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RESEARCH EDITORIAL

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# Invasive annual grasses—Reenvisioning approaches in a changing climate

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**Abstract:** For nearly a century, invasive annual grasses have increasingly impacted terrestrial ecosystems across the western United States. Weather variability associated with climate change and increased atmospheric carbon dioxide ($CO_2$) are making even more difficult the challenges of managing invasive annual grasses. As part of a special issue on climate change impacts on soil and water conservation, the topic of invasive annual grasses is being addressed by scientists at the USDA Agricultural Research Service to emphasize the need for additional research and future studies that build on current knowledge and account for (extreme) changes in abiotic and biotic conditions. Much research has focused on understanding the mechanisms underlying annual grass invasion, as well as assessing patterns and responses from a wide range of disturbances and management approaches. Weather extremes and the increasing occurrences of wildfire are contributing to the complexity of the problem. In broad terms, invasive annual grass management, including restoration, must be proactive to consider human values and ecosystem resiliency. Models capable of synthesizing vast amounts of diverse information are necessary for creating trajectories that could result in the establishment of perennial systems. Organization and collaboration are needed across the research community and with land managers to strategically develop and implement practices that limit invasive annual grasses. In the future, research will need to address invasive annual grasses in an adaptive integrated weed management (AIWM) framework that utilizes models and accounts for climate change that is resulting in altered/new approaches to management and restoration.

**Key words:** drought—ecology—extreme—resilience—resistance—restoration

## Distribution and Impacts of Invasive Annual Grasses with Climate Change

Millions of hectares of rangeland in the western United States are either dominated by or under threat of degradation from invasive annual grasses (Bradley and Mustard 2006; Bromberg et al. 2011; Brooks et al. 2016; Brunson and Tanaka 2011; D'Antonio and Vitousek 1992; Davies 2008, 2010; Davies et al. 2021a; Germino et al. 2016; Knapp 1996; Svejcar et al. 2017). The USDA National Resources Inventory, the largest inventory of nonfederal US lands, estimates that nationally between 2011 and 2015, nine invasive annual grass species were present on 30% of nonfederal rangelands. Ventenata (*Ventenata dubia* [Leers] Coss.) was observed on 8% of nonfederal rangelands in Oregon with trace amounts in Idaho and Washington. Medusahead (*Taeniatherum caput-medusae* [L.] Nevski) was present on nonfederal lands in Idaho (24%), Oregon (23%), California (18%), and Washington (9%) (USDA NRI 2018). The Bureau of Land Management (BLM) Greater Sage Grouse Plan Implementation Rangewide Monitoring Report estimates that percentage canopy cover of invasive annual grasses, such as cheatgrass (*Bromus tectorum* L.) and medusahead, is approximately 15% on BLM-administered lands (Herren et al. 2021). Although annual bromes, ventenata, and medusahead are just a few of the many invasive annual grasses on US rangelands, to date this group of three has the most cover and associated research.

Origins for the most prevalent invasive annual grasses in the United States can be narrowed down to Europe, northern Africa, and central to southwest Asia (Whitson 1991). Annual grass introduction to the United States likely occurred as seeds inadvertently transported in packing materials, ship ballast, the hair of livestock, or as contaminants of crop seeds (Salo 2005). Invasive annual grasses are well adapted to arid and semiarid western rangelands that are characterized by high variability in seasonal and interannual precipitation and temperature (Hardegree et al. 2018). Specific adaptive traits to this environment include prolific seed production, rapid establishment response to short periods of resource availability, rapid growth, preemptive utilization of site resources, and annual or winter-annual life cycles that facilitate survival during periods of seasonal drought (Arredondo et al. 1998; Balch et al. 2013; Davies 2008; Hardegree et al. 2010, 2013; Harris and Wilson 1970; Humphrey and Schupp 2001, 2004; Kulmatiski et al. 2006; Littell et al. 2009; Mangla et al. 2011;

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Mazzola et al. 2011; Melgoza et al. 1990; Reichenberger and Pyke 1990; Rimer and Evans 2006).

Landscape-level transformation from native to invasive annual grass communities has major negative environmental and economic effects on natural resource values, land management costs, and societal benefits from rangelands (Brunson and Tanaka 2011; Duncan et al. 2004; Epanchin-Niell et al. 2009; Maher et al. 2013; Riggs et al. 2001). Major impacts include (1) the loss of compositional, functional, and species diversity (Davies and Sheley 2011; Nasri and Doescher 1995); (2) disruption of forage cycles for livestock and wildlife through changes in seasonality and magnitude of herbaceous production (Bradley and Mustard 2006; Clinton et al. 2010); (3) a major increase in both the frequency and intensity of wildfires (Balch et al. 2013; Brooks et al. 2004; D'Antonio and Vitousek 1992; Davies and Nafus 2013; Eiswerth et al. 2009; Knapp 1996); (4) increased risk of postfire erosion (Pierson et al. 2011; Wilcox et al. 2012; Williams et al. 2014); and (5) degradation of wildlife habitat (Coates et al. 2016; Connelly and Braun 1997; Crawford et al. 2004; Garton et al. 2011). Invasive annual grasses can self-perpetuate by causing changes in abiotic and biotic conditions that reinforce site dominance and hinder the reestablishment of native perennial species (Balch et al. 2013; Blank et al. 2013; Bradley et al. 2018; Brooks and Matchett 2006; Boxell and Drohan 2009; Gasch et al. 2013; Norton et al. 2004; Owen et al. 2013; Pierson et al. 2011; Rau et al. 2011; Wilcox et al. 2012; Williams et al. 2014). For example, low-elevation perennial rangelands in deserts that span from the warm western to cold mountain and intermountain regions of the United States have been transformed to annual grasslands by cheatgrass, medusahead, and ventenata, along with red brome (*Bromus rubens*), Arabian schismus (*Schismus arabicus*), and common Mediterranean grass (*Shismus barbatus*) (Davies et al. 2021a; Fusco et al. 2019; Germino et al. 2016; Horn et al. 2017; Salo 2005; Suazo et al. 2012; Underwood et al. 2019). Economic impacts from the loss of productivity, wildfire suppression, costs of wildfire damage, decreased ecosystem services, and restoration costs have increased proportional to the impacts (BLM 2020; Brunson and Tanaka 2011; Davies et al. 2021b; Pilliod et al. 2021; USDA NRCS 2018).

Climate projections show elevated atmospheric carbon dioxide ($CO_2$) levels will lead to warming and more variable precipitation patterns, which could allow for further expansion of invasive annual grasses in the western United States, as shown in figure 1. Belowground, warmer temperatures and decreased water availability have been linked to less resistant and resilient native plant communities, increasing vulnerability to invasive annual grasses (Chambers et al. 2014b). In some regions, analyses have found cheatgrass moving up in elevation and increasing on north-facing slopes (Smith et al. 2022). Particularly in the western United States, an increase in fire frequency often favors the annual invader, producing a positive feedback cycle that is expected to accelerate as warming and drought lengthen fire seasons (Balch et al. 2013; Fusco et al. 2019; Underwood et al. 2019). Additional pressures from a rapidly warming climate and changing precipitation distributions could lead to widespread extinction of local native plant ecotypes in western regions, as these communities have insufficient time to evolve or migrate in an increasingly disturbed and fragmented landscape (Abatzoglou and Kolden 2011; Bradley 2010; Knapp 1996). Uncertainty in climate projections and the response of invasive annual grasses to these changes pose a greater challenge to the sustainability of invaded areas. Current and historical rehabilitation and restoration efforts in areas infested with invasive annual grasses have been relatively unsuccessful, particularly in the drier and lower-elevation range of the sagebrush steppe (Arkle et al. 2014; Brooks and Chambers 2011; Chambers et al. 2014a, 2014b; Davies et al. 2015; Knutson et al. 2014; Monaco et al. 2017; Pyke et al. 2013; Shackelford et al. 2021). As the climate becomes warmer and drier, even habitats that have been easier to rehabilitate, such as in the Great Plains, are likely to become more challenging.

## A Mechanistic Understanding of Annual Grass Invasion

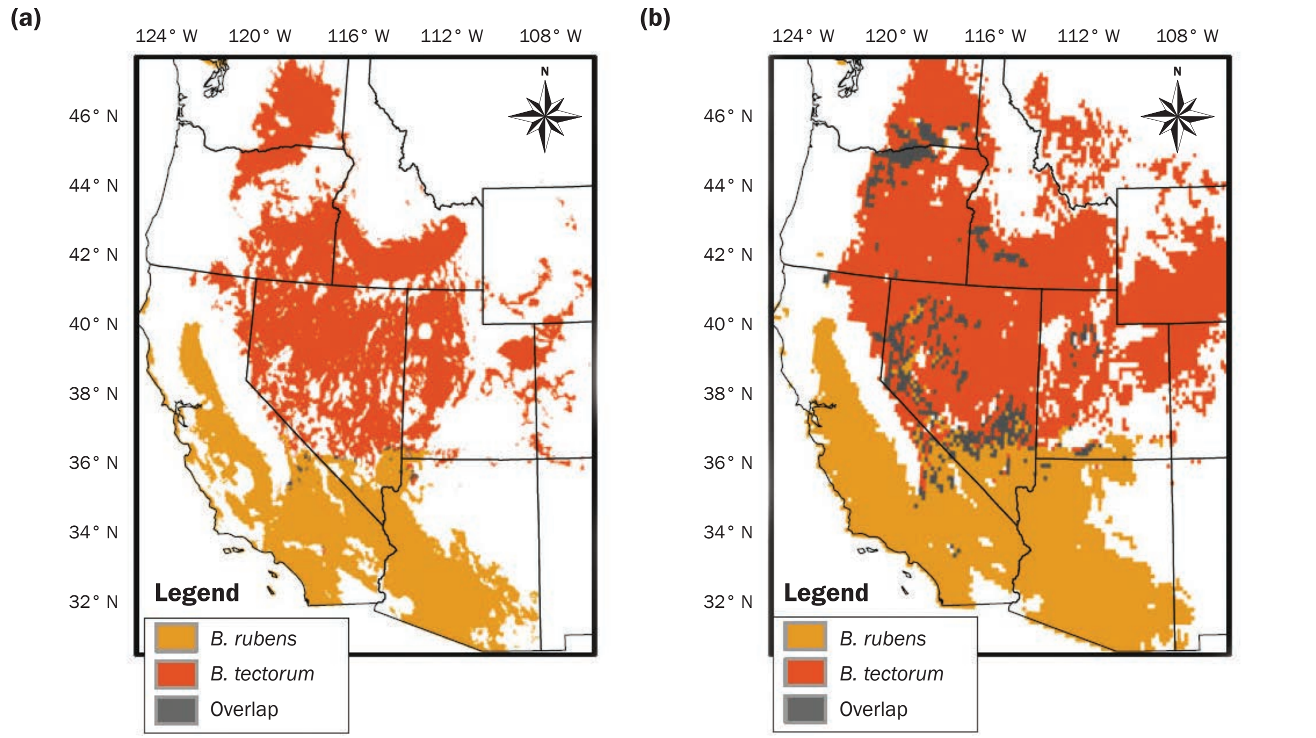
Perennial grasses provide the foundation for stability, resilience, and productivity of semiarid grassland and steppe ecosystems of the world (Chambers et al. 2017; Sanaei and Ali 2019). The perennial life history, in combination with relatively slow growth rates, allows these species to use limited water and nutrients efficiently, and to better resist drought (Ruppert et al. 2015; Wilcox et al. 2021). Unlike perennial grasses that must produce biomass to persist more than a single year, invasive annual grasses display a broad array of adaptive and functional traits to establish, spread, and persist in semiarid ecosystems (Chambers et al. 2007; Reisner et al. 2013; Seabloom et al. 2013). In particular, annual brome species exhibit transient but large seed banks, capitalize on altered soil resource availability and litter production, and contribute to frequent disturbance and the displacement of native plant species (Monaco et al. 2016). These impacts are possible because annual grasses are fast growing, rapidly acquire soil resources, maximize seed production, and senesce prior to seasonal resource-limiting periods (D'Antonio and Vitousek 1992; Norton et al. 2007). Thus, annual grass invaders are preadapted to thrive in semiarid ecosystems with recurrent and compounded disturbances that favor their persistence relative to perennial species, primarily at early growth stages (Mack 1981).

The capacity of invasive annual grasses to dynamically respond to resource availability in ways superior to perennial grasses is attributed to high phenotypic plasticity (Davidson et al. 2011), which is considered a primary mechanism allowing invasive annual grasses to expand their distribution and impacts in semiarid ecosystems (Drenovsky et al. 2012b; Funk 2008; Grime and Mackey 2002). For example, many invasive annual grasses display higher acquisition plasticity for mineral nitrogen (N) in heterogeneous conditions (James et al. 2009) and under variable growing temperatures, illustrating their ability to exploit transient warm periods in autumn and spring (Leffler et al. 2011). Thus, invasive annual grasses are adept at exploiting soil nutrients when seasonally available, after disturbance, or through atmospheric N deposition (Bilbrough and Caldwell 1997; Brooks 2003). At early growth stages, highly plastic invasive annual grasses acquire soil resources, which allows for competitive displacement of native species in a changing environment and co-opted successional dynamics through altered nutrient cycling (Evans et al. 2001; Hirsch-Schantz et al. 2014; Leonard et al. 2008).

Invasive plants often gain advantages by growing at different times of the season than native species (Wolkovich and Cleland 2011). In rangelands dominated by native perennials, annual bromes occupy a late-autumn through early-spring phenological niche, which can give them an advantage under the right climatic conditions, allowing access to

**Figure 1**

From Bradley et al. (2016), an example of invasive annual grass spread based on (a) current and (b) future climate conditions for cheatgrass (*Bromus tectorum*) and red brome (*Bromus rubens*). Note: current climate conditions are interpolated to a 4 km spatial resolution, while future climate conditions are scaled to a 12 km spatial resolution.




water and nutrients before being utilized by competitors. In cooler parts of annual brome geographic ranges, warming temperatures are likely to expand this autumn-spring phenological niche, thereby increasing competitiveness (Bradley 2009). This prediction is supported by studies showing that experimental warming facilitates cheatgrass invasion (Blumenthal et al. 2016; Compagnoni and Adler 2014; Zelikova et al. 2013). Shifts toward more winter relative to summer precipitation can similarly favor annual bromes (Bradley 2009; Prevey and Seastedt 2014; Zheng et al. 2019).

Invasive annual grasses have shown traits consistent with a drought-escape strategy for persisting during periods of low moisture availability, where species flower and reproduce early, completing their entire life cycle before drought conditions worsen (Blumenthal et al. 2020; Sherrard and Maherali 2006). This early flowering is facilitated by increased photosynthesis and attendant greater water-use-efficiency (Kimball et al. 2017). The strategy likely provides an advantage to invasive annual grasses in arid environments by providing a means of resource hedging under conditions of prolonged severe drought that are expected to become more common with climate change in many regions (Nguyen et al. 2016). Drought escapers are also more capable of quickly responding to pulses in plant available moisture than drought tolerators or avoiders because their physiological traits allow for rapid upregulation of photosynthates during pulse moisture events.

## Current Approaches for Management and Restoration of Invasive Annual Grasses

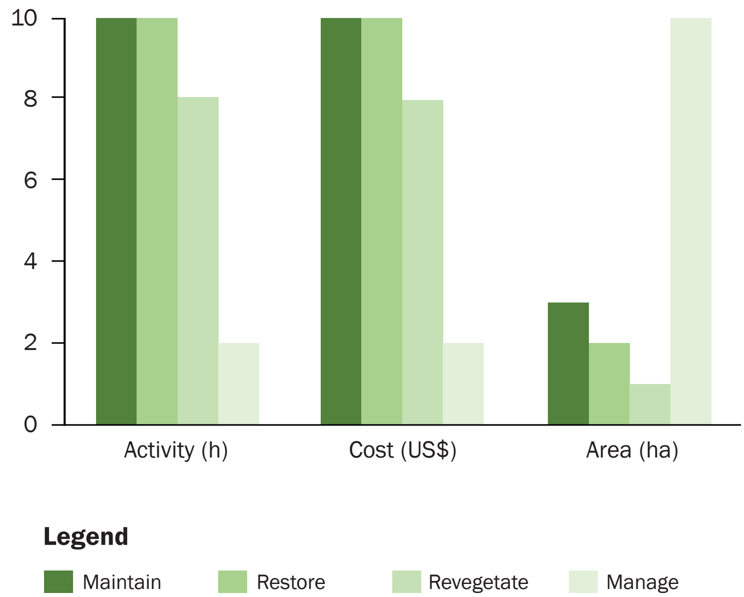
Invasive annual grass management options depend on the stage of invasion (DiTomaso et al. 2017). Prevention is employed prior to and at the introduction stage, whereas containment and control (to limit dominance) are management components administered during spread. Typically, at a later stage, restoration is designed and implemented to reduce impacts. Given the scope of invasive annual grasses and the impacts, successful management necessitates an ecosystem perspective that considers invasion as an ecological process, integrating the components of management through a comprehensive understanding of dynamics.

While prevention is often highlighted as the most effective and important step in managing biological invasions, both research and application of preventative measures against invasive annual grasses lag behind reactive crisis (e.g., postfire) management associated with containment, control, and rehabilitation. Prevention techniques include minimizing seed sources and dispersal, increasing ecosystem resilience and resistance, and developing spatially explicit prioritization plans to increase the adaptive capacity of land managers (Maestas et al. 2022). Preventative measures to minimize seed sources include controlling movement of livestock and people from invaded areas, using certified annual-grass-free forage, and monitoring travel corridors for wildlife-assisted dispersal of invasive annual grass seeds.

Most of the invasive annual grass management research and application is focused on containment and control, coupled with restoration, primarily seedling establishment, to improve ecosystem structure and function (Monaco et al. 2017). These management components address invasion reactively once invasive annual grasses have established and are focused on limiting or reducing dominance and further spread, which can be costly and time-intensive as depicted in figure 2. There remains a strong emphasis on single-use control approaches, such as herbicides, which have been effective to an extent at limited spatial and temporal scales, but can have associated trade-offs, such as nontarget effects of herbicide on native vegetation and other trophic guilds (e.g., pollinators). Additionally, herbicide effects can be short term. Furthermore, where annual grass invasion is driven by underlying environmental conditions (e.g., loss of perennial competitors), using herbicides is analogous to treating symptoms rather than the underlying problem and likely necessitate perpetual reapplication. Given the multiple ecosystem impacts of invasive annual grasses (e.g., altering processes and competitive interactions of perennial plant communities), they do not often recover after simple removal of invasive annual grasses, but also need the establishment of native plants (Chambers et al. 2007). As a result, there is an increasing focus on resilience-based control and restoration that occurs over the long term.

**Figure 2**

**Using Davies et al. (2021b) decision tree, the labor (h) and financial (US$) inputs needed and land area covered (ha) on a relative scale if (1) maintaining a native perennial community, (2) restoring a native perennial community, (3) revegetating with competitive plants (i.e., crested wheatgrass), or (4) managing an annual grassland.**




Ecological resilience is an emergent property of the abiotic and biotic components of the ecosystem and is governed by multi-scaled processes; process-based management focuses on maintenance and restoration of these processes at the scale of their function (Krueger-Mangold et al. 2006). A number of steps are required to restore the resilience of the invaded ecosystem and limit reinvasion or secondary invasion (Krueger-Mangold et al. 2006). For instance, in the Great Plains, cheatgrass and Japanese brome abundance varies considerably among years due to fall and early spring moisture relationships with germination and growth, respectively (Rinella et al. 2020). Control methods designed to increase invasion resistance, such as altering the timing of prescribed fire to provide a competitive advantage to native perennial grasses, have been effective in the Great Plains (Harmoney 2007; Vermeire et al. 2011, 2014, 2021). In sagebrush-bunchgrass communities of the Great Basin, prescribed grazing can increase the resilience to fire and subsequently improve postfire resistance to invasive annual grasses under certain conditions (Davies et al. 2015, 2017, 2020, 2021a). However, in areas where annual bromes have caused state-shifts of sagebrush shrublands to invasive annual grass dominated systems with modifications to ecosystem processes, the typical approach is restoration and revegetation with native species following intensive annual grass control or removal (Davies et al. 2021b; Freund et al. 2021).

Climate change and invasion are also altering the benchmarks for restoring resilient ecosystems. In some cases, invasions have created novel systems with only small fragments of historical ecosystems remaining intact (Hobbs et al. 2009). Plant communities, soils, and hydrology are sometimes changed so dramatically that it can be difficult to manage for a previously desirable assemblage. In addition, present and future climate conditions add to the novel dynamics, increasing resistance to attempts to restore historical species compositions (Coates et al. 2016; Hobbs et al. 2009; Seastedt et al. 2008). In landscapes with these conditions, managers have learned to prioritize getting the most goods and services from the existing situation, and this will need to continue with more urgency (Davies et al. 2021b). A greater number of managers may need to adapt to living with invasive annual grasses and find ways to increase the value of these invaded grasslands (e.g., limited grazing). Programs are needed to expand current education efforts and create new opportunities to help guide land managers on setting realistic targets based on research (Davies et al. 2021b; Ehrenfeld 2000). Because climate change is increasing the potential spread of invasive annual grasses, particularly in cooler microclimates (Smith et al. 2022), managers must be prepared to be more proactive even in areas where invasive annual grasses have not previously been problematic.

## Addressing Invasive Annual Grasses using an Adaptive Integrated Weed Management Framework

The ecological impacts and related socio-economic effects of invasive annual grasses present a complex and expanding problem for rangeland ecosystems, especially under the threat of increasing weather extremes due to climate change. In the future, management and restoration will likely consist of a science-based iterative process, such as adaptive integrated weed management, that leads land managers toward strategies with the highest probability of creating a desired plant community for a specific site (Hardegree et al. 2019; James et al. 2013; Sheley et al. 2006; Svejcar et al. 2017). To be sustainable, management and restoration strategies must be based on repairing, replacing, or establishing fundamental conditions and ecological processes that direct plant community change (James et al. 2010, 2013). The combining of adaptive management and integrated weed management (IWM) into a new "AIWM" framework will shape how practitioners approach the management and restoration of lands infested and threatened by invasive annual grasses and increasingly impacted by climate change. Several exciting areas of research within the AIWM framework are emerging and include models and scalability, novel control methods, and adaptation to climate change.

***Models and Scalability.*** Conceptual models that link site assessments to ecological processes/conditions and ecologically based principles can facilitate management for diverse, perennial plant communities in invasive annual grass dominated rangelands (Sheley et al. 2009). These models are based on identifying and repairing ecological conditions and processes that drive plant community change (James et al. 2010). Once an optimum series of treatments is identified and employed in an IWM-restoration program, adaptive management may alter treatments based on vegetation responses to prior activities (Hardegree et al. 2018; Leffler and Sheley 2012; Reever-Morghan et al. 2006; Sheley et al. 2009; Williams et al. 2009). Models are developed that compile old and new knowledge into a user-friendly AIWM framework for managing invasive annual grasses on rangelands (James et al. 2013).

Modeling situations and actions that allow for the prediction of desired outcomes need to be scaled to match the spatial extent of management. In an AIWM framework, annual grass invasions begin locally, but with widespread establishment, broaden to landscape scales. Networks of metapopulations across the landscape increase propagule pressure with invasion success dependent on size, connectivity, and dispersal mechanisms (Lurgi et al. 2016). Propagule pressure is an extremely important component of plant invasion dynamics (Colautti et al. 2006) that is active at the landscape level, but often managed at far smaller scales (Firestone and Jasieniuk 2013). Models should assess scaling with the appropriate management, which may include prevention, especially as climate change impacts invasions at large scales (Abatzoglou and Kolden 2011). An added component should be the matching of invasion dynamics and management scales with economic impacts. Newly developed inventory tools should accelerate research in matching scales of ecological data to processes driving annual grass invasions (Jones et al. 2020).

***New Tools: Potential Biological Control with Endophytes.*** The future of invasive annual grass management stands to benefit profoundly from genomics research and transgenic applications. Cheatgrass has been shown to benefit from associations with New World endophyte species that increase invasiveness (Aschehoug et al. 2014; Baynes et al. 2012). Fundamental research conducted on the biology and genomics of a New World endophyte would provide the basis for transformation to produce an RNAi (or other) molecule that is specifically deleterious to cheatgrass when colonized by the transformed endophyte. A genetic-drive mechanism (e.g., CRISPR-Cas9) could be employed to promote the spread of the introduced construct, curtailing cheatgrass throughout the geographic range of the endophyte. Other future applications of new and as yet developed technologies will be applied to the challenge of managing invasive annual grasses and reducing or eliminating their economic, environmental, and social impacts.

***Climate Change Adaptation: Using Weather Forecasting.*** A major issue complicating invasive annual grass management and restoration is highly variable and extreme weather (Hardegree et al. 2018). Effective invasive annual grass management requires an understanding of how precipitation patterns, for example, direct plant community establishment and assembly. Extreme variability complicates all aspects of IWM and especially the restoration of areas infested with invasive annual grasses. Short-term weather forecasting will be essential to decide when to implement invasive annual grass management, particularly for projects that include restoration (Hardegree et al. 2013, 2018). Federal restoration priorities are focused largely on abiotic resistance and resilience concepts, which relate primarily to long-term climatic patterns (Boehm et al. 2021; Pyke et al. 2013). However, variable weather patterns, particularly in the early stages (resistance) and postestablishment (resilience), need to be accounted for when implementing grazing, prescribed fire, chemical or biological control strategies, and the introduction of new sources of plant material.

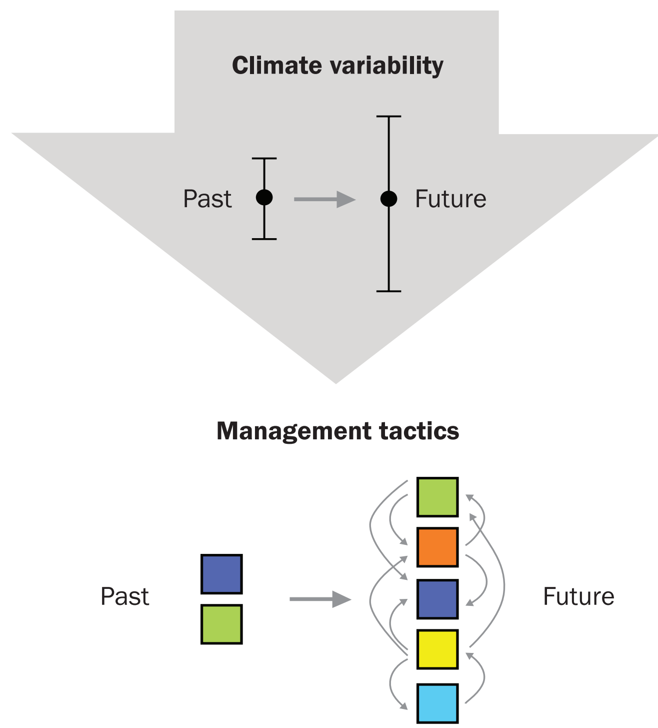
***Climate Change Adaptation: Plant Traits.*** Advances in plant trait research provide opportunities to improve both invasive species management and restoration (Laughlin 2014; Reich 2014). As climate changes, species with traits that allow adequate resource capture are a necessary component of the plant community. Thus, identifying such species and ecotypes with traits that establish in a predicted future environment could increase success rather than using species in restoration seed mixes that focus only on (functional) diversity (Clark et al. 2012). Trait-based approaches that link invasion dynamics with ecosystem processes are essential when addressing uncertain climate futures. Linking response traits of invasive plant species to changes in biotic and abiotic environmental factors will enable increased accuracy in plant trajectory predictions with rapid global change (Drenovsky et al. 2012a). Especially important is an understanding of trait plasticity and how it will contribute to invasions under current and future climates. Quantifying the level of plasticity will allow researchers to know the mechanisms of spread, which will help land managers to make more accurate assessments of prevention and restoration strategies (Zheng et al. 2019). The increasing availability of plant trait data also promises to help improve restoration success. Models are being tested that use widely available plant trait information to design restoration with particular ecosystem functions, such as drought resistance (Laughlin 2014).

## Conclusion

Effective management of invasive annual grasses requires an extensive understanding of the ecological dynamics of both invasion processes and ecosystem resistance and resilience. Since global change drivers, including increased temperatures, $CO_2$, N deposition, as well as altered precipitation and drought, are dynamic, addressing invasive annual grasses will require an AIWM framework with a strong integration of research and management, as represented in figure 3. The integration of extensive and diverse data into models can inform assessments of invasion risk and spread, assist in prioritizing management resources, and aid in monitoring management outcomes across various scales. An AIWM framework would greatly enhance the capacity of managers to adapt to the changing landscape of invasion, which in some cases may mean accepting the current condition. Regardless, an effective AIWM approach will require strategic planning that incorporates prevention, control, and restoration via sustainable integrated tactics that increase ecosystem resilience and resistance.

**Figure 3**

**Adapted from Birthisel et al. (2021), showing climate change effects on management tactics. In the past, adaptive management (AM) (dark blue box) and integrated weed management (IWM) (lime green box) were only practiced in isolation. In the future, the two approaches and others will need to be practiced in concert (e.g., AIWM) to effectively manage invasive annual grasses and restore perennial grass systems. Used with permission.**





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