

Mediterranean annual grasses in western North America: kids in a candy store

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In this issue of *Plant and Soil*, Blank and Sforza (2007) contribute to understanding of how exotic annual grasses invade ecosystems in the western United States. Their findings, that medusahead wildrye (*Taeniatherum caput-medusae* [L.] Nevski) was most productive on non-invaded US soil and that plants from US-derived seeds may have evolved to utilize higher nutrient concentrations, parallel other results that suggest soils of vulnerable western US ecosystems are functionally different (i.e., more available-nutrient rich) than soils where these weeds are native and noninvasive (Blumenthal 2005; Davis et al. 2000). While it has been well established that exotic annual grasses can perpetuate their own environment by

fostering increased available nutrients (e.g., Ehrenfeld and Scott 2001; Norton et al. 2003), we must remember, for the sake of ecological restoration, that initial invasiveness is caused by chronic disturbances that disrupt native nutrient and organic matter cycles and increase nutrient availability. The principal difference between western US ecosystems and those where invasive annual grasses are native is the amount of time during which chronic disturbances have occurred. In the Mediterranean region, intensive management of grass and shrubland ecosystems depleted nutrients long ago, so that native vegetation is adapted to a “here today, gone tomorrow” strategy. In ecosystems of the arid and semiarid western USA, perennial-plant-dominated native nutrient cycles were disrupted by intensive land use much more recently. Chronic disturbances in the form of extensive grazing and altered fire regimes began to unlock nutrients stored in soil organic matter (SOM) for millennia. When seeds of exotic annual grasses arrived they found that the candy store was open.

In this commentary, we review evidence for major shifts in ecosystem processes across the semiarid western USA and we call for more research that links results of ecological restoration efforts to the growing body of knowledge about interactions between invasive annuals and invaded environments.

In western US ecosystems vulnerable to weed invasion, the consequence of almost any type of ecosystem disruption is a shift from immobilizing,

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“conservative” nutrient cycling where nutrients from decomposing organic materials are rapidly taken up by diverse plant and microbial communities, to more mineralizing, “leaky” cycles with excess nutrients that are uncaptured by soil and plant communities (Haynes and Williams 1993; Schimel 1986). We believe that myriad disturbances across arid and semiarid western landscapes have the ultimate, synergistic effect of shifting nutrient cycling from conservative cycles dominated by uptake, immobilization, and storage in protected organic matter pools, to more open, “leaky” cycles where carbon and nitrogen are rapidly mineralized and excesses are potentially lost via leaching, greenhouse gas emissions (Norton et al. *in press*), or uptake by exotic weeds. Smith et al. (1994) found that undisturbed sagebrush-steppe plant communities, with diverse herbaceous, woody, and microbial components, have very conservative nutrient cycles with very little net nitrogen mineralization. It follows that relatively high concentrations of mineral nutrients observed by Blank and Sforza (2007) and others signify a shift from conservative to leaky nutrient cycling. Recent research by Davies et al. (2007) supports this notion by showing that maintaining high plant functional diversity decreases soil nutrient concentrations in semiarid bunchgrass-dominated plant communities, and that removal of individual functional groups increases mineral nitrogen concentrations.

Invasive annual grasses are equipped to thrive in mineralizing environments; and once established, they perpetuate and enhance mineralization-driven nutrient cycles (Ehrenfeld 2003; Sperry et al. 2006). Replacement of California’s xeric perennial grasslands by Mediterranean annual grasses was so complete before the beginning of the 20th century that we can only speculate about original plant communities (Bartolome et al. 1986; McNaughton 1968; Robinson et al. 1995). Conversion to annual grasses is now rapidly spreading in the sagebrush (*Artemisia* spp.)-steppe regions by cheatgrass (*Bromus tectorum* L.) and in the Mojave and Sonoran deserts by red brome (*Bromus rubens* L.; Brooks and Berry 2006; Salo 2004).

Mediterranean and Eurasian annual grasses take naturally (almost supernaturally, it seems) to our semiarid, resource-pulse-driven environments Andersson et al. 2002; Robocker 1973). Their phenology, root architecture, and litter decomposition rates differ from native vegetation in ways that create altered patterns of resource use and availability and allow them to persist

in previously perennial-dominated grass- and shrublands (Kulmatiski et al. 2006; Norton et al. *in press*).

However, as Blank and Sforza’s (2007) data and those of other research suggest, exotic annual grasses invade not only because they have key invasive traits, but primarily because management and disturbance has created an ideal backdrop for invasion. For example, long-term chronic disturbance from uncontrolled grazing accompanied introduction of invasive annual grasses in each case of widespread invasion of annual grasses (Brandt and Rickard 1994; Pickford 1932; Stromberg and Griffin 1996). Additional chronic disturbances that likely contribute to the success and persistence of invasive annual grasses include cultivation, altered fire regimes, altered watershed hydrology and erosion, elevated carbon dioxide, nitrogen deposition, and climate change. In studies of plant community responses to elevated carbon dioxide, for instance, exotic annual grasses respond more vigorously than native plants (e.g., Smith et al. 2000).

Invasive annual grasses are opportunistic and can rapidly utilize nutrients made available by combinations of lack of uptake and disintegrating soil organic matter (SOM) pools that characterize disrupted, leaky nutrient cycles (D’Antonio and Vitousek 1992). Once established, invasive annual grasses perpetuate and exacerbate ecological disturbance by promoting even more rapid mineralization (Chen and Stark 2000; Sperry et al. 2006). They create functional monocultures that constitute new ecological equilibriums (George et al. 1992). Annual grasses displace perennial native cool-season grasses in North American sagebrush-steppe and desert-scrub plant communities, producing more frequent wildfires so that non-sprouting shrub species are also eliminated and cannot recover (Baker 2006; Corbin and D’Antonio 2004; Humphrey and Schupp 2004). Many studies describe annual grass-soil feedbacks that alter soil structure (Norton et al. 2004; Young et al. 1999), biotic communities (Belnap and Phillips 2001; Hawkes et al. 2006), organic matter dynamics (Norton et al. *in press*), water relationships (Leffler et al. 2005), and, ultimately, soil nutrient cycling (reviewed by Ehrenfeld 2003; Sperry et al. 2006). In addition, medusahead wildrye, annual wheatgrass (*Eremopyrum triticeum* [Gaertn.] Nevski), and common Mediterranean grass (*Schismus barbatus* [Loefl. Ex. L.] Thellung) are secondary invasive annual grasses spreading throughout the exotic annual-

dominated plant communities that further threaten resiliency of altered ecosystems (Hironaka 1992; Monaco et al. 2005; Young and Clements 2005; Young et al. 1999).

The changes result in highly seasonal, resource pulse-dependent plant and microbial communities that are largely out-of-phase with nutrient availability (Bilbrough and Caldwell 1997; Norton et al. in press). In California's exotic annual grasslands, many ephemeral streams have unusually high nitrate concentrations resulting from decomposition of senesced exotic annual plants during the winter rainy season, as well as from losses of stored SOM (Lewis et al. 2006). Some studies suggest a priming effect where labile organic material high in carbon produced by invasive annual grasses stimulates a pulse of microbial activity that exploits C and N in stored SOM, depleting SOM and creating progressive soil degradation (Fierer and Schimel 2003).

Studies of invasive plants and their effects on new environments have contributed a great deal to basic understanding of plant–soil interactions (e.g., Blumenthal 2005; Chapman et al. 2006). With respect to ecological restoration, however, the tendency to attribute soil changes to invasive species, and forget original triggers for invasion (i.e., chronic disturbance and broken nutrient cycling) might be akin to analyzing how wheat crops alter soil properties but forgetting about effects of the plow. Weeds may have novel weapons that are more effective in their newly invaded ecosystems, or they may be well-equipped to capitalize on altered disturbance regimes, but it is becoming increasingly clear that counteracting them through restoration efforts must ultimately repair the primary ecosystem functions that have been disrupted.

The fact that the physical stage must be set for successful restoration of desirable plant communities is found in primary definitions of restoration ecology (e.g., Whisenant 1999), but is often overlooked in the zeal to restore altered plant communities by reestablishing native species. This is glaringly obvious in the case of riparian areas invaded by the exotic tree tamarisk (*Tamarix* spp.). Tamarisk initially displaces native willows (*Salix* spp.) and cottonwoods (*Populus* spp.) when stream channel entrenchment precludes annual flooding (channel-floodplain connection is lost) (Stromberg 1998). Plant community restoration is not successful unless hydraulic connectivity between channels and riparian areas is restored, and then

it is often unnecessary because native species respond rapidly (Briggs et al. 1994; Taylor and McDaniel 1998). In this case, hydraulic connectivity is a key functional characteristic that must be intact before restoration of invaded plant communities can be successful. Likewise, the disturbance regime, soil community, and nutrient cycling of annual grass invaded ecosystems must be set in place prior to reestablishing native species.

Ecological research and restoration experience suggest that conservative nutrient cycling of spatially and temporally diverse plant-microbe communities, may be the key functional characteristic that must be intact for successful restoration of native perennial plant communities in annual-grass-invaded grass- and shrublands. Cultivation and pesticide application that are part of many restoration seeding efforts have the opposite effect, causing further disturbance and release of available nutrients. Competitive introduced perennial grass species can begin to reverse the pulse behavior of annual communities by lengthening both uptake periods (Cox and Anderson 2004) and fire recurrence intervals (Keeley et al. 2005). As such, perennial forage grasses like crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] can be important tools toward restoration of diverse native-dominated plant communities. But planting exotic perennials as an end in itself often brings its own problems and results in low species diversity that may persist for decades (Marlette and Anderson 1986).

While we continue to need research that describes how invasive annuals alter soil environments, particularly with respect to basic soil building blocks that might be key components of restoration (structure, SOM content/composition), we also need critical analyses of restoration efforts with respect to how they alter soil processes toward or away from restoration goals.

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