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BIOLOGICAL INVASIONS BY EXOTIC GRASSES, THE GRASS/FIRE CYCLE, AND GLOBAL CHANGE

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INTRODUCTION

Biological invasions into wholly new regions are a consequence of a far reaching but underappreciated component of global environmental change, the human-caused breakdown of biogeographic barriers to species dispersal. Human activity moves species from place to place both accidentally and deliberately—and it does so at rates that are without precedent in the last tens of millions of years. As a result, taxa that evolved in isolation from each other are being forced into contact in an instant of evolutionary time.

This human-caused breakdown of barriers to dispersal sets in motion changes that may seem less important than the changing composition of the atmosphere, climate change, or tropical deforestation—but they are significant for several reasons. First, to date, biological invasions have caused more species extinctions than have resulted from human-caused climatic change or the changing composition of the atmosphere. Only land use change probably has caused more extinction, and (as we later discuss) land use change interacts strongly with biological invasions. Second, the effects of human-caused biological invasions are long-term: changes in climate, the atmosphere, and land use may be reversible in hundreds to thousands of years, but the breakdown of biogeographic barriers has resulted in self-maintaining and evolving

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populations in regions they could not otherwise have reached. Many of these changes must be considered irreversible (32). Finally, some biological invasions alter ecosystem processes in invaded areas, thereby causing functional as well as compositional change.

The fraction of successful invasions that alter ecosystem processes (defined here as whole-system fluxes of energy, the amount and pathway of inputs, outputs, and cycling of materials, and the ways that these vary in time) is not known. Such effects have been evaluated in very few cases, and most of those doubtless were selected for study because they were thought to involve changes in ecosystem processes. Vitousek (167) discussed three ways that biological invasion could alter ecosystems: (i) Invading species could alter system-level rates of resource supply. For example, the actinorrhizal nitrogen-fixer *Myrica faya* invades and dominates nitrogen-limited primary successional sites and increases both nitrogen inputs and the biological availability of nitrogen several-fold (168, 170). Other examples include *Tamarix* spp. in arid lands of the United States and Australia (65, 90, 112), *Mesembryanthemum crystallinum* in California and Australia (83, 171), *Carpobrotus edulis* in California (41), and Australian Acacia species in South Africa (185). (ii) Invading species could alter the trophic structure of the invaded area. Adding (or removing) a top carnivore can have disproportionate effects on ecosystem structure and function. This is the original basis of the keystone species concept (114), and it continues to be important in the development of trophic theory (28). Examples include the establishment of lamprey in the Saint Lawrence Great Lakes (5) and the introduction of the brown tree snake on Guam (135). (iii) Invading species can alter the disturbance regime (type, frequency, and/or intensity) of the invaded area. For example, feral pigs, *Sus scrofa,* alter rates of decomposition, nutrient cycling (166), and even watershed-level nutrient losses by "rooting" through soil (145). Plant invasions can alter fire frequency and intensity (92, 149, 164), including the introduced grasses that are the major topic of this review.

Invasions that alter ecosystem processes are important to ecological theory because such effects are less well characterized than are population or community level effects of invasion, and they represent a clear example of single species control over ecosystem processes. In addition, invasions that alter ecosystems represent a particularly significant threat to native populations and communities: they don't merely compete with or consume native species, they change the rules of the game by altering environmental conditions or resource availability. Finally, invasions that alter ecosystem processes over large areas could feed back to alter other components of global change (e.g. climate, atmospheric composition, and land use).

Grasses are one set of invading species that in the aggregate may be sufficiently widespread and effective to alter regional and even global aspects

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of ecosystem function. Grass invasions are important for several reasons: (i) As a group, grasses are moved actively by humans so invasions are common (e.g. 115); (ii) exotic grasses compete effectively with native species in a wide range of ecosystems; (iii) where they dominate sites, grasses can alter ecosystem processes from nutrient cycling to regional microclimate; and (iv) many species of grasses tolerate or even enhance fire, and many respond to fire with rapid growth. In turn, fire is a significant agent of both land use and atmospheric change regionally and globally (38, 81).

In this paper we make the case that grass invasions are widespread, that grasses are effective and aggressive competitors with native species, and that grass invasions have substantial ecosystem-level effects. We then discuss the regional and global significance of invasions in the context of the land use changes that are driving much of the earth's surface toward dominance by fire and grasses.

GEOGRAPHIC PATTERNS OF GRASS INVASION

General

Examples of alien grass invasion can be found on all continents, although examples from Eurasia and Africa are rare. These invasions can be divided into three categories: (i) spread of alien grasses into largely undisturbed native vegetation, (ii) spread of grasses into disturbed vegetation, and (iii) the longterm persistence of grasses in areas where they were originally seeded. Invasions into undisturbed sites are the most interesting from the point of view of developing a basic understanding of effects of individual species on ecosystems. However, invasions into human-disturbed areas and even the persistence of once-seeded grasses can be equally effective agents of local, regional, and global change.

North America

Alien grass invasions are most severe in the arid and semi-arid west and include invasions by European annual grasses and by perennial bunchgrasses of African, Eurasian, and South American origin.

Annual grass invasions began with the arrival of Europeans and were largely unplanned. Mack (94) details the expansion of ***Bromus tectorum*** (cheatgrass) throughout the Great Basin in conjunction with the introduction of sheep and cattle. Other European annual grasses whose invasion appears to be tied to grazing include ***Taeniatherum asperum*** (medusahead) (186) and ***Bromus rubens*** (red brome). Also, ***Bromus mollis***, ***B. diandrus***, and ***Avena*** spp. now dominate valley grasslands in California where they have replaced grazing-intolerant native bunchgrasses (10, 68). Other European annual species including ***Poa pratensis*** and ***Bromus inermis*** are common invaders of disturbed

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prairie throughout the Great Plains including Canada (156, 183, 184). In more mesic portions of North America the Asian annual grass *Microstegium vimineum* often forms dense monospecific stands on floodplains and adjacent disturbed and undisturbed mesic slopes throughout 14 eastern states (9).

Unlike the European annual grasses, perennial grass invaders were purposefully introduced as livestock forage or to prevent soil erosion. The Eurasian *Agropyron desertorum* (crested wheat grass) was seeded throughout the sagebrush steppe region because it was more tolerant of grazing than its native congener *A. spicatum* (24, 131). *A. desertorum* has maintained itself and spread into nearby shrublands (75, 124). The South African grasses *Cenchrus ciliarus* (bufflegrass) and *Eragrostis lehmanniana* (Lehmann lovegrass) were also seeded onto arid lands, maintained themselves in seeded sites even after livestock removal (16), and spread into nearby areas even in the absence of grazing (23, 37, 98). *Pennisetum setaceum,* also from Africa, is well established in areas of the Sonoran Desert (90).

Cortaderia jubata (Pampas grass) and *Ehrharta calycina* (Veldt grass) are perennial grasses that are common invaders of coastal habitats in California (138). *C. jubata* (from Argentina) is common in logged coastal forests and maritime chaparral (97, 138) and can invade without obvious human disruption of the habitat, particularly in areas with natural canopy gaps or after fire. *Ehrharta calycina* (from South Africa) invades disturbed and undisturbed coastal habitats in California (138). *Ammophila arenaria* (European beachgrass), also introduced for erosion control, has spread extensively so that it now dominates most beaches and foredunes in northern California, Oregon, and Washington (7, 177).

Central and South America

Alien grasses have invaded both natural and derived savannas (12, 15, 54, 115) in South America. Derived savannas result from forest clearing followed by burning; African grasses were introduced into them because of their tolerance of grazing (115, 144). Invasion of native grasslands by these grasses has been documented in Brazil, Colombia, and Venezuela where *Hyparrhenia rufa* (Jaragua) and *Melinis minutiflora* (Molasses grass) have displaced native pasture grasses such as *Trachypogon plumosus* (11, 36, 54, 113, 115, 144). Ecophysiological studies demonstrate that these grasses tolerate frequent defoliation better than native grasses (144). *Hyparrhenia* has also invaded Central American woodlands and pastures (77, 157). European annual grasses often dominate native grassland in Argentina after range degradation by cattle (39, 53).

Oceania

Alien perennial grasses of African origin are common throughout Oceania. Presently large portions of the Hawaiian islands are dominated by introduced

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grasses, including *Paspalum, Pennisetum, Melinus minutiflora, Hyparrhenia rufa, Cenchrus ciliarus,* and *Digitaria decumbens* (148). Two North American bunchgrass species, *Andropogon virginicus* and *Schizachyrium condensatum* are also common. Most of these grasses were introduced to support livestock; their spread may have been facilitated by the activity of feral goats which were also brought by early European colonists. Today these grasses persist and often spread in the absence of ungulates. Many of these same grasses are present on other islands in the Indo-Pacific region. For example, *Pennisetum polystachyon* dominates some lowland areas in Fiji (109). *Hyparrhenia rufa* and *Pennisetum clandestinum* are common on La Reunion (93), and *Pennisetum purpureum* covers 5000 ha in the Galapagos (89, 140).

In New Zealand, *Cortaderia jubata* along with its congener, *C. selloana*, has invaded thousands of hectares of forest plantations, but invasion appears limited to cut-over forests (57). *Ammophila arenaria* has also spread away from areas where it was planted and now dominates large sections of coastal dunes (79).

Australia

European annual grasses and African bunchgrasses are common alien species in Australia. Annual grasses invade both disturbed and undisturbed habitats and are largely successional (70, 71, 123). Perennial grasses of African origin were introduced as livestock forage. The most common of these, *Cenchrus ciliaris,* dominates many areas and has spread into adjacent native pastureland in northwestern Australia (37, 76). *Pennisetum polystachyon* is invading native savanna regions in northern Australia (59, 152), and two species of *Ehrharta* (African veldt grass) have invaded coastal communities in southwestern Australia (20). Relatively undisturbed shrublands and woodlands in this region are also invaded by the African species, *Ehrharta longiflora, Rhyncoletrum repens* (Natal red top), and *Eragrostis curvula* (weeping lovegrass) (20).

Aquatic grasses have invaded perennial and seasonally moist habitats throughout Australia and Tasmania (76). Reed sweetgrass, *Glyceria maxima,* and para grass, *Brachiaria mutica,* form large floating mats in ponds and other wet areas (76, 104), and the Eurasian saltgrass *Spartina townsendii* has invaded coastal salt marshes (76).

Eurasia and Africa

Much of tropical Asia and Africa is covered by derived grasslands and savannas (defined as once-forested regions in which grasses now dominate as a consequence of human activity) (146). However, relatively few examples exist of large-scale invasions by alien grasses from other continents or other areas within these continents. One example is the invasion of coastal salt marshes in Britain by the North American species *Spartina alterniflora* and the hybrid species *S. anglica* which formed through hybridization between *S.*

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alterniflora and the British native *S. maritima* (154). Other examples include the establishment of several European grasses in Mediterranean-climate regions of South Africa (27, 172), the spread of the South American species *Stipa trichotomea* and *Cortaderia jubata* in southern Africa (130, 179), and the naturalization of African *Panicum maximum* in India (136). Other African grasses are present in Asia, but they are less invasive (17). There are also examples of internal invasions, in which grasses from one region of a continent invade other areas: these include *Cenchrus ciliaris, Pennisetum clandestinum,* and *Eragrostis curvula* within Africa (37, 91).

In contrast to the rarity of grass invasions, several American shrubs and vines are aggressive invaders of Eurasian and African ecosystems (44, 92, 127).

EFFECTS OF GRASS INVASIONS

Framework

Grass invasions can have effects at multiple levels of ecological organization from population to the ecosystem. Table 1 suggests a framework for examining these effects and their interactions. The categories therein are not exclusive; competitive effects operating at the population level can also have ecosystem-level consequences. For example, where light absorption in a grass canopy prevents the establishment of tree seedlings, the interaction is competitive but the resultant ecosystem has the microclimate and flammability of a stable grass-dominated system. Conversely, ecosystem effects such as altered fire regimes will also alter competitive interactions by causing changes in resource availability.

Resource Competition

Where the canopy of an alien grass absorbs or intercepts incident light and thereby limits the establishment or growth of other species, this represents a

Table 1 A classification of possible population and ecosystem-level effects of grass invasions.

Resource competition (exploitation)	Effects on resource supply	Other ecosystem effects
Light absorption		Geomorphological effects
Water uptake	Altered water holding capacity	Microclimate effects
Nutrient uptake	Altered rates of mineralization and immobilization	Disturbance effects (e.g. fire)

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competitive rather than an ecosystem effect. Similarly, a reduction in water or nutrient availability to other species that results from utilization of those resources by grasses constitutes a competitive effect. In contrast, where grasses alter water or nutrient availability by altering boundary-layer humidity or rates of nutrient mineralization, this represents an ecosystem effect.

Grasses have long been recognized as good competitors against herbaceous and woody species (e.g. 22, 33, 84, 88, 141, 159, 161). In numerous studies, the establishment of large seeded and woody perennials has been found to be limited in the presence of dense grasses or grass litter. As a result, the invasion of grasslands by other perennial species often requires soil disturbance such as gopher mounds (41, 52, 63, 66, 120, 162, 163).

Rapidly growing grasses can reduce light at the soil surface and thereby reduce the photosynthetic ability of competitors (153, 155). For example, the grass *Miscanthus sinensis* colonizes abandoned fields in Japan, reducing light availability and daily carbon gain of oak seedlings and thus slowing the rate of encroachment of oak trees into grassland (153). Similarly, alien grasses in Texas reduce growth rates of seedlings of woody species such as *Baccharis neglecta* and *Prosopis glandulosa* by reducing light availability (21, 162).

Grasses are also effective competitors for water and nutrients. Alien grasses can interrupt succession through competition for water with native perennials (40, 42, 43, 49, 64, 101, 141). In California grasslands, European annual grasses are considered one of the major causes of poor oak recruitment (40, 64). Oak seedlings are extremely sensitive to soil water, and alien annual grasses rapidly draw down soil moisture and suppress oak seedling growth more dramatically than do native perennial grasses (40). Growth of seedlings of the native shrub *Baccharis pilularis* in California is also reduced by competition for soil water with European annual grasses (42, 43). The exotic perennial grasses *Agropyron desertorum* and *Dactylis glomerata* suppress pine reestablishment after wildfires in the southwestern United States, and at least part of this effect appears to be due to competition for water (49). Alien grasses have been used to reduce shrub seedling survival in the conversion of chaparral to grassland in the Mediterranean climate region of western North America, and their success has been attributed in large part to their ability to rapidly draw down soil moisture (141).

Efficient use of water is also a means by which alien grasses can outcompete native grasses. Eissenstat (47) and Eissenstat & Caldwell (48) found that the alien grass *Agropyron desertorum* drew down soil moisture more rapidly and to lower levels than its native congener *A. spicatum*. *Agropyron desertorum* has replaced *A. spicatum* in portions of the Great Basin (75) and competes more effectively for water with the dominant native shrub *Artemesia tridentata* than does *A. spicatum* (48). The alien grass *Bromus tectorum* is more abundant in stands of *A. spicatum* than in stands of *A. desertorum,* and this difference

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may occur because *B. tectorum* begins root growth at a time when established *A. desertorum* are rapidly drawing down soil moisture (48).

Alien grasses also have been shown to compete effectively with native species for soil nutrients. Elliott & White (49) observed more rapid disappearance of nitrate from soil in plots planted with an alien grass than in those with native grasses; they hypothesized that competition for nitrogen was one of the factors responsible for poor pine seedling growth in the presence of the aliens. Seedlings of native shrubs have reduced growth and lowered tissue nitrogen when grown in the presence (compared to the absence) of alien grasses after wildfire in a Hawaiian woodland (73). The abundant alien bunchgrass *Agropyron desertorum* is an effective competitor for phosphorus with the native shrub *Artemesia tridentata,* and it is more effective at phosphorus extraction from the soil than its native congener *A. spicatum* (25, 26).

The effective uptake of water and nutrients by grasses is likely the result of their dense shallow root systems (43, 119, 133, 175). The root systems of most woody species are deeper and less dense than those of grasses. Once individuals are large, woody species are generally thought to have access to moisture and nutrients from portions of the soil profile below grass roots (141, 150). Grasses may therefore be most effective as competitors against seedlings rather than saplings or adults of woody species. However, Knoop & Walker (84) demonstrated that grasses can also reduce water availability in the subsoil (30–130 cm) where shrub roots are common.

Replacement of native species and dominance by alien grasses may also result from demographic differences between native and alien species. For example, *Agropyron desertorum* appears to be able to replace *A. spicatum* in sites dominated by the latter in part because of higher seed output, lower seed predation, and the buildup of a large seedbank in *A. desertorum* (124).

Numerous studies have reported negative correlations between alien grass cover and diversity or growth of native species without elucidation of the mechanisms leading to these patterns (14, 16, 23, 33, 74, 110, 183, 184, 187). For example, Bock et al (16) found 10 common native plant species to be significantly reduced in the presence of the African grass, *Eragrostis lehmanniana* in Arizona, and Billings (14) found substantially reduced diversity of native herbs in dense stands of *B. tectorum.*

The elimination of native plant species through competition with alien grasses in turn affects the diversity and persistence of animal populations that rely on grasses for food or habitat (16, 100, 147, 184). For example, the elimination of native dune species by the aggressive alien beachgrass *Ammophila arenaria* has resulted in a dramatic decline in native insect species, including the elimination of several rare species (147). The replacement of native herbs and shrubs in the Sonoran desert by *Eragrostis lehmanniana* has resulted in a local decline in native bird and insect species (16, 100). The

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presence of introduced grasses in disturbed prairie in Canada has caused simplification of habitat structure and a shift in species composition of birds (184).

A major consequence of the competitive success of alien grasses is the slowing or alteration of succession. This interacts with increasing rates of human disturbance to increase the proportion of the Earth's surface that is successional. On a local and regional scale this can result in the loss of both plant and animal diversity and the fragmentation of natural systems which has both genetic and population consequences. Even where alien grasses eventually are replaced by woody species, the competitive success of grass prolongs the period during which successional systems are susceptible to fire, the consequences of which are discussed later.

Rates of Resource Supply

For soil resources, individual species can affect rates of resource supply as well as the amount of resource that is available (Table 1). Nitrogen fixation is an obvious example, but there are also more subtle pathways. For example, the litter of different species can differ in rates of decomposition and nutrient immobilization or release (52). These differences can establish feedbacks that affect both litter quality and the rates at which soil nutrients are released from organic matter into inorganic forms (96, 117).

In one study involving grasses, several native grass species grown in experimental monocultures were shown to produce nutrient-poor litter that led to reduced soil nutrient supply (176). In contrast, two Eurasian grasses, (*Poa pratensis* and *Agropyron repens)*, produced nitrogen-rich litter, and their soil had higher rates of nitrogen transformations (176).

The possibility of allelopathic effects of alien grasses fits uncertainly between competitive and ecosystem effects. To the extent that allelopathy alters nutrient dynamics (i.e. by suppressing nitrifying bacteria, 129) it should be considered an ecosystem effect. A number of common grass invaders (e.g. *Cynodon dactylon, Hyparrhenia* spp., and *Lolium* spp.) may be allelopathic (18, 53, 110, 148, 178), but the strength of these effects and their importance in field situations are uncertain.

Other Ecosystem Effects

Alien grasses can alter ecosystems through a number of pathways that are not obviously related to resource use or supply. Among these are: (i) geomorphological effects, (ii) microclimate effects, and (iii) disturbance effects, in particular fire regimes (which will be considered separately).

GEOMORPHOLOGICAL PROCESSES *Ammophila arenaria* (European beachgrass) alters dune formation patterns where it is planted or has invaded in North America, New Zealand, and Australia. Its ability to bind sand is greater

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than that of native species, and dunes formed by *Ammophila* tend to be steeper and taller than those formed by native species (8, 34, 69, 177). These changes may influence beach size, erosional patterns, and plant and animal diversity (8, 45, 60, 147).

Cynodon dactylon (Bermuda grass) invades stream courses in Arizona and appears to affect community development by increasing substrate stability during floods (46). Sites heavily dominated by *C. dactylon* retained more substrate during floods, including basal fragments of native aquatic macrophytes. Post-flood development of the aquatic macrophyte community proceeded more quickly in these sites than in those lacking *C. dactylon*.

The North American perennial bunchgrass *Andropogon virginicus* alters drainage patterns where it has invaded disturbed montane rainforest in Hawai'i (107). Its phenology, dense litter production, and low transpiration rates relative to forest species result in the accumulation of standing water and the formation of swampy areas. A number of introduced grasses in Australia have the opposite effect, colonizing ponds with water up to 2 m deep and thereby converting open water systems to wet grasslands (76).

MICROCLIMATE EFFECTS Grass invasion could alter microclimate on several scales. Grass litter can affect soil surface temperature and moisture and thereby influence seed germination, seedling growth, and nutrient transformations (52). For example, the buildup of litter of the alien grass *Bromus japonicus* in South Dakota decreases evaporation from the soil surface and favors further germination and establishment of *B. japonicus* (182). Similarly, litter of *Bromus tectorum* enhances seed germination of several alien species in desert shrublands because of improved water availability associated with the litter cover (51), and dense litter accumulations associated with the Eurasian grass *Lolium multiflorum,* reduced native species diversity in an Argentine grassland (53).

On a coarser scale, grass canopies are shallow and aerodynamically smooth in comparison to forest or woodland canopies. Where grass invasion leads to the replacement of woody vegetation by grassland, the pathway of energy partitioning leads to higher canopy and surface temperatures and lower relative humidities in grass-dominated systems (87, 143). These changes favor the growth of species with the C_4 photosynthetic pathway (mainly grasses), and also favor fire (160).

GRASS INVASION AND FIRE REGIMES

General

The most significant effects of alien grasses on ecosystems result from interactions between grass invasion and fire. A number of features make

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grasses and grass-dominated systems both relatively flammable and able to recover relatively rapidly following fire, in comparison to forests. First, the grass life form supports standing dead material that burns readily. Second, grass tissues have large surface/volume ratios and can dry out quickly. The flammability of biological materials is determined primarily by their surface/volume ratio and moisture content and secondarily by mineral content and tissue chemistry (132, 165, 174). The finest size classes of material (mainly grasses) ignite and spread fires under a broader range of conditions than do woody fuels or even surface leaf litter (80). Third, the grass life form allows rapid recovery following fire: there is little above-ground structural tissue, and so almost all new tissue fixes carbon and contributes to growth. Finally, grass canopies support a microclimate in which surface temperatures are hotter, vapor pressure deficits are larger, and the drying of tissues more rapid than in forests or woodlands. Thus, conditions that favor fire are much more frequent in grasslands. It is therefore reasonable to consider grasslands and fire as an "identity" (173) or to discuss the "pyrophytic grass life form" (108, 109). Indeed, human suppression of fire in natural grasslands is a disruption with major biological consequences.

Invasion can set in motion a grass/fire cycle where an alien grass colonizes an area and provides the fine fuel necessary for the initiation and propagation of fire. Fires then increase in frequency, area, and perhaps intensity. Following these grass-fueled fires, alien grasses recover more rapidly than native species and cause a further increase in susceptibility to fire. In fact land managers have seeded alien grasses for the purpose of increasing fire frequency and intensity in order to suppress woody species (141, 189).

Alteration of fire regimes clearly represents an ecosystem-level change caused by invasion. Fires themselves alter nutrient budgets profoundly; they volatilize some elements (notably carbon and nitrogen) while converting others into biologically more available, mobile forms for at least a short time (125). The selective loss of nitrogen in particular drives ecosystems toward nitrogen limitation (142, 169). Nutrient losses to streamwater, groundwater, and the atmosphere are also enhanced following fire (1, 137), and these can have significant effects on the chemistry of the atmosphere regionally and globally (38, 81).

Field Studies

A number of examples of effects of alien grasses on fire regimes have been described. These include:

HAWAI'I Several alien grasses have been implicated in increasing fire frequency and/or intensity in Hawai'i (148, 149). The best documented case involves invasion of the C_4 perennial grasses *Schizachyrium condensatum* and *Melinis minutiflora* in areas of seasonal submontane woodland in Hawaii

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Volcanoes National Park (74, 149). Invasion by *S. condensatum* took place in the late 1960s, and prior to that time grass cover in these woodlands was sparse. Areas that have never burned now support 80% cover of alien grasses, mainly *Schizachyrium*. The grass thoroughly fills the interstices of the native shrubs and grows into their canopies, providing continuous layers of fine fuel. Prior to the invasion, 27 fires burned an average of 4 ha/fire in 48 years, but in the 20 years following invasion, 58 fires have burned an average of 205 ha/fire (149).

In Hawaii, a single grass-fueled fire can kill most native trees and shrubs. *S. condensatum* recovers rapidly, however, and the alien grass *Melinis minutiflora* also invades the burned area (74). Grass cover and fuel loading in the resultant community are greater than before fire. *Melinis* is highly resinous and more flammable than *Schizachyrium;* its green leaves burn vigorously and can burn in 95% relative humidity (111). Subsequent fires are more likely, and when they occur they cause further increases in *Melinis* cover. Overall, grass invasion sets in motion a positive feedback cycle that leads from a nonflammable, mostly native-dominated woodland to a highly flammable, low-diversity, alien-dominated grassland. Most of the dominant native species and at least one candidate endangered plant species are eliminated by this fire cycle (74).

Similar processes have been observed elsewhere in Hawai'i. In dry lowland areas and other seasonal submontane sites, the alien grasses *Andropogon virginicus, Hyparrhenia rufa, Pennisetum setaceum,* and *Cenchrus ciliaris* are abundant, enhance fire, and grow rapidly in response to it. In subalpine areas, the C_3 alien grasses *Holcus lanatus* and *Anthoxanthum odoratum* both add fuel and respond more rapidly to fire than do native species (149).

WESTERN NORTH AMERICA The best documented example of ecosystem effects of alien grasses in North America is a *Bromus tectorum* invasion into the intermountain west. Historical evidence suggests that much of this region was dominated by perennial grasses when Europeans arrived and that fires were not common (82, 94, 95, 181). *Bromus tectorum* invaded the region as the habitat was degraded by livestock (14, 94, 180, 187). It is a highly flammable winter annual that dies and dries out in the spring, and spreads fires rapidly. Grass-fueled summer fires can sweep through *B. tectorum*-colonized shrubland, killing or damaging shrubs and perennial grasses (82, 151). *B. tectorum* recovers rapidly following fire and can suppress the growth of native species (101).

On a regional level, *B. tectorum* increases both the size and number of fires. Whisenant (181) estimates that the fire return interval in Idaho shrublands before *B. tectorum* invasion was 60–110 years. Since invasion, sites burn every 3–5 years. Earlier, sites in eastern Oregon dominated by *B. tectorum* were

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considered 500 times more likely to burn than those under other cover (121, 151). The net effect of *B. tectorum* invasion is thus a positive feedback from initial colonization in the interstices of shrubs, followed by fire, to dominance by *B. tectorum* and more frequent fire (151, 181).

More recently, *B. tectorum* has been spreading to higher elevation sites, with a consequent increase in grass-fueled fires and a reduction in area of some pinyon-juniper woodlands (14). In other sites, the increase in fires has led to increased flooding and erosion (82). Overall, invasion by *B. tectorum* and the attendant fires affect at least 40 million hectares, making this perhaps the most significant plant invasion in North America (181). Presently, fire resistant plants are being seeded in portions of the Great Basin in an attempt to interrupt this fire cycle (118).

Several other alien grasses appear to alter fire regimes in North America. *Tainiatherum asperum* is colonizing portions of *B. tectorum*'s range (186); it increases under frequent fire at the expense of *B. tectorum* and also appears to be fire-enhancing (102, 188). Zedler et al (189) demonstrated that seeding burned California chaparral with the alien annual *Lolium perenne* as an erosion control measure fueled a second fire in an area that had burned less than 1 year previously. Nadkarni & Odion (110) observed a similar result and found that only the seeded portion of the original tract of burned shrubland was consumed in a second blaze two years after the original fire. Normal fire intervals in chaparral are considerably longer (19, 67). Schmid & Rogers (139) report increased fire frequencies in the Sonoran desert over the last 30 years and attribute at least some of this increase to the accumulation of fuels by exotic grasses.

TROPICAL AMERICA Central and particularly South America supported extensive savannas when Europeans arrived, but the dominant native grasses were unable to support intensive ungulate grazing. A number of C_4 African grasses, most importantly, *Hyparrhenia rufa, Melinis minutiflora, Panicum maximum,* and *Brachiaria* spp., were brought in to support grazing in savanna regions and in cleared forests (115). All four of these grasses burn readily and resprout rapidly following fire; the consequent grass-fire interaction is thereby capable of maintaining cleared forest land as a derived savanna or grassland (15, 99), preventing succession back to forest. In addition, *H. rufa* and *M. minutiflora* are able to invade otherwise intact native-dominated savanna ecosystems (11).

In Central America, *Hyparrhenia* has received the most attention from ecologists, since when it is not heavily grazed it forms tall, dense stands that burn readily and intensely (77, 85, 122). In contrast, fires in comparable sites dominated by native grasses are patchy and less intense (85). *H. rufa*-fueled fires can burn into successional and even intact tropical dry forest and

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represent a serious threat to preservation of this ecosystem in Guanacaste National Park in Costa Rica and elsewhere (78). Bilbao & Medina (13) and Coutinho (35) reported, surprisingly, that long-term fire suppression leads to colonization by *H. rufa* and *M. minutiflora* in some Brazilian and Venezuelan savannas. The difference is due to the very low soil fertility of the natural savannas; these alien grasses require more nutrients than native *Trachypogon* species (11), and fire suppression over time leads to increased nutrient availability (99). Cleared forest sites support much greater nutrient availability (13).

Nepstad et al (113) describe more complex interactions between alien grasses and fire near Paragominas, Brazil. Pastures there are cleared from forest, burned, and planted to the alien grass *Panicum maximum*. As the initial pulse of soil fertility declines, other species including *H. rufa* colonize the pastures. Grass/fire interactions can lead to arrested succession at this stage, or succession can proceed to a depauperate forest.

AUSTRALIA Several alien grasses have been identified as participating in a positive feedback with fire in Australia. The most significant of these is *Cenchrus ciliaris,* which produces 2–3 times as much flammable material as native grasses in central Australian watercourses (86). Colonization by *C. ciliaris* alters these watercourses from their historical role as a barrier to fire to one of being a "wick" for fire (76). Fire frequency in the region has increased as a consequence (86).

In northern Australia, the African perennial grass *Pennisetum polystachyon* maintains more litter and carries more intense fires than the native annual *Sorghum intrans,* which it is replacing in portions of Kakadu National Park (59, 152). There is concern that this invasion will allow fires to penetrate into and thereby alter areas of hitherto nonflammable monsoon vine forests (92).

The now familiar *Melinis minutiflora* also invades disturbed areas within the moist tropical zone near Cairns, Australia. In this region, cyclones frequently destroy intact native forest, thereby producing enough fuel to carry fires. Native grasses colonize the burned sites but now are being replaced by *Melinis*. The flammability and large litter mass of *Melinis* supports a grass/fire cycle that arrests succession at the grass stage (152). In southwestern Australia, *Ehrharta calycina* invasion initiates a grass-fire positive feedback cycle (6, 29, 30).

OTHER AREAS We did not locate any clear examples of alien grass/fire cycles in Eurasia or Africa, with the exception of the Mediterranean climate region of South Africa (27). These continents have supported human populations and anthropogenic fires for much longer than others, and they contain

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extensive, frequently burned areas dominated by native grasses. Many of these areas result from human clearing of forested areas (i.e. the extensive, economically destructive *Imperata* grasslands of Asia), and they are maintained by a positive feedback between grasses and fire.

The long history of human presence in Africa and Asia probably has had substantial effects on the grasses themselves. African grasses in particular have evolved with hominids for millions of years. They have also evolved with intense ungulate grazing and show adaptations to grazing that also confer adaptation to fire. These include perennating organs near or below the ground and a rapid growth response to defoliation (31, 72). It is therefore not surprising that Africa and to a lesser extent Asia are donors rather than recipients of fire-adapted alien grasses. Interestingly, the New World vine *Chromolaena odorata* was introduced to Asia and Africa specifically to interrupt the native grass/fire cycle and has become an aggressive invader on both continents (44, 50, 136).

LAND USE CHANGE, INVASION, AND FIRE: ARE THERE GLOBAL CONSEQUENCES?

Globally, the effects of alien grasses on fire and ecosystems must be viewed within the context of human-caused land use change (103), which has increased the importance of both fire and grasses world-wide (109). Humans often clear wooded lands in order to create grassland for domestic animals; fire is used as a tool in land clearing and the maintenance of cleared areas. Even where human land use merely involves selective logging, it increases both the amount and the flammability of combustible material on sites (62, 160), thereby greatly increasing the probability of fire and further land conversion (Figure 1). By increasing fire and grasses separately, both are increased synergistically through the grass-fire positive feedback cycle.

Land use change in the Americas, Australia, and Oceania is increasing fire and grazing to historically unprecedented levels and thereby selecting for grasses (many of them African and Eurasian) that are able to tolerate fire and grazing. In some cases (i.e. Hawai'i), grass invasion alone is sufficient to initiate grass/fire cycles that convert woodland to grassland (Figure 1). In a greater number of cases, the aliens increase the amount of biomass consumed during fire and/or the length of time flammable grassland persists before woody plant encroachment. The availability of alien grasses can even contribute significantly to human decisions to initiate land use change. For example, intensive cattle grazing could not be supported without African grasses in many areas of tropical America (115, 116).

Overall, there is abundant evidence that grass invasions and the grass-fire cycle arrest or alter succession in many regions, leading to substantial changes

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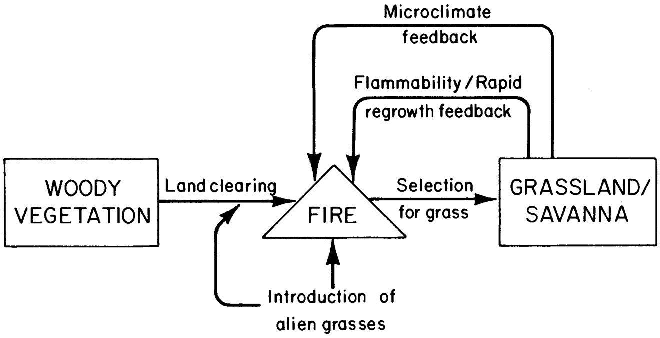

Figure 1 Conceptual diagram of land clearing and the grass-fire cycle (modified from Fosberg et al {54}), to illustrate the influence of alien grass invasion. In some cases grass invasion itself is sufficient to initiate grass-fire positive feedbacks: more often, it interacts with human-caused land use change.

in regional population, species, and landscape diversity in the Americas, Australia, and Oceania. These changes represent a significant challenge to conservation biology. How important are alien grass invasions as agents of regional and global functional change? Several of the studies reviewed here demonstrate that their effects on local ecosystem function can be profound. Is the overall effect of many local changes in ecosystem function sufficient to affect climate, water quality, or the composition of the atmosphere regionally or globally? We cannot answer that question unequivocally, but there are several plausible ways that grass invasions could have or could come to have regional or global consequences.

Two possible regional effects are alterations to climate caused by conversion of forest to grassland, and alterations to the oxidant chemistry of the atmosphere caused by fires. Using a simulation model of regional climate, Lean & Warrilow (87) and Shukla et al (143) suggested that complete conversion of the Amazon Basin forest to grassland would alter regional climate by increasing temperature and decreasing humidity and precipitation. These changes would also increase fire frequency and favor the persistence of grasses with the C_4 photosynthetic pathway. The simulations they created represent an extreme case, but partial conversion would still have significant climatic effects. To the extent that African grasses are essential to the initiation or maintenance of Amazonian forest clearing, grass invasion would contribute to any regional change. Similar regional climatic changes would not necessarily be expected elsewhere in the Americas, because much more of the precipitation is recycled through the biota within the Amazon basin than elsewhere (134).

Recent measurements have demonstrated that biomass burning has significant regional effects on the chemistry of the atmosphere and of precipitation

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during the dry season in west Africa and South America (3, 4, 55). Ozone levels in particular approach those in eastern North America and northern Europe, where significant effects on regional vegetation and agricultural yields have been demonstrated (128). Grass invasions contribute to regional atmospheric change in tropical America to the extent that burning reflects grasslands dominated by African grasses or forests being cleared to plant African grasses.

On a global level, grass invasions could contribute to functional change if alien grass-fueled fires added significantly to the increasing concentrations of radiatively active (greenhouse) or stratospheric ozone destroying gases in the atmosphere. Andreae (2) estimated that biomass fires globally contribute 6–8% of the total sources of the relatively stable gases methane, nitrous oxide, and carbonyl sulfide. The proportional contribution of the human-caused increase in fires to the human-caused increase in gas concentrations may be somewhat greater, but it probably does not exceed 15% for any of these gases. (We do not discuss CO_2 here because grass regrowth following fire is so rapid that grassland or savanna fires, unlike land clearing fires, do not represent a significant net source of CO_2).

Andreae (2) estimates that tropical forests, savannas, and grasslands now account for about 40% of the biomass burned globally; about half of that is now in Africa and so does not involve alien grasses. If half of the remainder involves alien grasses (probably an overestimate), then their overall contribution to increased gas concentrations could be .15 (maximum proportion of the increase in concentrations of stable gases that result from fire) × .4 (proportion of global biomass combustion that occurs in tropical forests, savannas, and pastures) × .25 (proportion of tropical biomass combustion that involves aliens) or approximately 1.5% of the total increase. It therefore appears likely that while human-altered grass/fire cycles may be a significant source of gases that drive climate change, the contribution of alien grasses to the total is relatively small.

CONCLUSIONS

The effects of alien grasses on ecosystem function (fire, nutrient loss, altered local microclimate, prevention of succession) are significant on the local scale and are becoming increasingly important on regional and global scales. Moreover, the interaction of competition with alien grasses, fire, and the prevention of succession now represents a substantial global threat to biological diversity on the genetic, population, and species levels. However, the number of cases in which ecosystem effects of grass invasions have been intensively studied (as opposed to described or speculated about) is small. A thorough understanding of additional cases, leading to a better overall

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understanding of the process, would be useful to the development of basic ecological principles as well as to the management of these invasions.

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