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African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology

David G. Williams[1,*] & Zdravko Baruch[2]
[1]*School of Renewable Natural Resources, University of Arizona, Tucson, AZ 85721, USA;* [2]*Departamento de Estudios Ambientales, Universidad Simón Bolívar Aptdo, 89000, Caracas 1080, Venezuela;* [*]*Author for correspondence (e-mail: dgw@ag.arizona.edu; fax: +1-520-621-8801)*

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Abstract

Clearing of natural vegetation for pastures and the deliberate introduction of African grasses constitute significant threats to the biological diversity of the tropics, subtropics, and warm temperate regions of the Americas. African grasses have escaped from cultivated pastures and revegetated rangeland sites and invaded natural areas at alarming rates. Invaded ecosystems tend to be biotically impoverished and differ markedly from adjacent non-invaded areas in structure and function. Effects of pasture creation and invasion by African grasses on ecosystem processes (transformation and flux of energy and matter) are primarily related to loss of woody species and changes in the fire regime. However, the ecophysiological attributes of the African grasses (e.g. high biomass allocation to leaves, high growth rate, and high leaf-level gas exchange rates) also have important consequences. Here we describe the extent of pasture creation with African grasses and their invasive spread in the New World and review ecological effects of these land-cover changes. We highlight a number of comparative ecophysiological studies within the context of mechanisms responsible for invasion by African grasses and resulting ecosystem change.

Introduction

Conversion of native forest, woodland, savanna, and grassland to pasture for livestock grazing in tropical and subtropical regions of the Western Hemisphere represents an extensive and significant human-caused land-cover change. Effects of this pasture conversion on regional and global biogeochemical cycles and climate are widely recognized (Gash et al. 1996; Houghton et al. 1996). Of equal significance is that these pastures have been developed using imported C_4 African grasses. These aggressive non-native grasses have spread from cultivated pastures and from revegetated rangeland to natural areas at alarming rates. Encroachment of African grasses into native savanna, forest edges, and grassland in many instances has altered fire regimes and produced significant changes in the flow of energy, nutrients and water through these ecosystems (Luizão et al. 1989; D'Antonio and Vitousek 1992; Fisher et al. 1994; Maass 1995; Baruch 1996; Gash et al. 1996; Johnson and Wedin 1997; Ley and D'Antonio 1998; Ibarra-Flores et al. 1999).

Consequences of structural changes in native communities resulting from fire and land clearing are difficult to distinguish from the direct ecological effects of African grasses that accompany these disturbances (D'Antonio and Vitousek 1992). Direct effects of African grasses on ecosystem processes are likely to be subtle compared to disturbance and land clearing that often precedes their invasion. Nevertheless, African grasses may contribute directly to changes in ecosystem processes. Despite calls for selection and development of native tropical grasses for pastures (McIvor and McIntyre 1997) and warnings about the use of introduced species in these situations (Lonsdale 1994; Low 1997), the introduction and spread of African grasses continue. These grasses will proceed to escape from cultivated areas and invade forest edges, savanna, and grassland without direct human assistance. We review here the extent of African grass invasion in the Americas using examples from savanna and forest in central and South America and desert grassland and thorn woodland in the North American Southwest. We also examine how land-cover change leading to dominance by African grasses and the unique ecophysiological characteristics of these alien grasses alter ecosystem function and dynamics.

History of introduction and invasion of African grasses in the Americas

Conversion of neotropical forest and savanna to pastures dominated by African C_4 grasses has resulted in dramatic losses of native vegetation. Approximately 53×10^6 ha of humid tropical forest have been converted to pasture in the Brazilian Amazon Basin alone (INPE 1999). Seasonally dry forest once covered 20–50% of the tropics in South and Central America, but today it is found only in small fragments within a matrix of derived grassland and savanna (Murphy and Lugo 1986; Janzen 1988). Approximately 10×10^6 ha of this forest type in Central America and Mexico have been converted to pasture for grazing (Maass 1995). Consequently, only 2% of dry tropical forest in the New World remains intact (Janzen 1988). As much as 40×10^6 ha of native tropical savanna have been converted to pastures in Colombia, Venezuela, and Brazil (Fisher et al. 1994). In sum, more than 100×10^6 ha of the humid and subhumid neotropics have been converted to grassland dominated by African C_4 grasses. This enormous area is increasing due to persistent forest clearing and pasture creation, and subsequent spread of these grasses into natural areas.

C_4 African grasses were introduced to the Americas inadvertently as early as the 17th century, even before they were widely used to establish grazing pastures (Parsons 1972). Many more introductions took place in the 19th and early 20th centuries, ostensibly to enhance livestock production; these grasses have invaded savanna and forest edges throughout the neotropics (Parsons 1972; Baker 1978). Among the early-introduced African grasses in the humid tropics of Central and South America, five are prominent: *Melinis minutiflora* Beauv., *Hyparrhenia rufa* (Nees) Stapf., *Panicum maximum* Jacq., *Brachiaria mutica* (Forsk.) Stapf. and *Pennisetum clandestinum* Hochst. (Table 1). These grasses escaped from planted areas and eventually became invaders, aided in part by the opening of native communities by fire and deforestation. More recently, large tracts of native tropical savanna and cleared forest have been sown with the nutritious and productive varieties of the African grasses *Andropogon gayanus* Kunth, *Pennisetum purpureum* Schumach., *Chloris gayana* Kunth, *Digitaria decumbens* Stent, and several species of *Brachiaria* (*B. decumbens*, *B. humidicola*, *B. brizantha*, and *B. dictyoneura*) (Table 1). At present, there is no evidence that the recently introduced *A. gayanus* and *Brachiaria* spp. have invaded neighboring areas (Fisher et al. 1995). However, it may take as long as 100 years after introduction before these grasses' ability to spread naturally can be assessed (Low 1997). In tropical Australia, *A. gayanus* and *B. decumbens* (together with the recognized neotropical invaders *M. minutiflora*, *H. rufa* and *B. mutica*) have been cited as environmental weeds (Lonsdale 1994; Low 1997; McIvor and McIntyre 1997); these species may also become invaders in tropical America.

Introduction and spread of African grasses have also occurred in semi-arid and arid regions of North and South America (Cox et al. 1988) where selection and importation of African C_4 grasses is used for rangeland improvement and revegetation. Arid and semi-arid rangeland on several continents was severely degraded by episodes of intense drought and overgrazing during the late 19th and early 20th centuries. A worldwide search was undertaken to find and develop grass species for rehabilitation of these sites and to enhance forage production for livestock (Cox et al. 1988). Four C_4 African grasses eventually were selected because of their drought tolerance, ease of establishment relative to native grasses, and high productivity. These 'miracle grasses' were: buffelgrass [*Pennisetum ciliare* (L.) Link. (syn. *Cenchrus ciliaris*)], Lehmann lovegrass (*Eragrostis lehmanniana* Nees), weeping lovegrass [*E. curvula* (Schrad.) Nees] and kleingrass (*Panicum coloratum* L.) (Table 1). The geographic scale of African grass introduction and spread since the 1940s in these dry regions of North and South America has been substantial and rivals the spread of introduced grasses in the wet tropical regions of the hemisphere.

P. ciliare is one of the world's most notorious invaders, yet it is also the most popular of the African

Table 1. Biogeographical and ecological characteristics of the prominent African grasses introduced to the Americas.

Latin name	Common name	Origin	Distribution in Americas	Ecological relationships	Life history/ growth form	Reproductive system[a]	Mode of spread	Reference(s)[b]
Andropogon gayanus Kunth	Gamba grass	Tropical and, sub-tropical south of Africa Sahara desert	Humid tropics, Central and northern Brazil	Drought and, fire tolerant frost sensitive	Perennial, large caespitose	A	Seed	1, 6
Brachiaria brizantha (A. Rich) Stapf	Signal grass, pasto alambe	Humid tropical Africa	Humid tropics	Frost and grazing tolerant, but will not withstand fire	Perennial/ rhizomatous	A	Seed	1, 6
B. decumbens Stapf	Signal grass	Great lakes Plateau, East and Central Africa	Humid tropics, sub-tropics, Caribbean	Drought sensitive, withstands heavy grazing	Perennial/ stoloniferous	A	Seed, stolons	1
B.mutica (Forsk.) Stapf	Pará grass, Capim angola	Tropical Africa	Humid tropics, sub-tropics	Semi-aquatic, persists in flooded areas, not tolerant to heavy grazing	Perennial/ stoloniferous	A, S	Stolons	1, 2, 6
Chloris gayana Kunth	Rhodes grass, pasto Rhodes	Sub-tropical Africa	Humid Tropics and sub-tropics	Tolerant to salinity, frost, drought, fire and grazing	Perennial/ stoloniferous	S	Seed, stolons	1, 2
Digitaria decumbens Stent	Pangola grass, pasto pangola	South Africa, Pangola River	Humid tropics in Central and South America, Florida	Tolerates heavy grazing, but is susceptible to frost	Perennial/ stoloniferous	Sterile	Stolons stolons	1
Eragrostis curvula (Schrad.) Nees	Weeping lovegrass, pasto llorón	Southern Africa, sub-tropics to tropics	Semi-arid North and South America, sub-tropics and warm temperate regions	Very tolerant to salinity and drought, moderate grazing tolerance	Perennial/ caespitose	A	Seed	1, 3, 6
E. lehmanniana Nees	Lehmann lovegrass	Tropical and sub-tropical South Africa	Semi-arid southwest North America, warm temperate and sub-tropical regions	Very drought tolerant, populations respond well to fire	Annual–perennial/ caespitose	A	Seed	1, 3

Table 1. Continued.

Latin name	Common name	Origin	Distribution in Americas	Ecological relationships	Life history/ growth form	Reproductive system[a]	Mode of spread	Reference(s)[b]
Hyparrhenia rufa (Nees) Stapf	Jaraguá	Tropical and South Africa and Madagascar	Humid and sub-humid tropics, Central and South America, Cuba	Tolerant to drought, grazing and fire	Perennial/ caespitose	FA	Seed	1, 2, 6, 7
Melinis minutiflora Beauv.	Molasses grass, gordura	Tropical West Africa, Angola to Camaroon	Tropics of Central and South America, West Indies, Puerto Rico	Moderately drought tolerant, but not tolerant to heavy grazing or frequent fire	Perennial/ caespitose	A	Seed	1, 2, 6, 8, 9
Panicum coloratum L.	Kleingrass, Makarikari grass	Tropical and sub-tropical South Africa	Tropics, sub-tropics, and warm temperate regions,Brazil, Venezuela, Texas	Frost sensitive, but somewhat drought tolerant	Perennial/ caespitose–stoloniferous	S, A	Seed, stolons	1, 3, 6
P. maximum Jacq.	Guinea grass, pasto Guinea, zacatón	Tropical Africa to sub-tropics of South Africa	South eastern US, West Indies, Tropics of Central and South America	Intolerant to drought, salinity and heavy frost, tolerant to fire and moderate grazing by livestock	Perennial/ caespitose	FA	Seed	1, 2, 6
Pennisetum ciliare (L.) Link. (= *Cenchrus ciliaris*)	Buffel grass	Hotter and drier parts of eastern and southern Africa	Semi-arid and arid tropics and sub-tropics, North Mexico, southwestern US	Sensitive to prolonged frost, but very tolerant of drought, fire, and heavy grazing	Perennial/ caespitose	A, S	Seed	1, 3

P. clandestinum Hochst. ex Chiov.	Kikuyu grass	High grassland of East and Central Africa	Humid regions in southern US, Central and South America	Intolerant to high temperature (16–21°C opt.) and sustained frost, but is very tolerant to grazing	Perennial/ rhizomatous and stoloniferous	A, S, some races sterile	Stolons and rhizomes	1, 2, 6
P. purpureum Schumach.	Napier grass, elephant grass	Sub-tropical and tropical Africa	Tropics and sub-tropics	Drought fire and frost sensitive, but can tolerate fire and heavy grazing	Robust perennial/ caespitose–rhizomatous	A, S	Seed	1
P. setaceum (Forsk.) Chiov.	Fountain grass	Eastern and North Africa, semi-arid to arid regions	Arid and semi-arid southwestern North America	Very tolerant to fire and drought, resists grazing	Perennial/ caespitose	A	Seed	1, 5
Rhynchelytrum repens (Willd.) C.E. Hubbard	Natal grass	Tropical Africa to sub-tropical South Africa, Madagascar	Semi-arid to humid sub-tropics of US and South America	Drought and fire tolerant	Annual–Perennial/ caespitose	??	Seed	6
Sorghum halepensis L.	Johnson grass	Mediterranean North Africa	Sub-tropics and warm temperate North and South America	Top-killed by frost, but regenerates from rhizomes, drought and grazing tolerant	Stout perennial/ rhizomatous	S	Seed, rhizomes	1, 6

[a] Reproductive system: S = sexual; FA = facultative apomixis; A = apomixis.

[b] Data were synthesized from numerous sources [1 = Skerman and Riveros (1989); 2 = Parsons (1972); 3 = Cox et al. (1988); 4 = Baker (1978); 5 = Williams et al. (1995); 6 = Bogdan (1977); 7 = Baruch (1994); 8 = Klink (1994); 9 = Pivello and Nortan (1996)].

grasses planted to enhance livestock production in the dry tropics and subtropics. This grass is used to convert thornscrub and succulent desert vegetation to grassland in Texas and northern Mexico; it is now the dominant herbaceous cover on roughly 10×10^6 ha (Yetman and Burquez 1994; Burquez et al. 1996). In Sonora, Mexico 1.2×10^6 ha of desert vegetation have been converted to buffelgrass pasture. An additional 6×10^6 ha (1/3 of the state's area) has been targeted for conversion to buffelgrass (Navarro 1988). The region undergoing the most extensive conversion to *P. ciliare* covers most of the Sonoran Desert subdivision Plains of Sonora – an ecologically diverse region with extraordinary examples of plant adaptive modification and radiation (Shreve 1951). Thus, bufflegrass constitutes a singular threat to the biological diversity of the Sonoran Desert.

Although not yet as prominent as buffelgrass, the C_4 South African grass *E. lehmanniana* has spread in desert grassland and scrub in Mexico and the southwestern US. Widespread reductions in grass cover and encroachment of woody plants and cacti in desert grassland late in the 19th century (Humphrey 1958; Bahre 1995) prompted seeding trials with African grasses (Crider 1945). *E. lehmanniana* was successful in these trials and now is used extensively to revegetate degraded areas. This grass has spread beyond the initial seeded areas and is invading desert grassland even without disturbance by livestock or humans (McClaran and Anable 1992). In Arizona, the area covered by *E. lehmanniana* more than doubled (to 340,000 ha) between 1950 and 1984 (Cox and Ruyle 1986; Anable et al. 1992).

The agronomic incentive for African grass introductions and pasture conversion is overwhelming (Humphreys 1994; Clements 1996), especially in the Western Hemisphere. Of the world's total cattle inventory, 20% (250 million head) are in the American tropics (Rao et al. 1993). In Colombia, liveweight gains of cattle can be as much as ten fold greater in converted pasture of the African grass *A. gayanus* than in native savanna (Rao et al. 1993). High production of *A. gayanus* and several other African grasses is attributed somewhat to their tolerance to the acidic, nutrient-poor soils that characterize most of tropical America (Rao et al. 1993) and their tolerance to grazing (Simoes and Baruch 1991; Klink 1994).

Similar enhancements of livestock production by African grasses are reported from arid and semi-arid regions of North America. Conversion of Sonoran Desert vegetation to *P. ciliare* in northern Mexico can allow stocking rates to triple (Burquez et al. 1996). Pastures dominated by *E. lehmanniana* in southern Arizona produce forage more consistently in dry years than do native grass pastures and thus serve as drought 'insurance' for ranchers (Cable 1971). Ranchers in Arizona often devote part of their ranch to *E. lehmanniana* pasture for this purpose.

Not every African grass was introduced deliberately to the New World for pasture development or rangelend improvement. *P. maximum* (Guinea grass) and *B. mutica* (Pará grass) may have been introduced inadvertently to the West Indies and Brazil as early as 1684 from slave ships (Parsons 1972). Others have been introduced more recently for ornamental purposes. The very attractive and aggressive fountaingrass [*Pennisetum setaceum* (Forsk.) Chiov.], for example, is widely planted in urban areas in southern California and Arizona. This fire-enhancing grass has escaped cultivation in the Tucson area and has spread to nearby Saguaro National Park (D.G. Williams, personal observation). The aggressive, fire-enhancing behavior of fountaingrass and its continuous cover over large areas in the Hawaiian Islands (Williams et al. 1995) suggest that this species could become a serious problem in the American Southwest.

Effects of African grass invasion on the flow of energy, nutrients, and water

Although the list of plant invaders worldwide is extensive (Groves and Burdon 1986; Drake et al. 1989; Mooney and Drake 1989), little is known about the effects of invaders on ecosystem processes. The little we do know about effects of African grasses on ecosystem processes can nonetheless direct policy makers and land managers to the potential consequences of these invasions (Vitousek et al. 1997) and offers guidance for management at the local scale (Pivello and Norton 1996; Walker and Smith 1997).

African grasses have the potential to affect ecosystem function by 1) altering productivity or trophic structure, 2) altering microclimate and shifting the rates of consumption and supply of light, water and mineral nutrients, 3) increasing the frequency and intensity of fire, 4) altering competitive interactions, and 5) compromising ecosystem stability.

Comparative ecophysiological studies suggest that some effects of single species on ecosystem processes are governed by traits at the level of tissues and organs (Grime 1979; Chapin et al. 1993). Thus, understanding the effects of African grasses requires examination of their ecophysiological traits and comparing these traits to those of native species in invaded ecosystems. A promising approach compares performance of invaders to that of their native congeners to distinguish those few ecophysiological traits that confer invasion success (Mack 1996). This method is more precise than tabulating common attributes of invaders from broad floristic surveys (Baker 1974). The latter approach has been widely criticized for its inability to predict the outcome of any specific introduction and for the numerous exceptions to any unique suite of traits expressed by plant invaders (Noble 1989; Mack 1996). For instance, many of the African grasses introduced to the Americas are either obligate or facultative apomicts (Table 1), yet the aggressive invader *Sorghum halepensis* L. is strictly sexual. Similar exceptions can be found for any common trait among African grass invaders.

Plant invasions provide examples of how a single species may control ecosystem function and dynamics (Vitousek and Walker 1989; Vitousek 1990; D'Antonio and Vitousek 1992), and there is growing recognition that ecophysiological traits have important ecosystem consequences (Wedin and Tilman 1990; Hobbie 1992; Lawton 1994; Wardle et al. 1998; Williams et al. 1999). For elucidating the effects of an invader, it may prove more useful to make comparisons between the invader and representatives from dominant plant functional groups within the invaded ecosystem, rather than comparisons with native congeners alone (Chapin et al. 1996; Hooper and Vitousek 1998; Williams et al. 1999). The specific goal is to uncover *how* invaders alter the processing of nutrients, energy, and water within invaded ecosystems. Unfortunately, few ecophysiological studies have been conducted that compare non-native African grasses and native plants.

Plant traits that have important effects in ecosystems and those that allow a species to invade the ecosystem are often the same. Changes in ecosystems brought about by an invasion allow the invasion to proceed. For instance, with African grass invasions, positive feedback with fire promotes continued invasion and vegetation change (D'Antonio and Vitousek 1992). Plant ecophysiological traits (e.g. large aboveground biomass, high herbaceous productivity) that promote changes in fire regime are the same traits that allow the African grass to persist and proliferate in the new range.

The ecophysiological traits relevant for understanding ecosystem effects of invasions vary. Some traits integrate several ecosystem processes. For example, traits related to tissue decomposition and nitrogen mineralization (e.g. tissue C : N ratio, lignin : N ratio) are also important in trophic level interactions (Wardle et al. 1998). Traits involved with energy and water exchange (e.g. leaf area ratio, stomatal behavior, drought response) also characterize potential changes in primary productivity and canopy transpiration following invasion. Furthermore, a general understanding of how an invader alters ecosystem processes should recognize species–environment responses. The most useful ecophysiological comparisons between invaders and natives are those that assess responses over a range of environmental (biotic and abiotic) conditions. Plasticity is an important component of these responses (Williams et al. 1995), but it has not been addressed within the context of ecosystem effects of invasions.

Effects of African grasses on fluxes of materials and energy at the ecosystem level depend on how resources are captured and processed and how coincident land disturbance alters the abundance of other species. Here we highlight some of the ecophysiological differences between African and native grasses and illustrate how traits of the African grasses are manifested at the ecosystem level. We focus on studies that involve natural gradients or experimental manipulations of resource supply or disturbance.

Gas exchange, water relations, and growth of African grasses

Periodic drought limits plant growth and establishment in many New World ecosystems currently being invaded by African grasses. Generally, the introduced African grasses are intensive water users that have high maximum photosynthetic rates and produce abundant biomass when water is available but cease growth and gas exchange at moderate drought levels. In greenhouse and field comparisons between the native C_4 grass *Trachypogon plumosus* Humb. & Bonpl. from neotropical savanna in Venezuela and the African invaders *Hyparrhenia rufa* and *M. minutiflora*, the African grasses consistently expressed higher maximum stomatal conductance, photosynthesis, and transpiration rates than the native *T. plumosus* (Baruch et al. 1985; Simoes and Baruch, 1991;

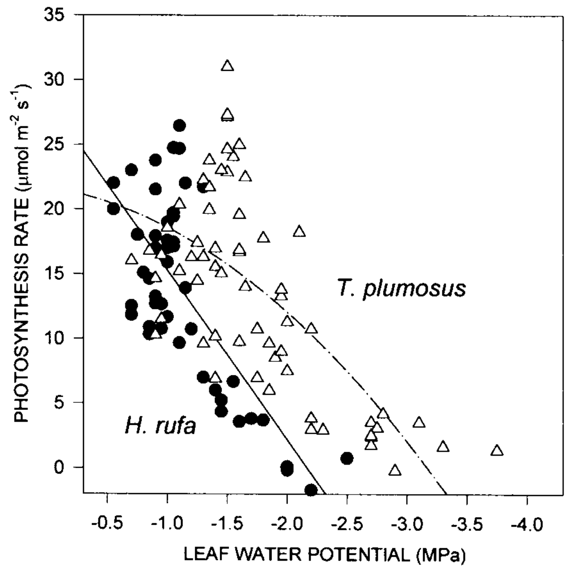

Figure 1. Relationship between photosynthetic rate and leaf water potential in the alien *Hyparrhenia rufa* and the native *Trachypogon plumosus* in Venezuela neotropical savanna. Circles = *Hyparrhenia* [$A = 24.42 - 1.31\Psi$ ($r^2 = 0.56$)]; triangles = *Trachypogon* [$A = 21.68 - 0.13\Psi - 0.01\Psi^2$($r^2 = 0.48$)] [Reproduced with permission from Baruch and Bilbao (1999); © Springer-Verlag.]

Baruch and Fernández, 1993). *H. rufa* apparently avoids drought in these subhumid savannas; its leaf senescence is rapid with cessation of the rainy season. In contrast, *T. plumosus* maintains net positive photosynthetic rates at leaf water potentials well below that tolerated by *H. rufa* (Figure 1) and persists longer into drought periods (Baruch and Bilbao 1999).

Similarly, the aggressive African grass *P. setaceum* at semi-arid coastal sites on the island of Hawaii had higher maximum photosynthetic rates under favorable greenhouse conditions than the native Hawaiian grass *Heteropogon contortus* (Williams and Black 1994). These two species also co-occur in southern Arizona where *P. setaceum* is escaping cultivation and invading upland Sonoran Desert vegetation (Burgess et al. 1991). *P. setaceum* maintained higher maximum leaf gas exchange rates than did *H. contortus* even after several cycles of water limitation and irrigation (Figure 2). As in the *Hyparrhenia–Trachypogon* comparison, the native *H. contortus* can however maintain positive photosynthetic rates at much lower leaf water potentials than can *P. setaceum* (Williams and Black 1994). *P. setaceum*, similar to *H. rufa*, is an intensive water user but has limited tolerance to water deficits.

African grasses allocate proportionally more of their total biomass to assimilating surfaces than do the native grasses in invaded ecosystems. For example, 44% of total plant biomass in *P. setaceum* was partitioned into leaf blades compared to only 30% in *H. contortus* after 98 days of glasshouse growth (Figure 3) (Williams and Black 1994). The proportion of biomass in leaf blades did not vary with watering treatment or plant size in either of these grasses. Preferential allocation of biomass to leaves favors greater whole-plant carbon fixation and growth. Consequently, *P. setaceum* accumulated much more total plant biomass than *H. contortus* by the end of the study (Figure 3) (Williams and Black 1994). Similar differences in biomass allocation patterns between native and African grasses are reported from neotropical savanna. *H. rufa* and *M. minutiflora* invest a greater proportion of total biomass to leaves during the peak growing season compared to the native *T. plumosas* in upland and lowland savanna ecosystems in Venezuela (Figure 4) (Baruch et al. 1989; Baruch and Bilbao 1999). Consequently, *H. rufa* and *M. minutiflora* have higher growth rates and also produce more biomass in these field settings (Figure 5 and Table 2) (Baruch et al. 1989; Klink 1994; Baruch and Bilbao 1999). Biomass production of cultivated African grasses in the Neotropics is even greater than the production of the invaders or native grasses (Table 2).

Effects of African grasses on ecosystem water balance

The conversion of native forest to pasture and the establishment of African grasses can significantly alter water balance of ecosystems and watersheds. The magnitude and direction of impact will be determined by the physiognomic and life form changes associated with invasion or conversion and the management in the derived grassland. Deliberate conversion of mesic and dry tropical forest to African grass-dominated pasture produces radical changes in hydrologic balance. Conversion of mesic and dry tropical forest to these pastures increases runoff, warms the air above the canopy, and lessens the amount of energy dissipated through transpiration (Maass 1995; Gash et al. 1996). These effects are produced primarily by the extreme structural changes of the vegetation, rather than specifically the introduction of African grasses themselves. However, due to the massive area that has been converted to African

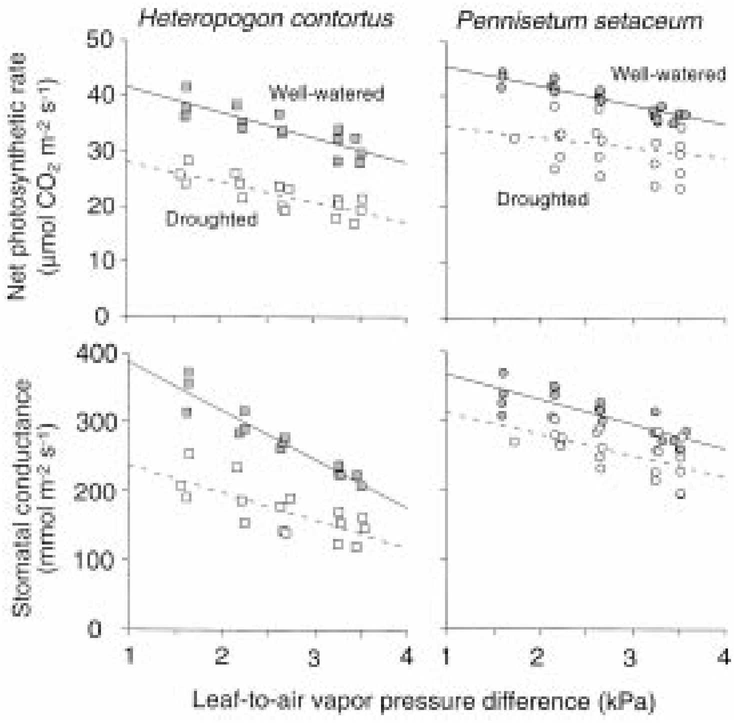

Figure 2. Response of stomatal conductance and net photosynthetic rate to leaf-to-air vapor pressure difference in the Hawaiian native *Heteropogon contortus* and the alien *Pennisetum setaceum*. Plants were grown for 90 days in a glasshouse before measurement and were subjected to periodic water limitation (open symbols) and well-watered (closed symbols) treatments [Reproduced with permission from Williams and Black (1994); © Springer-Verlag.]

grass dominance (100×10^6 ha), these changes have potentially large effects on regional and global climate.

By contrast, invasion of African grasses into native grassland or savanna will likely increase evapotranspiration and rainfall interception and decrease soil water recharge and runoff by virtue of the higher LAI in African grass stands and these grasses' more rapid canopy development during the rainy season (Daubenmire 1972; San José et al. 1998). In some cases these effects will be compounded by the higher leaf-level transpiration (Williams and Black 1994) and deeper root systems (Daubenmire 1972; Fisher et al. 1994) of African grasses. Averaged daily net radiation was 1.1 fold higher over pasture of *B. decumbens* than in native grasslands in Venezuela during a typical rainless day in the wet season. Differences in canopy closure among these grasses had a major effect on partitioning energy into sensible and latent heat fluxes. Transpiration dissipated 85% of available energy in the *Brachiaria* pasture but only 64% of available energy in the native grass stand (San José et al. 1998). Similar changes may occur with invasion by *E. lehmanniana*

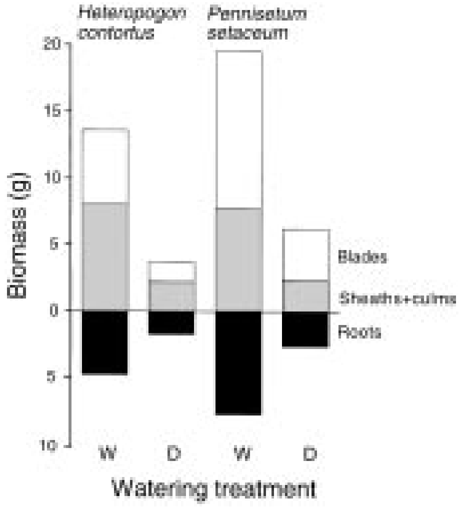

Figure 3. The distribution of biomass among roots, culms + sheaths, and leaf blades in the Hawaiian native *Heteropogon contortus* and alien *Pennisetum setaceum* after 98 days of growth in a glasshouse. Plants were subjected to periodic water limitation (D) and well-watered (W) treatments [Reproduced with permission from Williams and Black (1994); © Springer-Verlag.]

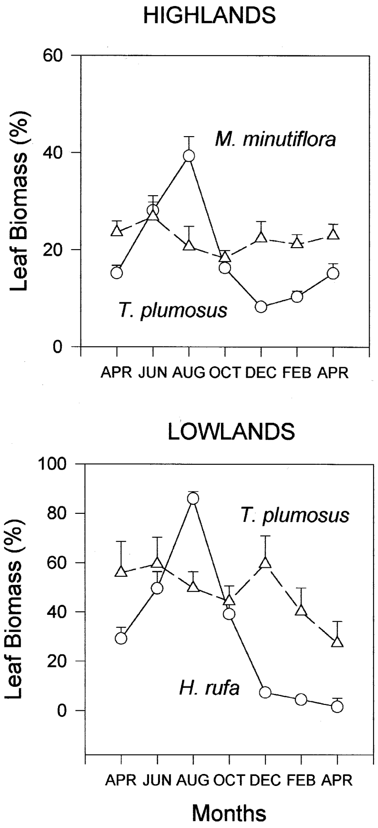

Figure 4. Percentage of total plant biomass allocated to leaves throughout one growing season in two populations of the native grass *Trachypogon plumosus* and the African spp. *Melinis minutiflora* and *Hyparrhenia rufa* from highland and lowland savannas of Venezuela.

and *P. ciliare* in the American Southwest because these invasions enhance herbaceous cover.

Nutrient use by African grasses

Scarcity of soil nutrients also occurs in many areas that have been converted to pasture or invaded by African grasses in the New World (Frost et al. 1986; Medina and Silva 1990; Rao et al. 1993). African pasture grasses selected for introduction are either adapted for production with low nutrient supply (*M. minutiflora, H. rufa*) or have high nutrient requirements and respond with tremendous growth when fertilized (*A. gayanus, E. curvula, P. clandestinum, Brachiaria ruziziensis, P. maximum*) (Humphreys 1981). However, even those African grasses adapted to low nutrient supply tend to have greater responsiveness to nutrient additions than the native grasses they displace (Baruch et al. 1985; Bilbao and Medina 1990; Fisher et al. 1992). Baruch and Gómez (1996) found that tissue N and P content in the native *T. plumosas* and the alien *H. rufa* did not differ markedly, but *Hyparrhenia* tended to preferentially allocate these nutrients to leaves. Consequently, nutrient-use efficiency (biomass gain per unit of nutrient taken-up from soil) was higher in the alien grass. The African grass *P. clandestinum* was more responsive to added nitrogen than the native grasses *Paspalum*

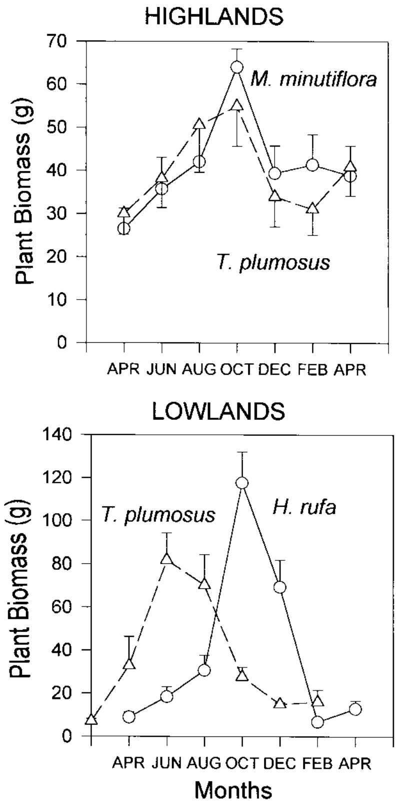

Figure 5. Biomass production during one growing season by two native *Trachypogon plumosus* populations and the African grasses *Melinis minutiflora* and *Hyparrhenia rufa* in highland and lowland savannas of Venezuela.

Table 2. Specific leaf area (SLA), photosynthetic nitrogen-use efficiency (PNUE) and leaf construction costs (glucose equivalents per gram) of the alien *Hyparrhenia rufa* and the native *Trachypogon plumosus* during the peak of seasonal growth in field grown plants in lowland savannas of Venezuela (adapted from Baruch and Gómez 1996).

	SLA ($m^2 g^{-1}$)	PNUE (μmol CO_2 g $N^{-1} s^{-1}$)	Leaf C Costs (eq. gluc. g^{-1})
H.rufa	0.034 ± 0.0008	40.3 ± 1.4	1.26 ± 0.01
T. plumosus	0.020 ± 0.0002	31.8 ± 2.6	1.38 ± 0.02

dilatatum and *Axonopus affinis* (Mears and Humphreys 1974). In general, African grasses introduced to the Americas require more nutrients than native grasses in order to achieve their higher growth potentials, but they also appear to use nitrogen more efficiently. The preferential invasion of African grasses on the most fertile soils in neotropical savanna supports this observation (Baruch et al. 1989). Soil nutrient additions, furthermore, promotes establishment of *H. rufa* on soils where it normally does not occur in these savannas (Pieters and Baruch 1997).

Effects of African grasses on ecosystem nitrogen and carbon

Generalizations about how African grass invasion and forest-to-pasture conversion alter carbon and nitrogen balance can be made readily in some circumstances but not in others. Outcomes are straightforward when radical changes in physiognomy or lifeform accompany invasion or pasture conversion. Net losses of carbon from ecosystems generally follows loss of woody vegetation. Conversion of tropical forest to pasture in the Amazon Basin, for example, results in immediate C losses of between 268 and 670 mg/ha (Lucas et al. 1996). Burquez et al. (1996) reported above ground C losses of 4–16 mg/ha following conversion of Sonoran Desert vegetation to *P. ciliare* – a remarkably high figure for arid ecosystems. On the other hand, conversion of native savanna dominated by *T. plumosus* to pasture dominated by *H. rufa* enhanced aboveground biomass by aproximately 100% (Baruch 1996). Direct effects of grass invasion on soil nitrogen and carbon biogeochemistry and ecosystem water balance are more subtle, especially when introduction of an African grass causes little change in the community's life forms.

Management of African-grass pastures in the tropics has a large influence on the dynamics of soil carbon and nitrogen (Humphreys 1994). Large disturbances associated with pasture creation is coincident with African grass introduction or invasion and these are difficult to address independently in terms of their effects on ecosystem carbon and nitrogen. In Costa Rica, Johnson and Wedin (1997) found that soil C stocks were depleted and soil organic matter had lower quality in derived grassland dominated by *H. rufa* than in adjacent dry tropical forest. Soil C : N ratios were higher and N mineralization rates were lower in the derived grassland. Loss of tree species from these ecosystems likely was the principal cause of these changes, but the impact of *H. rufa* may also be significant. The tolerance of this grass to low nutrient supplies and its relatively high C : N ratio would promote a positive feedback so that rates of nitrogen cycling and nitrogen availability would decline as the abundance of *H. rufa* increased, thereby enhancing further the relative dominance of this grass. Conversely, invasion by African grasses has the potential to establish a positive feedback with nutrient cycling in exactly the opposite direction. Asner and Beatty (1996) found that soils in non-invaded shrubland in Hawaii had lower N availability compared to soils that had been invaded by *M. minutiflora*. C : N ratios of the litter were negatively correlated to nitrogen availability index as estimated with resin bags. Foliar and litter C : N ratios for *Melinis* were 35 and 46, respectively, whereas those of the native shrubland averaged about 50 and 71.

Redistribution and loss of soil N and C following the establishment of African grass pastures depend on the agricultural practice, life zone, soil texture, and length of time since pasture creation (Maass 1995). Pasture soils had higher levels of soil carbon than did forest soils in the humid region of Rondônia in the Amazon Basin (Neill et al. 1996). δ^{13}C ratios of soil organic matter in this study suggested that African grass-derived C was increasing more rapidly than forest-derived carbon was being lost. The lower-quality carbon from grass in this case apparently caused net C sequestration in soil organic matter (Wedin and Tilman 1996). From a similar forest and pasture comparison in Rondônia, Piccolo et al. (1994) observed large differences in litter C : N ratios. Forest litter had an average C : N ratio of 21. In five-year-old and twenty-year-old pasture dominated by the African grass *B. brizantha,* litter C : N values ranged from 149 to 166.

Fisher et al. (1994) also found that cultivated African grasses increase soil carbon stocks in tropical savanna. The African grasses produced a net gain by sending carbon deeper in the soil compared to native grasses. Because soils are a major compartment for C storage in terrestrial ecosystems, conversion of neotropical savanna to African grass-based pastures and the resulting increase in carbon sequestration, potentially leads to important changes in global carbon cycling. Fisher et al. (1994) suggested that the added C to deep soil layers by African grasses in South America could sequester up to 507 Mt C per year more than sequestered in native savanna. Davidson et al. (1995), however, disputed these projections of soil C sequestration, noting that equilibrium rates of carbon input and soil respiration in the new African grass-dominated pastures studied by Fisher et al. (1994) were not yet established, and thus sequestration was difficult to extrapolate to other areas with different-aged pastures.

Effects of African grass invasion on soil C and N in arid and semi-arid ecosystems also can be significant and appear to be different from most effects in more humid regions. Ibarra-Flores et al. (1999) investigated effects of buffelgrass (*P. ciliare*) establishment on soil C and N in three climatic regions in Mexico. Total soil C and N levels declined by an average of 40% and 25% respectively, among 13 sites in the Sonoran Desert of Northwest Mexico. However, some sites showed increases in total soil C and N following conversion to buffelgrass pasture. The five sites examined by these investigators in the seasonally dry Yucatan Peninsula showed declines in soil C and N of approximately 40% following conversion to buffelgrass. Soil C : N ratios, however, were not different in buffelgrass pastures than in native vegetation for any of the regions studied by these investigators. Removal of biomass by cattle and volatilization by fire likely contribute to the lowered soil C and N in these pastures.

Williams (unpublished data) measured total soil N and C, cover of herbaceous dicots, and cover of the South African grass *E. lehmanniana* at seven desert grassland sites on the Santa Rita Experimental Range in southeastern Arizona. *E. lehmanniana* had not yet invaded two of the sites, but had been a dominant member of the herbaceous community from between five and 30 years at the other five sites. Cover of herbaceous dicots was negatively correlated with cover of *E. lehmanniana* (Figure 6); a decline observed at other desert grassland sites (Bock et al. 1986). Plant traits that determine rates of nutrient cycling and soil carbon storage can differ between herbaceous dicots and C_4 grasses. Herbaceous dicots tend to have lower tissue C : N ratios and higher nitrogen requirements for growth than C_4 grasses (Field 1991; Hooper and Vitousek 1998). The lowest soil C : N ratios in the Santa Rita Experimental Range study were in sites not yet invaded by *E. lehmanniana*. Despite this outcome, no significant correlation was observed between *E. lehmanniana* cover and soil C : N ratios (Figure 7). Conversely, cover of the herbaceous dicots was negatively correlated to soil C : N ratios and may be an important link between *E. lehmanniana* invasion and potential nutrient cycling changes (Figure 7).

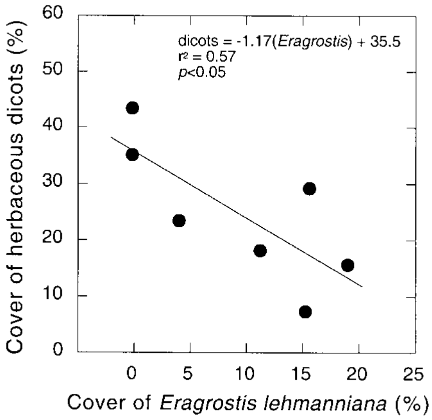

Figure 6. Relationship between cover of *Eragrostis lehmanniana* and that of herbaceous dicots among seven desert grassland sites on the Santa Rita Experimental Range in southeastern Arizona. Data were collected using 20 × 50 cm plot frames along a single 50 m transect at each site.

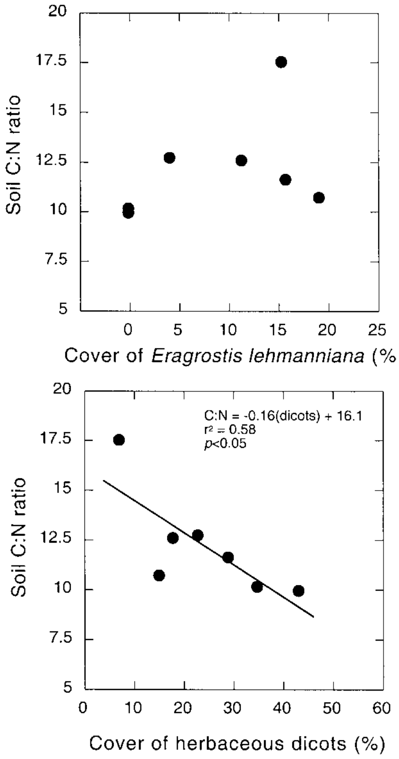

Figure 7. Relationships between cover of herbaceous dicots and *Eragrostis lehmanniana* (from Figure 6) and soil C : N ratio. Soil C : N ratios are for total soil organic matter collected from 25 random locations along 50 m transects at each of seven sites on the Santa Rita Experimental Range in southeastern Arizona.

Input of nitrogen to ecosystems via biological N fixation is potentially altered by African grass invasion. Displacement of native legumes by alien grasses should reduce N accretion in converted pastures and invaded sites. However, nitrogen fixation by free-living bacteria (asymbiotic N fixation) in the rhizosphere and roots of several African pasture grasses can be significant (Boddey and Döbereiner 1988). In Brazil, ^{15}N labelling demonstrated that pastures of *B. humidicola* and *B. decumbens* potentially fixed as much as 30 and 45 kg N ha^{-1} yr^{-1}, respectively; these values represent 30% and 40% of the total nitrogen requirement for these grasses (Boddey and Victoria 1986). The native Brazilian grass *Paspalum notatum* showed no significant levels of asymbiotic N fixation. Picollo et al. (1994), using natural abundance ratios of ^{15}N, found evidence for greater N fixation in pastures dominated by *B. brizantha* and *P. maximum* compared to adjacent forest in Rondônia, Brazil. More recently, however, Ley and D'Antonio (1998) found reduced rates of asymbiotic N fixation in tropical dry forest that had been converted to *M. minutiflora* grassland in the Hawaiian islands. In this case, volatilization of N by fire and reduced N fixation following invasion by *M. minutiflora* is impoverishing these already nitrogen-poor ecosystems. Asymbiotic N fixation in African grasses may vary with site conditions, host specificity, the availability of inoculates, and the techniques used to measure fixation rates (Boddey and Döbereiner 1988).

Production and emission of trace gasses containing nitrogen represent an important pathway for nitrogen loss from ecosystems and has implications for global atmospheric chemistry and climate (Vitousek 1994). Range expansion of African grasses and especially increase in these pastures in the American tropics potentially enhances emissions of the 'greenhouse' gas nitrous oxide (N_2O). Matson and Vitousek (1995) summarized work conducted in Jalisco, Mexico that compared N_2O emissions from pastures and intact dry tropical forest. Although unfertilized upland pastures of *P. maximum* were not different from intact forest in seasonal patterns and fluxes of N_2O, fertilized lowland pastures had very high N_2O emissions. In another study, Luizão et al. (1989) found that fertilized pastures of the African grass *B. humidicola* had threefold greater annual N_2O flux than did adjacent forest in the central Amazon. Without direct application of fertilizer, it seems unlikely that African grass expansion in the Americas will enhance N_2O fluxes. However, greater nitrogen inputs could occur by planting legumes, a common practice in tropical pasture management (Humphreys 1994), or from asymbiotic N fixation in the grasses. The extent to which greater nitrogen inputs accompany African grass invasion will determine if these transformed ecosystems in the New World will be a significant source of rising atmospheric N_2O (Matson and Vitousek 1990).

Effects of African grasses on disturbance by fire and herbivores

African grasses introduced to the Americas are tolerant and responsive to fire (Cable 1965; Daubenmire 1972; Sumrall et al. 1991; Low 1997) and grazing (Daubenmire 1972; Simoes and Baruch 1991; McClaran and Anable 1992). These traits can alter disturbance cycles in ecosystems when African grasses invade.

Response to fire

Many African grasses introduced to the Americas promote and are stimulated by fire. In many cases, African grasses respond more positively to fire disturbance than native grasses. For example, the African *H. rufa* had greater regrowth and photosynthetic enhancement following fire than the native *T. plumosus* (Table 3) (Baruch and Bilbao 1999). However, *H. rufa* displayed greater mortality, and the surviving individuals of this African grass were smaller and reached their peak biomass later in the wet season compared with *T. plumosus*. Greater fire damage to *H. rufa* may have resulted from higher combustion temperature in stands of this grass compared to temperatures in stands of *T. plumosus* stands (Bilbao 1995). Fire damage to adult *H. rufa* was offset by tremendous regrowth and recruitment of new individuals from seed; these responses favor colonization of burned savannas (Table 3) (Baruch and Bilbao 1999). Responsive seed germination also favors recruitment of *E. lehmanniana* over native grasses in burned desert grassland sites in Arizona (Sumrall et al. 1991)

The large standing necromass left by the African grasses at the end of the dry season facilitates the combustion and increases the intensity of fires. As a result, larger losses of nitrogen and sulfur through volatilization occur in African grass-dominated savanna than in native savanna in the tropics (Medina 1993; Bilbao 1995). Invasion of African grasses in New World tropical savannas, dry tropical forests (Janzen 1988), and aridlands (Cable 1965; Sumrall et al. 1991; Burquez et al. 1996) is promoted by fire which in turn promotes more frequent and intense fires (D'Antonio and Vitousek 1992). African grasses are a particular threat along forest edges as they carry successive hot fires that progressively destroy the forest (Low 1997). When African grass pastures are heavily grazed by livestock, little standing necromass is left through the dry season; the fire potential is reduced. For this reason, and because domestic livestock facilitate seed dispersal of woody plants (Brown and Archer 1987), grazing may be important for managing African grass invasions and restoring native ecosystems that contain fire-sensitive woody species.

Response to herbivory

African grasses are often more tolerant to defoliation than indigenous grasses (Table 3) (Hodgkinson et al. 1989; Simoes and Baruch 1991; Sarmiento 1992; Baruch and Bilbao 1999). Simoes and Baruch (1991) in a controlled environment study clipped *H. rufa* and *T. plumosus* plants to a 8 cm height at weekly intervals. Although experimental defoliation reduced total plant biomass relative to controls in both species, only the former compensated partially for the loss (Figure 6). Greater compensatory response in *H. rufa* than in the native *T. plumosus* has been attributed to the larger proportion of assimilates allocated to leaf and tiller production and higher leaf growth rate in *H. rufa* (Simoes and Baruch 1991). However, Klink (1994) found that African grasses were no more tolerant of defoliation than native grasses in the Brazilian savannas. He compared responses of five native caespitose grasses (*Axonopus barbigerus*, *A. marginatus*, *Echinolaena inflexa*, *Schyzachyrium tenerum*, *Trachypogon polymorphus*) and two caespitose (*A. gayanus*, *H. rufa*) and two stoloniferous African grasses (*B. decumbens*, *M. minutiflora*) to experimental defoliation in the field. The responses (tillering, basal growth, height growth) overlapped considerably between African and native grasses. *M. minutiflora* expressed reduced tillering under defoliation treatments. These results, taken together with those of Simoes and Baruch (1991), suggest that the role of defoliation tolerance in an invasion depends on the match between the invader and invaded ecosystem.

Future global changes that may affect African grass invasions and their consequences

Although any increase in atmospheric CO_2 concentration will tend to affect C_3 plants more than C_4 plants (Poorter 1993; Poorter et al. 1996), relationships between the C_4 native and African grasses could also be altered. The generally higher growth rates of the latter would be further enhanced by an increase in atmospheric CO_2 concentration. High CO_2 concentration promotes stomatal closure (Tyree and Alexander 1993). Therefore, the relatively higher stomatal conductances and transpiration rates of species, such as *H. rufa*, *M. minutiflora*, and *P. setaceum*, would decrease proportionally more than in natives such as *T. plumosus* and *H. contortus*. Lower transpiration under elevated CO_2 may potentially decrease soil water use (Field et al. 1997) to a greater extent by the former. Both effects would constitute a relative advantage for these African grasses and accelerate their invasion and dominance. Seneweera et al. (1998) examined the response of *P. coloratum*, one of the rangeland 'miracle grasses' planted throughout the Americas, to

Table 3. Biomass of whole plants and caryopses, germination percent, and seedling density of the alien *Hyparrhenia rufa* and the native *Trachypogon plumosus* under defoliation and fire treatments in lowland savannas of Venezuela. For each species, values followed by the same letter are not significantly different under $P < 0.05$. Caryopsis weight of *M. minutiflora* is 0.64×10^{-4} g. Adapted from Baruch and Bilbao (1999).

Species	Treatment	Plant dry weight (g)	Caryopsis weight × 10^{-4}(g)	Germination (%)	Seedling density (m^{-2})
H. rufa	Control	117.70 ± 14.44 (a)	2.94 ± 0.38	74.3 ± 5.0	—
	Clipped	92.36 ± 20.30 (ab)	—	—	—
	Burned	75.67 ± 18.47 (b)	—	—	~9700
T. plumosus	Control	81.93 ± 12.46 (a)	8.10 ± 0.20	33.0 ± 7.0	—
	Clipped	27.88 ± 6.83 (b)	—	—	—
	Burned	65.59 ± 9.82 (a)	—	—	~12

CO_2 enrichment. Growth enhancements were achieved under high CO_2 concentrations (1000 μl/l), but only under conditions of high atmospheric VPD or low soil water availability. No enhancements were detected for plants grown with ample water or in humid air. Effects of invasions therefore may be exacerbated further in semi-arid and arid regions with future CO_2 levels but may not change in the humid tropics.

Other anticipated global changes include climate warming, precipitation redistribution, and enhanced levels of nitrogen deposition that together may produce accelerations in African grass invasions and range shifts (Lodge 1993; Ehleringer et al. 1998; Wedin and Tilman 1996). Range expansion of African grasses could occur at high latitudes and elevations where minimum seasonal temperatures limit their survival. For example, the distribution of buffelgrass (*P. ciliare*) in the American Southwest is limited by minimum temperatures of 5 °C (Cox et al. 1988). This species may expand its distribution northward in the future with only modest changes in air temperature. However, agronomists are unwilling to wait for global warming; efforts are underway to develop frost tolerant buffelgrass varieties and hybrids for release in the US (Stair et al. 1998). The distribution of African C_4 grasses in semi-arid regions of North America are also limited in many locations by the amount of precipitation falling in summer (Cox et al. 1998). Expansion or intensification of the summer 'monsoon' in the American Southwest as predicted from global circulation models, consequently, could cause range expansions of C_4 African grasses into regions that have so far been resistant to these invasions (Ehleringer et al. 1998).

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