Invasive grasses and forbs have invaded this fuel break in the Santa Ynez Mountains above Santa Barbara. Photograph by C. D'Antonio.

INVASIVE SPECIES AND FIRE IN CALIFORNIA ECOSYSTEMS

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Invasive plant species occur throughout all floristic regions of California, but their spatial extent, diversity, and impacts within these regions vary considerably. Alterations of natural disturbance regimes have made communities more susceptible to these invasions (Brooks et al. 2004). Fire is a natural and chronic disturbance in many California plant communities and has been observed to promote and be promoted by invasive species in several of the communities.

Fire regimes—the type, frequency, intensity and timing of fire—have played an important role in the evolution of California plant communities, but human influences have changed fire regimes, sometimes in ways that shift the relative dominance of native and non-native species. Invasive plants may be directly responsible for changes in fire regimes through increased biomass, changes in the distribution of flammable biomass, increased flammability, and altered timing of fuel drying, while others may be "fire followers" whose abundances increase as a result of shortening of fire return intervals.

California's shrublands, woodlands, grasslands, wetlands, and forests occupy different elevation and moisture zones, creating unique fire regimes that have benefitted particular invasive species. Plant associations that differ in physiognomy, fire regimes, and fuel types may vary in their resistance and resilience to fire. Fire regimes have been best studied in conifer forests and shrublands, but are poorly understood in California's grasslands. The role of fire in riparian or other wetland systems is particularly poorly known, presumably because these habitats have long been considered barriers to fire due to the high moisture content of soil and vegetation.

Most evidence indicates that the strongest impacts of invasive plants on fire regimes in California occur in coastal sage scrub, deserts, and riparian areas. The subject of how fire regimes are being changed in these systems will be addressed later on. In general, one of the least reversible and most significant impacts on native species occurs when introduced plant species alter the frequency of fire. In the intermountain west, cheatgrass (*Bromus tectorum*) has affected more areas than any other invasive plant. Plant ecologists observed in the mid-1900s that invasion by cheatgrass increased fire frequencies by creating continuous standing fuel between shrubs in these lightning-prone habitats. This, in turn, has led to a decline in native species and increased invasion by cheatgrass, setting in motion a cycle that is difficult to break.

For example, work by Steve Whisenant, now at Texas A&M University, quantified alterations in fire frequency and the dramatic loss of native species in Idaho's Snake River Plains as a result of lightning-caused summer fires fueled by dead cheatgrass. Could this happen in California? Red brome (*Bromus madritensis* ssp. *rubens*) and other invasive annual grasses increase fire frequencies in the western Mojave Desert in California, and cheatgrass has been part of the fuel in sagebrush fires in the Owens Valley. But so far, few sites have burned multiple times and it is not yet clear if a grass/fire cycle as has developed in the central Great Basin will develop in the California deserts.

The California Invasive Plant Council plant inventory lists 104 species that have the potential to alter fire dynamics or whose abundance is increased following fire. However, for many of these species, there is little published evidence to corroborate these accounts. Some of these species most likely influ-

Purple veldtgrass (*Ehrharta calycina*) in burned coastal sage scrub site at Vandenberg Air Force Base, approximately 15 years after fire. Fire is a natural disturbance in these ecosystems, but *Ehrharta* regenerates very rapidly after fire and appears to suppress the recovery of native species. Photograph by C. D'Antonio.

Abundant invasive, nonnative annual grasses growing between and within a stand of native species at a recently burned chaparral site in Ronald W. Caspers Wilderness Park, Orange County. Photograph by C. D'Antonio.

ence some aspect of fire regimes, but many may not. Here, we focus on the invasive plants that are well known for their interaction with fire, and provide case histories of invasion by the most problematic of these plants in the major upland and wetland ecosystems of California. We primarily address those invasive species that appear to alter fire regimes, rather than focusing on the many more non-native species that appear to opportunistically benefit from the presence of fire in our landscapes.

SHRUBLANDS

When one thinks of fire in California, one immediately thinks of the massive conflagrations that occur in central and southern California chaparral and sage-scrub ecosystems, particularly because of their close proximity to dense population centers. These closed-canopy shrublands—particularly intact chaparral—are in fact relatively resistant to invasion by non-native species. However, non-native plants are increasingly closely tied to fire dynamics and to ecosystem responses to fire in some regions.

Under natural conditions, chaparral communities retain most fuels in the canopy layer and have relatively long fire intervals (greater than 20 years). Contrary to common perception, foliar tissue does not easily ignite except under super-heated conditions or when leaf tissue moisture is low. However, several weedy forbs and grasses tend to thrive at the disturbed edges of these shrublands along roads, power lines, and fuel breaks where shrubs are removed. The invasive, annual grasses that often colonize these areas dry out much earlier in the spring than the native shrubs, and with their high surface area to volume ratio, are more prone to ignition than the native vegetation. Mediterranean grasses such as *Bromus* species and slender oats (*Avena barbata*) are particularly implicated since they act as wicks, spreading fast-moving fire into the canopies of larger shrub vegetation.

Monotypic giant reed stand (*Arundo donax*) in the Santa Clara River, Ventura County. A human-initiated fire burned through several kilometers of the riparian zone, fueled primarily by giant reed. The dead trees remaining are cottonwoods and willows. Photograph by A. Lambert.

Human activity also tends to be focused on these edges, making ignition far more likely to occur. (Lightning is uncommon in these systems and is rarely implicated in ignitions except at high elevations.) Jon Keeley and others have noted that the frequency of ignition has dramatically increased as a consequence of human activity, and the presence of these weedy plants exacerbates this interaction. In essence, the widespread presence of annual grasses—both because of their earlier seasonal drying compared to shrubs and their high surface area to volume ratio—has enhanced the volume of readily ignitable fuel and increased the seasonal duration when fuels are readily susceptible to ignition.

At historic fire frequencies, shrublands are generally resilient to fire. Chaparral species are well-known to regenerate from both resprouting of perennial root crowns and germination of seeds in the soil when heated and/or exposed to smoke. But increasing fire frequencies in these systems, especially near urban centers, has led to a loss in native species that rely on seed regeneration due to insufficient recovery time between fires for shrubs to reach reproductive age. For example, researcher Anna Jacobsen, who studied repeated short-interval fire in the Santa Monica Mountains, has found that return intervals of less than 12 years cause substantial reductions in shrub densities, including loss of obligate seeding shrubs and a decline in some of the resprouter species. The eventual result is a habitat that contains an open mosaic of exotic annual grasses and a few resprouting shrubs. Thus, increased fire frequency results in a conversion of native shrublands to a more open, grass-invaded system with scattered woody plants. The application of prescribed fire for "brush removal" in wildlands similarly contributes to counterproductive vegetation type conversion.

Shrublands along California's

Tamarisk resprouting following a fire at the Cibola National Wildlife along the lower Colorado River. Photograph by A. Lambert.

foggy central coast are also affected by an increase in the abundance of the fire-responsive African perennial veldtgrass (*Ehrharta calycina*). This species was introduced at least 40 years ago for erosion control in sandy soils. It produces relatively continuous fuel that promotes the spread of fire through coastal chaparral and sage scrub, but it also responds rapidly to fire. This species also promotes fire and it increases in density following fire in similar Mediterranean climate areas of Southwest Australia. The result in California is that many habitats which burned either in accidental or prescribed fires are becoming heavily dominated by low diversity stands of veldtgrass. This conversion is most apparent on Vandenberg Air Force base where *Ehrharta* was widely planted in the 1900s and has spread widely. Such coastal chaparral and shrublands on unique marine terrace soils (in this case, sands) are well known for their high endemism (being unique to a particular geographic region). So an increase in fire occurrence and an increase in the growth of highly competitive grasses after fire could lead to the decline of endemic species.

DESERTS

Invasive grasses have played an even more fundamental role in altering fire dynamics and causing native plant declines in desert ecosystems. In general, deserts are among the least invaded ecosystems in North America, in terms of the number of non-native species that have become established and the proportion of the flora they represent (Rejmanek and Richardson 1994). Roughly 5% of the flora is comprised of exotic species, presumably owing to physiological stresses caused by the harsh climate and moisture conditions. However, a few ecosystem-changing grass species are increasing the frequency of fires in California deserts. The exact species differ in each desert, but all threaten the future sustainability of these fragile ecosystems.

In the Great Basin systems east of the Sierra Nevada, cheatgrass (*Bromus tectorum*) is the primary species of concern, thriving where soil disturbance from historic livestock grazing has promoted its establishment in the interspaces between shrubs like sagebrush (*Artemisia tridentata*), bitter brush (*Purshia tridentata*), and rabbit brush (*Chrysothamnus spp.*). Lightning strikes often ignite fires in the region, but whereas historically these would have burned short distances and then died out because of the discontinuous fuels, cheatgrass now provides a continuous fuelbed between senescent (end of aging process when plant tissues become dormant, dry, or are dropped) sagebrush, resulting in very large fires.

In the Mojave Desert, the same impact is caused by low-growing Mediterranean grasses (*Schismus barbatus* and *S. arabicus*), as well as by red brome. All are annual grasses that fill in the space between shrubs. In the Sonora/Colorado Desert, senesced red brome is implicated in supporting fast moving surface fires and shortening fire intervals (Rogers and Steele 1980, Phillips 1992). Many desert plant species are not adapted to fire, so are gradually being replaced by monotypic stands of annual grasses. Large-scale type conversion of endemic desert plant communities is more prevalent in Arizona and Nevada to-date, but recent fires in the Owens Valley and areas of the Mojave show that our desert ecosystems are not immune to such irreversible impacts.

Sahara mustard (*Brassica tournefortii*) is a short-lived forb that poses a serious threat to desert ecosystems. While it has not yet caused serious fire events in sand-dominated sections of the Mojave, this large, multi-branched plant is forming nearly continuous stands and is already crowding out annual wildflowers. It will almost certainly become fuel for destructive wildfire in the future.

GRASSLANDS

California's grasslands have a history of human management that has impeded accurate documentation of fire cycles. Early human inhabitants used fire to reduce woody plant cover and maintain grassland habitats for hunting, and to promote growth of particular species. After Euro-American colonization, grasslands were maintained by intensive livestock grazing, and fire was used to convert shrublands to grasslands. Today fire frequencies are low in these ecosystems, likely lower than prior to European settlement.

California grasslands are dominated by European annual grasses, even in regions that have not burned for decades. Prescribed fire has been used as a tool in some invaded grasslands to try to manage against non-native grasses, but results have been mixed as demonstrated in a meta-analysis conducted by D'Antonio and Bainbridge (Corbin et al. 2004). While it appears that a single fire can reduce non-native grasses, this effect is short-lived, and only recurrent fire or fire combined with grazing can keep down non-native grasses. At the same time, some non-native forbs such as species in the genus *Erodium* and black mustard (*Brassica nigra*) are promoted by fire. Thus, the use of fire in grasslands to enhance native species must be carefully done, and consideration of what non-native species are in the local seedbank is a key element. But overall, fire is not considered a key factor in the maintenance of invasive plant dominance, nor an appropriate management tool for eliminating non-native species in most California grasslands.

FORESTS

In California, there is a general pattern of decreasing numbers of non-native plant species with increasing elevation (Keeley et al. 2011). Fuel management practices in coniferous forest ecosystems have generally decreased fire frequency, but at the same time have increased the severity of wildfires compared with other fire-prone systems. Woody fuel accumulation (of native species), livestock grazing, and logging—which creates even-aged stands replete with ladder fuels—have altered fire regimes from historical low- or mixed-severity understory fires to larger, more intense crown fires. These high-intensity fires create crown gaps and appear to occur more frequently than in the past. Montane coniferous forests in California generally have a lower diversity of invasive species and a different composition of invasive species than lower elevation woodlands and grasslands. Many of the invasive species problems in forest ecosystems have been attributed to management practices that reduce fire frequency.

Cheatgrass (*Bromus tectorum*) appears to be one invasive plant that is an increasingly common invader of some of the drier coniferous forest ecosystems in California such as Ponderosa pine woodlands. Keeley has documented its occurrence in the understory of Ponderosa-dominated sites where it becomes abundant after fire. However, it is not clear that cheatgrass has any long-term impact on these ecosystems. Abundant cheatgrass growth during the early years after fire when tree seedlings are small could result in an increased probability of fire occurrence, to the detriment of the young woody plants, but data to support this is lacking.

RIPARIAN SYSTEMS

Riparian ecosystems encompass a wide variety of habitats, from small springs and vernal pools to large rivers, coastal marshlands, and natural and man-made lakes, and support much of the biodiversity found in California. Riparian vegetation is defined by plants with regular access to groundwater or soil moisture, so typically, riparian plants have higher foliar moisture than upland plants. Higher moisture content imparts greater resistance to and reduced damage from fire, so riparian areas are often considered to be functional barriers to the spread of wildfire (Pettit and Naiman 2007). However, several invasive plants in California riparian systems are changing these dynamics. For example, giant reed (*Arundo donax*) and tamarisk (*Tamarix* spp.) are well known to be highly flammable, yet both species recover rapidly from fire by regrowth from below-ground plant parts. By contrast, cottonwoods, willows, and other native woody plants are much less tolerant of direct exposure to fire. Recent studies suggest that the invasive plants mentioned above are making riparian systems fire-prone.

Giant reed is a large, bamboo-like grass from southern Eurasia that is altering the diversity and function of riparian corridors throughout coastal California. In Southern

TABLE 1. NON-NATIVE, INVASIVE PLANTS POTENTIALLY ASSOCIATED WITH CHANGE IN FIRE REGIME OR FUEL CONDITIONS IN CALIFORNIA

Common Name	Scientific Name	Habitat*	Habitats of Concern and Comments
ANNUAL GRASSES			
barbed goatgrass	*Aegilops triuncialis*	G, C, W	Spreading into serpentine grasslands where it could promote fire in otherwise sparse vegetation
wild oats	*Avena fatua, A. barbata*	G	Ignition on trails, roads, disturbance corridors
ripgut brome	*Bromus diandrus*	G, C, W	Widespread and abundant, particularly in nitrogen-rich soils
red brome	*Bromus madritensis* ssp. *rubens*	G, D	Desert and desert washes in Mojave
cheat grass, downy brome	*Bromus tectorum*	D	Primarily high desert, but also in parts of lower Mojave and Sierra Nevada
foxtail barley	*Hordeum murinum* ssp. *leporinum*	G	Widespread, could change fuel continuity in some sites
Mediterranean grass	*Schismus arabicus, S. barbatus*	D	Produces continuous fine fuels in arid shrublands, esp. Mojave desert
medusahead	*Taeniatherum caput-medusae*	G, D	Common in grasslands of North Coast ranges and north Central Valley, spreading into high desert
PERENNIAL GRASSES			
beach grass	*Ammophila arenaria, A. breviligulata*	[1]	Creates dense fine fuels in coastal dunes, where fire typically would not burn
giant reed	*Arundo donax*	R	Low gradient floodplains; drought tolerant, highly fire-promoting
jubata grass, pampas grass	*Cortaderia jubata, C. selloana*	G, C	Primarily coastal habitats; could influence fuel continuity
veldt grass	*Ehrharta calycina*	G	Sandy soils, especially dune shrublands on central coast
smilo grass	*Piptatherum miliaceum*	G, C, W, R	Expanding range; can invade into disturbed chaparral. Future significance unclear, but could change chaparral fire regime.
ravenna grass	*Saccharum ravennae*	D, R	Emerging concern in North Coast riparian scrub; considered fire hazard in Arizona
fountain grass	*Pennisetum setaceum*	G, C	Roadsides, also coastal dunes. Some horticultural cultivars sterile. Highly invasive and fire promoting in Hawaii.
FORBS			
fivehook bassia, forage kochia	*Bassia hyssopifolia, B. scoparia (formerly Kochia)*	D, R	Alkaline habitats and disturbed areas where it forms continuous stands
black mustard	*Brassica nigra*	G, C, R	Widespread in disturbed sites and coastal shrublands; high standing biomass. Flammability poorly known.

Sahara mustard	*Brassica tournefortii*	D	Favors sandy substrates and dunes
thistles	*Carduus spp., Cirsium* spp., *Cynara cardunculus, Silybum marianum*	G, C, W, R	Could be ladder fuels in open woodlands; disturbed soils
yellow starthistle	*Centaurea solstitialis*	G, R	Large stands provide continuous fuel, but flammability poorly known
tumble or tansy mustard	*Descurainia sophia*	D, R	Impacts appear to be minor, but locally more invasive in northeast CA
perennial pepperweed, tall whitetop	*Lepidium latifolium*	R	Dense stands of standing biomass in wetland margins; range expanding
Russian thistle	*Salsola tragus*	D, R	Forms dense stands in disturbed alkaline sites; tumbleweeds can accumulate along fence lines and structures, causing a build-up of fuels
SHRUBS			
Scotch broom	*Cytisus scoparius*	C	Coastal scrub, oak woodland, perennial grasslands; could enhance fuel accumulation
French broom	*Genista monspessulana*	C, R	Coastal scrub, oak woodlands, grasslands, particularly in understory, creating additional dry biomass
Spanish broom	*Spartium junceum*	C, R	Coastal scrub, grasslands, wetlands, oak woodland, forests; mostly found in open canopy
gorse	*Ulex europaeus*	G, C	Coastal bluffs and grasslands; may not be highly flammable but adds substantial biomass to grasslands
TREES			
tree-of-heaven	*Ailanthus altissima*	C, W, R	Fire tolerant, litter burns
Tasmanian blue gum	*Eucalyptus globulus*	W, R	Coastal habitats; spreads from plantations and can enhance fire intensity; source of firebrands near urban areas
Peruvian peppertree	*Schinus molle*	C	Southern CA coastal hillsides; promoted by fire
athel	*Tamarix aphylla*	D, R	Limited distribution; evergreen species; lower fire risk than deciduous congeners
tamarisk, saltcedar	*Tamarix ramosissima, T. chinensis, T. parviflora,* etc.	D, R	Major fire hazard throughout western states; replaces less flammable riparian vegetation
fan palms	*Washingtonia robusta, W. filifera*	R	Native to isolated desert springs; spreads from ornamental plantings; source of firebrands near urban areas
VINE			
cape ivy	*Delairea odorata*	R	Coastal, both riparian and fog-affected chaparral; hanging dry biomass could be fuel, esp. when killed back by frost

The plants listed above have known impacts or greatest potential to influence fire regimes, or to become fire hazards as their populations increase. Other invasive plants with little or no available fire-related information were not included.
*G = grassland, C = chaparral, W = woodlands, D = desert, R = riparian
[1] Occurs only in coastal beach dunes

California, giant reed has fueled fires around urban areas and facilitated fire spread to natural areas, and is alleged to reduce the ability of river courses to act as natural barriers to fire. Coffman and her collaborators at UCLA examined the regrowth rates of giant reed and nearby native woody vegetation following a 300-hectare fire in the Santa Clara River (Ventura and Los Angeles Counties) in 2005. Giant reed grew three to four times faster following fire, and within one year its density was 20 times greater than native species. This suggests that rapid regrowth of the highly flammable biomass creates an invasive plant-fire cycle that ultimately leads to a decline in native species in these ecosystems.

In more arid regions, tamarisk or saltcedar (*Tamarix* spp.) is considered to be one of the most destructive invaders of the southwestern U.S. This shrubby tree was introduced from Eurasia in the 1800s for erosion control, windbreaks, and other horticultural uses. It now dominates desert riparian corridors such as the lower Colorado River and parts of the Owens River where water and land management have degraded conditions for native cottonwood, willow, and/or mesquite vegetation. Tamarisk has also displaced some native riparian woodlands in relatively healthy watersheds such as Coyote Creek in Anza-Borrego State Park. The relatively long intervals between flood events allow tamarisk seedlings to reach maturity, and subsequently to inhibit establishment of native plants.

In these locations, wildfires have become frequent. For example, on the Colorado River bordering California and Arizona, Bureau of Reclamation researcher David Busch has shown that over a third (approximately 37%) of riparian vegetation burned during a 12-year period. Such fires occur in the fall/winter period when the deciduous plants drop foliage which builds up into a flammable litter layer. They also occur during the growing season when tamarisk is also susceptible to ignition and may burn with greater intensity owing to volatile compounds in live, green foliage. In a cooperative study of tamarisk-fueled fires by the University of California and the U.S. Geological Survey, Gail Drus found that across the desert regions there is a correlation between the relative abundance of tamarisk and extent of native plant mortality. In other words, as tamarisk becomes more abundant, there is a greater loss of native vegetation during fire and acceleration toward eventual monocultures of this widespread invader. Interestingly, the introduction of the tamarisk leaf beetle (*Diorhabda* spp.) for biological control of tamarisk may protect native plants because, even in the absence of tamarisk mortality, by reducing tamarisk canopy density, the threat of fire to native plants is reduced (Brooks et al. 2008).

Comparatively little is known about most invasive plants in California and their relationship to wildfire. The above examples are the best observed cases of invasive plants changing the dynamics of fire in California ecosystems, although some are still anecdotal. Further scientific evaluation is necessary to accurately identify the mechanisms that lead to these changes or to determine whether changes are reversible. Current evidence suggests that annual and some perennial grasses have the strongest effects on fire regimes and act as ecosystem transformers. In many ecosystems, the dense growth habit and flammable tissue of invasive grasses create continuous drier fuels that are lacking in uninvaded communities. Further research should evaluate the effect of these and other invasive life forms (forbs, shrubs, trees, etc.) on fire regimes to guide management efforts to conserve and restore California native plant communities.

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