 1960s cannot be attributed to browsing alone but appears associated with the combined effects of browsing and fire (55). Similarly, the fire regime associated with wildebeest grazing cannot maintain the grassland state unless browsers are present in sufficient numbers. The fire mechanism can be subtle and complex, involving in one example interactions between frequent fires, windstorms, and basal bark-scars left by gnawing rodents (206). In savannas where grazing and browsing animals (domestic or wild) are of little consequence, fire may operate more directly to influence tree-grass mixtures and may slow, but not prevent, complete tree domination (77). The fact that such sites persist as savanna rather than forest or woodland may indicate that portions of the landscape do not provide physical or nutritive conditions required for tree establishment.

MODELS OF TREE-GRASS INTERACTION

The coexistence of apparent competitors can be accounted for in three ways. All three models have been proposed for savannas. Niche separation models posit that competitors avoid competition by using resources that are slightly different, obtained from different places, or obtained at different times. Balanced competition models admit interspecific competition but propose that it is weaker than intraspecific competition. Both niche separation and balanced competition can lead to a stable coexistence and are therefore known as equilibrium models. Disequilibrium models assume there is no stable equilibrium but that frequent changes in the environment (disturbances) prevent the extinction of either competitor by restarting the race or by biasing it alternately toward one or another competitor.

Niche Separation by Depth

The observation that the fibrous root systems of grasses intensively exploit a relatively small proportion of the soil profile, whereas woody plants extensively explore a larger volume, extending deeper, prompted Schimper (142) to suggest "moisture in the subsoil has little influence on the covering of grass; only moisture in the superficial soil is important to it" and that woody plants are favored by a moist subsoil "regardless of whether rain falls during a period of activity or rest." This perception formed the basis for Walter's explicit model for tree-grass coexistence in savannas (192). He assumed water was the limiting factor and hypothesized that trees had roots in both the topsoil and subsoil, while grasses rooted only in the topsoil. This difference would result in a stable equilibrium if grasses have a greater water use efficiency than trees. Stable tree-grass coexistence is theoretically possible even if there is not complete rooting depth separation (and there seldom is), as long as there is a sufficient degree of separation in relation to the pattern of water distribution in the profile and the relative water use efficiencies (188, 189).

Walter's two-layer hypothesis predicts that in any environment with a given climate and soil there should be a characteristic tree-grass ratio. Trees should be advantaged on soils of low water-holding capacity, such as sands, and under wetter climates, since both of these conditions lead to more water reaching the deeper soil layers. Conversely, shallow soils underlain by impervious layers, water-retaining clays, and arid environments should disfavor trees. Evidence for the supposition that grasses and woody plants use different water resources in the soil profile exists for shrub-steppe (96, 133, 161) and tree savannas (76, 88, 93, 156). In addition, it appears that tree species with rapid root development are capable of achieving this resource partitioning with grasses very early in their life cycle (37, 39). However, the two-layer hypothesis cannot account for the large variation in the tree-grass ratio within a single climate-soil combination (22).

The rooting depth distribution data for savannas only partly supports the two-layer hypothesis as well. Trees do tend to have a maximum and modal rooting depth deeper than that of grasses, but grass roots can be more abundant in absolute terms than tree roots to depths of up to a meter (148). Most roots of trees and grasses are in the upper soil horizons (84), which makes ecological sense in semi-arid environments because that is where water and nutrients co-occur. Some species of savanna trees send roots down to great depths or exploit fissures to gain access to resources accumulating beneath bedrock or claypans. However, it seems unlikely that all trees on a savanna landscape obtain the bulk of their water from these deep sources. Indeed, many woody species are quite shallow-rooted or plastic with respect to rooting patterns, and their physiological activity may be closely coupled to soil moisture availability in upper horizons (10, 50, 59, 76, 123, 152, 175). These shallow-rooted trees may increase in abundance with heavy grazing, apparently favored by an increase in water availability in the surface soils resulting from reductions in grass biomass (155). In humid savannas of West Africa (1000 mm annual rainfall; 2-month dry season), patterns of root distribution and soil water depletion are similar for trees and grasses, with each life-form obtaining water primarily from the top soil layers during both rainy and dry periods (95).

Niche Separation by Phenology

The characteristic climate associated with tropical savannas is alternating warm dry seasons with hot wet seasons. Might this seasonal pattern of growth opportunity provide a potential axis of niche separation for trees and grass? This model is conceptually similar to the model developed by Westoby (199) for coexistence of grasses, shrubs, and forbs in episodically wetted arid shrublands.

Deciduous savanna trees achieve full leaf expansion within weeks of the onset of the rainy season (148). In moist savannas, leaf expansion of the C_3 trees may precede the rains by up to several weeks. The peak leaf area of C_4 grasses is achieved only several months after the onset of the wet season. Trees that flush early do so, it is hypothesized, by using carbohydrates and nutrients carried over from the previous growing season and residual water deep in the soil. Grasses initiate growth from stored reserves, but full leaf growth appears more dependent on factors affecting current season photosynthesis. Thus, trees expand their leaves rapidly in a synchronous flush from preformed buds, whereas grasses initiate leaves sequentially and at staggered intervals over the growing season (14), the rates and dynamics being influenced by environmental conditions (161). Deciduous trees may also retain leaves for several weeks after grasses have senesced. As a result, trees can monopolize resources early and late in the growing season (132). Evergreen trees, which dominate many neotropical and temperate savannas, may have lower nutrient requirements, higher nutrient retention, and higher concentrations of secondary compounds than grasses and cast deeper shade year-round than deciduous trees. These features may more than offset their low photosynthetic rates and give them an advantage over grasses, especially on nutrient poor sites.

Using a model that includes the grass rooting-depth niche entirely within the tree niche, we would predict dominance by trees wherever seasonality is strong, protracted, and predictable. In arid unpredictable environments dominated by small rainfall events, the opportunistic strategy of grasses would be favored (161), while in continuously moist environments (such as those occupied by forests), a continuous growth, overtopping strategy is favored. Within its area of applicability, the model predicts greatest advantage for trees where there is greatest potential for between-season carryover of resources, which is in the moister savannas and on deeper, sandier soils. As in the rooting-depth niche separation model, these predictions are broadly consistent with what is observed, but many local exceptions occur.

Balanced Competition

If balanced competition occurs, the superior competitor becomes self-limiting at a biomass insufficient to eliminate the poorer competitor. It is reasonable to expect greater competitive overlap between trees than between trees and grasses, and, similarly, greater competitive overlap between grasses than between grasses and trees. Since mature trees generally dominate over grasses, the model predicts that all savannas should trend toward a woodland with a sparse understory of grasses. Those not currently in this state are unstable and presumably are held away from the equilibrium point by disturbances such as fire or browsing (7, 125).

The theory that a form of balanced competition would result if mature trees could outcompete grasses, but grasses could outcompete establishing trees, is supported by evidence from competition experiments. The model predicts two meta-stable states, one a dense woodland with little or no grass, and the other a dense grassland with no trees. Rapid and dramatic transitions from open grassland to thickets have been observed following heavy grazing and the exclusion of fire (140, 155, 156, 178, 182). Spontaneous reversions to grassland have rarely been observed, but that may be an artifact of the longevity of trees. It is possible to keep a cleared savanna treeless by repeated burning. Meta-stable models lend themselves to description as "state and transition" models (55, 200).

Spatially Explicit Models

These models are built on the observation that the interactions between coexisting organisms (trees and grasses in this example) are not spatially homogeneous. Whereas the other models consider trees and grasses as abstract classes that have a vertical structure (rooting and canopy layers, for instance) but no lateral structure, the spatially explicit models contend that where each individual plant occurs is as important as what its life-form is. In practice, because of the large-scale difference between trees and grasses, only the trees are usually treated spatially explicitly, and the grasses are combine into a zoned layer. The "ecological field theory" approach (205) describes a plant community as a mosaic of overlapping spheres of influence, each showing some pattern in relation to the plant at its center. The performance of the entire community or of any community component measured at a landscape patch scale is the integral of these spatially varying fields of growth opportunity.

Spatially explicit models (139) provide a plausible explanation for the nonlinear relationship between grass production and tree cover described in the *Tree Density and Herbaceous Production* section. As a simplified example, imagine that every tree is the center of a circular area with a radius equivalent to the maximum root extension. The first tree in a grassland might suppress grass growth within this circle, causing the grass production on the landscape to decrease. A second tree would have an additional influence but would also have some small probability of partly overlapping with the area of influence of the first tree, so the incremental reduction in total area grass production would be slightly less. Extend this scenario to a large number of trees, and the result is an exponentially declining relationship between grass production and tree density very similar to that actually observed.

The model can be made more sophisticated with trees of different sizes occurring in nonrandom patterns and with spheres of influence having differing decay functions, giving rise to curves with different degrees of concavity. As would be expected in a high-fertility, moist site where the rooting radius could be small, the influence zone would be small, and the curve more nearly linear than on sites where the radius of influence is large. This concurs with field observations.

The anomalous convex tree-density–grass-production curves observed on some sites (151, 165) could also be generated with this approach, by including in the model zones of facilitation as well as zones of competition. By varying the relative strengths of competition and facilitation and their rate of decrease with distance from the tree stem, almost any shape of relationship between grass production and tree density could be simulated.

A Synthesis Model

All the models outlined above are at least partly correct, but no single model can account for the variety of phenomena at all savanna locations, or even the range of behaviors exhibited at one location in different seasons or stages of succession. A comprehensive model of tree-grass relationships in savannas must combine elements of all of them (168, 187).

It is further useful to divorce the issue of co-existence of trees and grasses in the long term from the issue of resource partitioning in the short term, since the two may bear little relationship to one another outside of computer simulations. The dynamics of savannas, and probably many other ecosystems, are driven to a large degree by factors such as climate that originate outside the tree-grass system (157). The vegetation structure is therefore only to a small degree the result of the cumulative effect of competition for resources. Co-existence of trees and grass in this view is largely a result of the interaction of a variety of stresses and disturbances, acting differentially on trees and grass and patchily in time and space. Equilibrium niche theory is useful for understanding patterns of resource partitioning in between these stress periods.

Niches of grass and tree archetypes differ in both rooting depth and phenology. Life-history and growth form within the archetypes also vary substantially. Deep-rootedness is very important for some tree species, but not all, and some grasses have a less opportunistic growth pattern than others. On average, there is probably more opportunity for phenological separation than for depth separation, simply because so much of the soil activity is concentrated in the topsoil that any plant without most of its roots there has little chance of capturing resources. Phenology and rooting depth are not unrelated because possession of a large and deep root system is one reason why trees can expand their leaves early and rapidly and retain them for longer into stress periods.

We suggest that the rapid, synchronous deployment of leaves and fine roots by trees allows them almost exclusive access to the nutrients (particularly nitrogen) mineralized in the early part of the growing season. The nutrients can be stored in the tree biomass for use throughout the season, and when the leaves are dropped, a large fraction of their nutrient content is reabsorbed into the permanent tissues (148, 175). Grasses do the same, but to a lesser degree because of their limited storage capacity, and therefore they are usually highly responsive to added nitrogen. Trees, especially the nitrogen-fixing species, may be limited much more by the availability of phosphorus than of nitrogen (79).

Nutrients are mineralized, transported to the root, and taken up only in the presence of water. Most of the observations advanced to suggest water is the main resource competed for by savanna vegetation (for instance, the near-linear relation between net primary production and annual rainfall) can apply equally to nutrients. A simplistic "law of the minimum" view of competition is not useful in this context. Multiple-factor limitation is the norm, either sequentially or simultaneously (48). The arrangement of various savanna types within the axes of plant-available moisture and plant-available nutrients has been the focus of recent discussion (22), but quantification of these variables remains elusive. In reality, savanna structure is hierarchically constrained: by climate at regional-to-continental scales; by topographic effects on rainfall and landscape water redistribution, and by geomorphic effects on soil and plant-available water at landscape-to-regional scales; and finally by water redistribution and disturbance at local and patch scales (51).

CONCLUSIONS

Tree-grass interactions in savannas cannot be predicted by a simple model. They include elements of competition and facilitation, varying complexly in both time and space. Coexistence is permitted by a combination of niche separation, stronger intra–life-form than inter–life-form competition toward the extremes of dominance, a balanced asymmetry of competition, and most importantly, frequent levelling disturbances, particularly fire.

Experimental evidence suggests all mixtures of mature trees and grass are unstable in savanna environments. In the absence of disturbances such as repeated fires, clearing by humans, or feeding by large herbivores, the tree cover increases at the expense of grass production until it is limited by tree-tree competition. The amount of grass remaining in the system when this endpoint is reached depends on the match between the tree growth strategy and the growth opportunities offered by the environment. In moist, relatively predictable environments the match is good, and a closed woodland with almost no grasses will result. In arid, unpredictable environments, substantial quantities of grass may occur in some years.

Tropical nonhydromorphic grassland states are meta-stable where fires are sufficiently frequent and intense to prevent trees from escaping the flame zone. How easily the trees can escape depends on factors that include intensity of browsing, rainfall, soil texture, and soil fertility. Moist fertile environments support a vigorous grass growth that, if not grazed, leads to frequent intense fires. These environments often support large herds of migratory grazers, which crop the grass very short and browse the small trees. In these environments, extensive grassland patches can occur (the Mitchell grasslands in Australia and the Serengeti grasslands in Africa may be examples), suggesting a relatively robust meta-stable state. They can nevertheless be invaded by trees if tree propagules are present and grass cover is reduced.

Semi-arid environments on sandy, low-fertility soils are seldom treeless, suggesting a very weak or absent meta-stable grassland state. Many semi-arid areas on relatively fertile loamy or clayey soils were relatively treeless in precolonial times but were encroached rapidly and apparently irreversibly when grazed continuously by cattle. The encroachment often occurred in relatively discrete episodes, following a prolonged period of drought during which no fires were possible.

Resource partitioning patterns do not explain coexistence of trees and grasses in savannas, but they do account for the observed patterns of primary production. In particular, horizontal spatial interactions in the rooting zone are the key to understanding the nonlinearities in the relationships between tree and grass primary production.

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