Discussion

Living with exotic annual grasses in the sagebrush ecosystem ☆

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ABSTRACT

Exotic annual grasses dominate millions of hectares and increase fire frequency in the sagebrush ecosystem of North America. This devastating invasion is so costly and challenging to revegetate with perennial vegetation that restoration efforts need to be prioritized and strategically implemented. Management needs to break the annual grass-fire cycle and prevent invasion of new areas, while research is needed to improve restoration success. Under current land management and climate regimes, extensive areas will remain annual grasslands, because of their expansiveness and the low probability of transition to perennial dominance. We propose referring to these communities as Intermountain West Annual Grasslands, recognizing that they are a stable state and require different management goals and objectives than perennial-dominated systems. We need to learn to live with annual grasslands, reducing their costs and increasing benefits derived from them, at the same time maintaining landscape-level plant diversity that could allow transition to perennial dominance under future scenarios. To accomplish this task, we propose a framework and research to improve our ability to live with exotic annual grasses in the sagebrush biome.

1. Introduction

Exotic annual grass invasion has caused unprecedented ecological degradation in rangelands throughout the world (D'Antonio and Vitousek 1992; Mack 1981; Purdie and Slatyer 1976; Brooks et al., 2004). A particularly devastating example of the negative impacts of exotic annual grass invasion and dominance can be found in the 62 million ha sagebrush (*Artemisia* L.) ecosystem of western North America, where cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* (L.) Nevski) have invaded tens of millions of hectares (Pellant and Hall 1994; Meinke et al., 2009; Brady et al., 2018). Cheatgrass, by itself, is estimated to be present in high abundance across almost a third (21 million ha) of the Great Basin (Bradley et al., 2018). In addition, perennial plant communities of the Great Basin are transitioning to exotic annual grasslands at a rate of almost 200,000 ha per year (Smith et al., 2021). A large portion of the area invaded by exotic annual grasses is or was sagebrush rangeland. These exotic annual grasses are converting previously perennial-dominated communities into annual-dominated communities (Knick and Rotenberry 1997;

Davies et al., 2011), changing the seasonality, productivity, and inter-annual variability of herbaceous production in these regions (Clinton et al., 2010; Bradley and Mustard 2005).

Exotic annual grass invasion is particularly destructive because native plants and plant community diversity decline exponentially with increasing abundance of exotic annual grasses (Fig. 1; Davies 2011). Native plants decline with exotic annual grass invasion in part because exotic annual grasses are highly competitive with native vegetation (Nasri and Doescher 1995; Rafferty and Young 2002). Exotic annual grasses often grow earlier and more rapidly than many native species and preempt resources, especially at the seedling stage, resulting in the exclusion of native species (Melgoza et al., 1990; Humphrey and Schupp 2004). Exotic annual grasses can also increase wildfire frequency, to the detriment of native vegetation intolerant of more frequent fire (D'Antonio and Vitousek 1992; Brooks et al., 2004), by increasing the amount and continuity of fine fuels as well as period of time that these fuels are dry enough to readily burn (Knapp 1995; Brooks 2008; Davies and Nafus 2013). This is particularly impactful for native shrubs such as sagebrush that do not resprout after fire, and rely on longer fire return intervals to

Fig. 1. Native perennial-dominated sagebrush community (top) and exotic annual grass invaded community (bottom) in the Great Basin, USA.

reach reproductive age (Young and Evans 1978). Thus, more frequent fire prevents reestablishment of sagebrush and is detrimental to most other native perennial plants, leading to near monocultures of exotic annual grasses and the development of an exotic annual grass-fire cycle (D'Antonio and Vitousek 1992; Eiswerth et al., 2009).

In addition to the loss of plant diversity, invasion by exotic annual grasses has been devastating to wildlife species that depend on sagebrush habitat. The increased fire frequency associated with exotic annual grass invasion has resulted in wide-spread loss of sagebrush-occupied lands (Stewart and Hull 1949; D'Antonio and Vitousek 1992; Davies et al., 2011; Balch et al., 2013). This in turn has been a major factor contributing to the decline of sagebrush-associated wildlife (Crawford et al., 2004; USFWS 2013). For example, sage-grouse require sagebrush-occupied rangelands for all their seasonal habitats and during the winter sagebrush can comprise up to 98% of their diet (Patterson 1952; Wallestead et al., 1975). Thus, exotic annual grass invasions are negatively impacting sagebrush-associated wildlife by reducing habitat availability and important food sources.

In addition to ecological effects, the increased fire frequency associated with exotic annual grass invasion contributes to an increased economic cost of fire (suppression, property loss, rehabilitation, etc.) in the United States. Exotic annual grasses, especially cheatgrass, have increased the area burned annually in the Great Basin and likely contributed to mega-fires becoming more prevalent in the last decade and a half (Balch et al., 2013). The cost of wildfire suppression has risen sharply in the last two decades. Federal wildfire suppression in the

United States averaged over $2 billion for the last five (2015–2019) years (NIFC 2020). In the sagebrush ecosystem, livestock producers have lost infrastructure and part to all of their forage base in some of these fires. Thus, exotic annual grasses have a substantial economic cost as well as an ecological cost.

The exotic annual grass problem in the sagebrush ecosystem is likely to become more severe in the near future. While historical evolutionary and ecological dynamics in the sagebrush steppe favored dominance by perennial species (West 1983), the compounding of anthropogenic disturbances and the introduction of exotic annuals in these systems are currently favoring annual life history strategies. For example, increasing atmospheric CO_2 concentrations can increase exotic annual grass productivity, leading to increased fuel loads which may increase fire intensity and frequency (Ziska et al., 2005). Further, most models of climate change anticipate conditions that are expected to favor exotic annual grasses because of warmer winters and altered precipitation patterns as well as an earlier onset of fire season and more wildfires (Abatzoglou and Kolden 2011; Creutzburg et al., 2015). Applying these climate predictions to the landscape predicts stable or increasing cheatgrass cover in much of the Great Basin through 2070 (Boyte et al., 2016). Increased human activity in Great Basin ecosystems since European settlement (Morris and Rowe 2014) has resulted in increased chances for ignition events, and humans are responsible for an estimated 75% of fires in cheatgrass systems (Bradley et al., 2018). The likelihood of a sagebrush system transitioning to annual dominance increases with the number of repeat fire events (Mahood and Balch 2019; Ellsworth et al., 2020). Thus, while some invaded or disturbed sagebrush systems can return to pre-disturbance vegetation given sufficient time for recovery (Hironaka and Tisdale 1963; Morris and Leger 2016; Prach and Walker 2019), the ongoing intensification of disturbance factors, particularly increasing fire frequency, favors exotic annual grasses becoming an even bigger threat to the sagebrush ecosystem.

The vast nature of the exotic annual grass invasion and likely expansion in the near term necessitates that resource managers find strategies to cope with exotic annual grasses. While restoring all exotic annual grass-invaded sagebrush communities would be ideal, this isn't likely to be successful or feasible considering the contemporary scale of the invasion and the ongoing environmental and disturbance patterns that reinforce it, coupled with the difficulty of establishing native perennial species under current conditions. In fact, there are no cost-effective treatments for exotic annual grass control within the large areas already invaded (Stohlgren and Schnase, 2006), let alone to rapidly restore these lands. Efforts to control exotic annual grasses and reestablish native plant communities have also often been unsuccessful (Young 1992; Monaco et al., 2005; Davies et al., 2015). However, there is some evidence that highly targeted or resource-intensive treatments can result in greater success (Porensky et al., 2018; Davidson et al., 2019). Given the economic constraints to implementing intensive treatments across wide areas, a more strategic approach must be applied to stem the continued conversion of sagebrush rangelands to exotic annual grasslands and prioritize where limited restoration resources should be applied. This will require making some difficult decisions, including accepting that some areas will be managed as exotic annual grasslands, which we suggest referring to as Intermountain West Annual Grasslands, at the same time we emphasize proper management of native perennial-dominated communities, which may require management changes (e.g. remove feral grazing) in biodiverse, culturally important, or critical habitat areas. Another tough decision will be to decide where and when inexpensive, introduced perennial vegetation will be seeded instead of native species to either prevent exotic annual grass dominance after disturbance or to replace exotic annual grasses with perennial vegetation. Improvements in native plant establishment and persistence are also needed to increase restoration success, and we need to consider how post-seeding management decisions, like when to defer or resume livestock grazing activities or manage feral horse activities, affect the immediate success and long-term persistence of
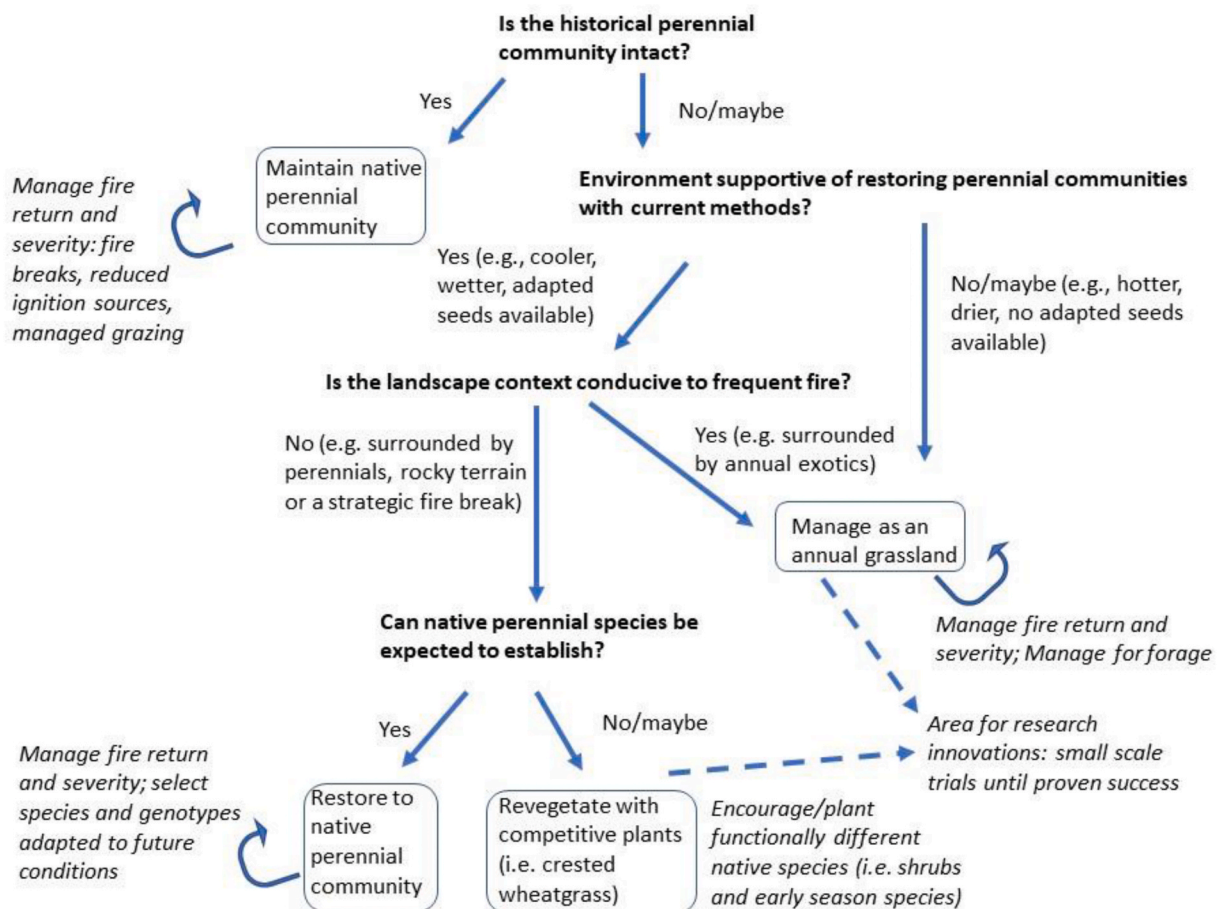
expensive treatments.

In this paper we outline a framework for living with exotic annual grasses in sagebrush habitats at risk or already invaded by exotic annual grasses. This includes: 1) preventing exotic annual grass dominance of new areas, and maintaining the integrity of high-priority areas, 2) breaking the annual grass-fire cycle in already invaded areas, 3) judiciously using introduced perennial species to prevent exotic annual grass invasion and revegetate invaded-areas where native seedings are unlikely to be successful or are not feasible, 4) improving restoration with native species, including considering more intensive methods to restore native species in strategically-located refugia, and 5) recognizing invaded landscapes that will likely remain exotic annual grasslands and managing them as such. To assist with management decisions, we provide a decision support flowchart (Fig. 2). We also suggest research along multiple avenues that will improve our ability to live with exotic annual grasslands. Finally, we consider lessons learned in the California Annual Grasslands, comparing and contrasting dynamics in these two converted ecosystems.

2. Preventing exotic annual grass dominance

Preventing exotic annual grass dominance is undoubtedly more efficient than trying to restore annual grass-dominated sagebrush communities. Maintaining abundant perennial vegetation is key to limiting exotic annual grasses (Chambers et al., 2007; Davies 2008; Davies and Johnson 2017). Perennial grasses are particularly important to keeping exotic annual grasses in check because their resource acquisition

patterns overlap substantially with annual grasses (James et al., 2008). Thus, management needs to focus on limiting disturbances that substantially reduce perennial vegetation, especially perennial bunchgrasses.

Pre-fire plant community composition largely drives post-fire composition, with degraded sagebrush communities converting to exotic annual grasslands and more intact communities often remaining perennial-dominated (Ellsworth and Kauffman 2017; Barker et al., 2019). Maintaining perennial bunchgrass dominance of the understory is, therefore, vital to limiting exotic annual grass dominance post-fire. Critical to maintaining large perennial bunchgrasses is well-managed grazing because grazing by domestic livestock and feral horses can have strong influences on plant community composition. Wide-scale spread of exotic annual grasses was spurred by extreme overgrazing coupled with drought in the early 1900s (Young and Allen 1997). Heavy, repeated grazing, particularly in the spring, of sagebrush communities should be avoided, as this can be detrimental to large perennial bunchgrasses and favor exotic annual grasses (Stewart and Hull 1949; Laycock 1967; Mack 1981). Well-managed grazing is characterized by moderate levels of use (40–50% utilization of available forage), particularly in the growing season, and limiting repeated growing season use (Davies et al., 2014). Sagebrush rangelands with well-managed livestock grazing can have similar vegetation characteristics to ungrazed areas (West et al., 1984; Copeland et al. IN PRESS). While livestock grazing exclusion can increase perennial dominance in some areas, well-managed grazing can result in similar increases (Copeland et al. IN PRESS), with the benefit of maintaining historical land use and

Fig. 2. Decision support flowchart for living with exotic annual grasses in the sagebrush biome. Adapted from Hobbs et al. (2014) framework for guiding major decision regarding interventions in historical, hybrid, and novel ecosystems.

sustaining local economies.

Grazing can also influence post-fire community composition indirectly by altering fuel loads and associated fire severity. Though intact sagebrush plant communities can remain dominated by perennials post-fire, severe fires, often caused by fuel accumulations, can kill perennial species and shift dominance to exotic annual grasses, even if fire is infrequent. Long-term grazing exclusion can increase the possibility of substantial fire-induced mortality of perennial bunchgrass because of increased fine fuel and structural changes to perennial bunchgrasses (Davies et al. 2009, 2016a, 2018a). Exotic annual grasses can dominate these areas after substantial fire-induced mortality of perennial bunchgrasses (Davies et al. 2009, 2016a). Thus, grazing exclusion is not necessarily a solution to preventing exotic annual grass dominance. Mortality of perennial bunchgrasses in a fire also increases with over-abundant woody vegetation. The majority of perennial bunchgrass mortality occurs under shrub canopies (Boyd et al., 2015), because of elevated temperature and longer burn duration (Boyd and Davies 2012; Davies et al., 2016b). Similarly, as conifer encroachment increases in sagebrush communities, wildfire severity and, subsequently, post-fire exotic annual grass dominance increases (Bates et al., 2014; Urza et al., 2019). Fuel management appears to be, at least at times, needed in sagebrush communities to reduce the probability of post-fire exotic annual grass dominance.

There is a strong and justified focus on the role of fire in degrading sagebrush habitats, but the sagebrush ecosystem evolved with periodic fire that shifted dominance from woody vegetation to herbaceous vegetation (Wright and Bailey 1982; Miller and Rose 1999). This fire-driven pattern of shifting dominance and succession has been interrupted by exotic annual grasses, such that contemporaneous fire, particularly fire with short return intervals, can favor exotic annual grasses and be the catalyst for converting sagebrush communities to exotic annual grasslands (D'Antonio and Vitousek 1992; Chambers et al., 2007). As such, reducing fire frequency may be particularly important to maintain existing perennial vegetation, particularly in areas with low resilience and resistance and high risk of anthropogenic ignition (Bradley et al., 2018). Concern over annual grass invasion has prompted some to suggest preventing all fires in sagebrush communities (e.g. USFSW 2013); however, this is unrealistic as most sagebrush communities will inevitably burn (Davies et al., 2012). Furthermore, many sagebrush communities burn without converting to exotic annual grasslands, and fires may be important for creating heterogeneity and diversity (Fig. 3; Davies and Bates 2020). Moreover, undesirable shifts in plant community composition may also occur with fire exclusion. For example, as fire return intervals lengthen, native conifers can expand from historical fire safe areas into sagebrush communities (Miller and Rose 1999; Miller et al., 2000; Weisberg et al., 2007). Conifer encroachment degrades sagebrush-associated wildlife habitat, reduces forage production, and increases erosion (Miller et al., 2000; Pierson et al., 2007). Prolonged exclusion of fire may also alter the response of plant communities to fire (Varner et al., 2005; Thorpe and Stanley 2011). Thus, instead of preventing all fires, the focus should be on ensuring plant communities can tolerate periodic fire, determining the types of post-fire management that best favor perennial plant recovery, and preventing severe and frequent fire. This would include determining the optimal timing, duration, and stocking rates of livestock after fire in relatively intact sagebrush communities, which deserves further study, as does the impacts of feral horses on post-fire dynamics.

3. Breaking the annual grass-fire cycle

Once exotic annual grasses dominate an area, breaking the exotic annual grass-fire cycle should become a management priority. Frequent fires associated with exotic annual grass invasion precludes fire-intolerant native species, such as sagebrush, from reestablishing in these communities and further reduce remaining native species that are generally not adapted to this novel fire regime (D'Antonio and Vitousek

Fig. 3. Top panel: Extensive post-fire forb response on an unseeded area of the Martin Fire, in June 2019. This area of Humboldt County, northern Nevada, burned in 2018, and is the largest wildfire in the state, as of 2020. Bottom panel: post-fire recovery of sagebrush community in Elko County, northern Nevada in June 2016, 10 years after the East Suzie fire burned this area. This site was seeded with a mix of widely-available native grasses and forbs, receives ~300 mm of annual precipitation, and has recovered to perennial dominance, with little to no invasive annual grass understory.

1992). Frequent fires in annual grass-dominated areas often results in fires spreading to adjacent areas (Balch et al., 2013), which may result in subsequent invasion and dominance by exotic annual grasses. Therefore, breaking the exotic annual grass-fire cycle is needed to prevent further degradation of already invaded areas and limit expansion of annual grass dominance into adjacent areas. It is also vital to limit frequent fires in annual grass-dominated areas to reduce the risk to human lives and property and maintain more stability in the forage resource provided by annual grasses.

Limiting fires is challenging in exotic annual grasslands because of the highly flammable and spatially extensive fine fuels they contain. Strategically deploying fire suppression resources to reach fires faster can improve suppression efforts and increase the safety of fire operations personnel, but lands at risk of wildfire are vast and often not easily accessed. Fuel breaks (mechanical or chemical) and green strips can be vital to improving suppression efforts and limiting fire spread from ignition hotspots, like roadways (Omi 1979; Pellant 1994; Shinneman et al., 2019). However, fuel breaks and green strips are costly and logistically challenging to implement, and without constant management, they can revert to annual dominance (Shinneman et al., 2019). Ultimately, the potential use and importance of fuel breaks should be

viewed within the context of a fire/fuels management system that includes practices to manage fuels within the much larger areas between fuel breaks.

In extensive rangelands, grazing is often the most feasible tool to manage fine fuels (Davies et al., 2016b). Spring grazing of exotic annual grasses can be effective at reducing fine fuel and decreasing fire probability (Diamond et al., 2009). However, exotic annual grass production is highly variable from year to year with at times a 10-fold difference in consecutive years (Hull and Pechanec 1947), and therefore, it can be difficult to achieve the desired reduction in fine fuels in high annual grass production years, when such reduction is most needed. In response to this need, extending the grazing period in the fall and winter may be a method to help reduce excess fine fuels in highly productive years, as well as give managers more time to overcome logistical challenges, while reducing the impacts of grazing on perennial plants (Schmelzer et al., 2014). Though fall or winter grazing would not decrease fine fuel in the summer fire season immediately following a wet spring, it would decrease fine fuel loads in subsequent years. This is important as most big fire years occur following several above-average plant production years (Pilloid et al., 2017). In addition, the reduction of litter associated with dormant-season grazing of exotic annual grasses can decrease their seedbank and reduce safe sites for germination, and this method has shown some promise for promoting perennials in exotic annual grasslands (Schmelzer et al., 2014; Perryman et al., 2020). Furthermore, it is possible that targeted grazing in combination with seeding of grazing-tolerant perennial species could begin to transition some of these highly invaded sites back to perennial dominance (Porensky et al., 2018).

While breaking the annual grass-fire cycle is a clear challenge in these systems, a combined approach of strategically placing fire suppression resources, fuel breaks and green-stripping, and strategic grazing to manage fuels can reduced the severity, frequency and extent of the annual grass-fire cycle. Research to determine where these treatments are most effective in exotic annual grass-invaded landscapes would be valuable to improving fire management.

4. Use of introduced perennial vegetation

While multiple Federal and State agencies have policies that require the use of native vegetation in seeding projects, there are widely-practiced exceptions to these policies for reasons such as cost, seed availability (especially common in large fire years), and the recognition that using the most valuable seed resources on highly degraded lands can be an inefficient use of limited seeds (National Academy of Science 2020). To-date, the most commonly planted introduced species in sagebrush communities have been crested wheatgrass (*Agropyron cristatum* [L] Gaertm.) and its close relatives (desert wheatgrass, *Agropyron desertorum* [Fisch.] Schult. and Siberian wheatgrass, *Agropyron fragile* [Roth] P. Candargy), hereafter, collectively referred to as crested wheatgrass. Crested wheatgrass has been seeded on 6–11 million hectares of rangelands in western North America, though not exclusively in sagebrush communities (Lesica and DeLuca 1996; Ambrose and Wilson 2003; Hansen and Wilson 2006). It was originally planted in sagebrush communities to reduce halogeton (*Halogeton glomeratus* [M. Bieb.] C.A. Mey), a forb that is toxic to sheep, and to increase livestock forage (Miller 1943, 1956; Frischknecht and Harris 1968; Vale 1974). Crested wheatgrass is still seeded after wildfire in former sagebrush communities largely because of its ability to suppress exotic annual grasses (Arredondo et al., 1998; Davies et al., 2010), but also because it is less expensive and establishes better than widely-available commercial varieties of native species, particularly in hotter and drier sagebrush communities (Asay et al., 2003; Pellant and Lysne 2005; Boyd and Davies 2010; James et al., 2012; Davies et al., 2015). Crested wheatgrass has also been seeded to prevent the development of an annual grass-fire cycle and used in green-stripping programs to break up continuous exotic annual grass fuel (Pellant 1994).

The seeding of crested wheatgrass, instead of native bunchgrasses, has come under intense scrutiny, especially given the desire to maintain native plant communities for sagebrush-associated wildlife. The competitiveness of crested wheatgrass, which makes it ideal for suppressing exotic annual grasses, can also lead to it forming monotypical plant communities, resulting in less valuable wildlife habitat (Looman and Heinrichs 1973; Christian and Wilson 1999; Heidinga and Wilson 2002; Hamerlynck and Davies 2019). Though varying levels of native vegetation can be found in crested wheatgrass stands (Nafus et al. 2016, 2020; Williams et al., 2017), these communities have substantially less diversity and abundance of native vegetation compared to intact sagebrush communities (e.g. Davies et al., 2006; Davies and Bates 2010). However, some of the lack of native vegetation in crested wheatgrass stands is an artifact of many of these communities being severely degraded prior to seeding crested wheatgrass and the treatments used to prepare the ground for seeding (Nafus et al., 2016). Degraded communities would have also likely transitioned to exotic annual-dominated communities after fire without establishment of perennial grasses (either native or introduced).

The current management issue is that crested wheatgrass is seeded in some areas to prevent conversion to exotic annual grasslands after fire, but it is also seeded in areas where seeding is likely not needed or native species may achieve similar success. Adding seeds of crested wheatgrass to seed mixes with native species is also common, and, in the event native species are capable of establishing at a site in a given year, such practices may increase the likelihood that more expensive native species are outcompeted at the seedling stage as co-planted crested wheatgrass recruits much more vigorously than native bunchgrasses (Nafus et al., 2015; Hamerlynck and Davies 2019), resulting in an inefficient use of native seed. Improved knowledge of pre-fire plant community composition and fire severity could substantially improve efforts to determine if burned areas require seeding to maintain perennial dominance, through improved pre-fire data collection and better matrices to assess post-fire conditions. In areas that need seeding, the next step would be to determine if native species are likely to successfully establish at that site and if seeds of these natives are available (Fig. 2). In areas with greater precipitation and higher elevation, currently available native seed sources can be successfully seeded in some sagebrush communities to prevent exotic annual grass dominance (Fig. 3; Davies et al., 2019; Urza et al., 2019). However, successful establishment of native perennials is less likely as sites become hotter and drier (Fig. 4). This is in part due to the majority of widely available native seeds being sourced from cooler, wetter areas (Jones and Larson 2005). More direct comparisons of the
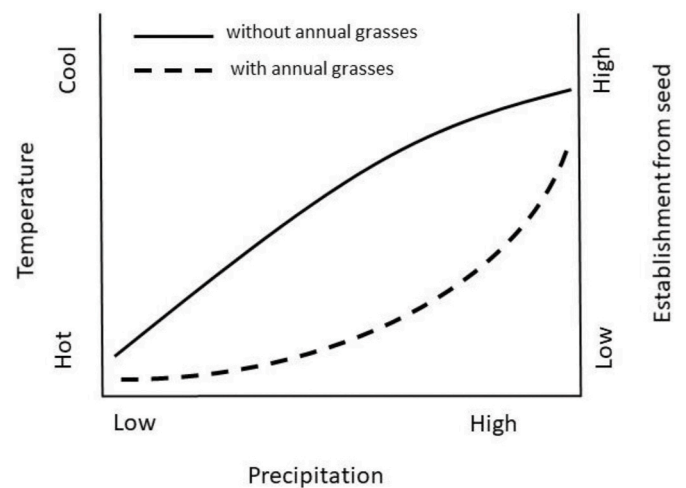

Fig. 4. Theoretical probability of successfully establishing native perennial vegetation in sagebrush communities across temperature and precipitation gradients with and without exotic annual grasses.

relative establishment of native species of different origins and crested wheatgrass across a range of environmental variation is needed to determine where native species are likely to be as successful as introduced species. This could also be used to ascertain the probability of native species establishment across environmental gradients, to help managers evaluate if the risks and costs are worth the potential rewards of seeding native species at given locations.

In areas where crested wheatgrass is seeded, efforts should be made to establish sagebrush and manage crested wheatgrass stands to promote other types of native vegetation. This could create crested wheatgrass-sagebrush communities that provide better habitat for sagebrush-associated wildlife than monotypic crested wheatgrass grasslands. Increased abundance and cover of sagebrush and other natives in crested wheatgrass stands corresponds to increased floristic and structural diversity and better habitat for native wildlife (Vale 1974; Reynolds and Trost 1981; Parmenter and MacMahon 1983; McAdoo et al., 1989). Efforts to establish native vegetation in crested wheatgrass stands by seeding native vegetation with and without crested wheatgrass control have, however, largely failed, and can elevate the risk of substantial increases in exotic annual grasses if crested wheatgrass is successfully controlled (Hulet et al., 2010; Fansler and Mangold 2011; Morris et al., 2019). In contrast, transplanting sagebrush seedlings into crested wheatgrass stands can substantially increase sagebrush cover and density (Davies et al. 2013, 2020). Grazing crested wheatgrass stands can also promote native vegetation, likely by reducing the competitive advantage of crested wheatgrass (Nafus et al., 2016). However, native species that are functionally similar to crested wheatgrass may not fare well, regardless of management, because competition from crested wheatgrass may limit resources available to them. Native species with resource use acquisition patterns that have less overlap with crested wheatgrass or largely complete their life-cycle when resources are not limited, such as shrubs and early growing species, are more abundant in crested wheatgrass communities (Nafus et al., 2020). Thus, if crested wheatgrass is seeded, efforts should be made to promote native vegetation within these areas, particularly species that differ functionally from crested wheatgrass, which would increase ecosystems services such as wildlife habitat, biodiversity, and resource capture.

5. Improving success with natives

The first opportunity for success with native species is to allow them to naturally recover when possible. Seeding into areas that will naturally recover without intervention may be counter-productive (Ratzlaff and Anderson 1995). Thus it is critical to determine if seeding is necessary prior to seeding. This will also prevent expending limited resources on unnecessary actions. However, native species often need to be seeded to restore native plant communities. Success of native species establishment from seed in sagebrush communities and other arid and semi-arid rangelands can be low (Svejcar et al., 2017; Svejcar and Kildisheva 2017).

The success of seeding native plants can be substantially increased with 1) using plant materials adapted to site environmental characteristics, 2) advancements from plant breeding and selection, and seed enhancement technologies, and 3) planning for additional treatments should initial efforts fail. All these efforts will require substantial investments and a commitment to restoring exotic annual grass-invaded sagebrush rangelands. These efforts, however, could substantially increase the likelihood of successful restoration.

A critical component to successfully restoring native species is seeding populations that are adapted to local environmental conditions and have characteristics that help them thrive in disturbed environments. Locally sourced plants generally have greater survival and fitness, likely because they harbor adaptations to local conditions (Baughman et al., 2019). What exactly constitutes "local" varies by species, and the need to balance the use of locally-adapted seeds with the constraints of commercial seed production is an ongoing discussion

(National Academy of Science, 2020). Seed transfer zones, which have a long history of use in production forestry, are a method to accomplish this, by delineating zones where managers can source and deploy plant materials that are well-adapted to site characteristics (St. Clair et al., 2013; Bower et al., 2014; Havens et al., 2015). When creating seed transfer zones, there is a deliberate effort to balance evidence of local adaptation with practical considerations of the need to increase seed for widespread use (e.g. Johnson et al., 2015). However, as climate changes or sites become heavily disturbed, even locally collected seed may not perform well (Havens et al., 2015). Plant materials from southern ecotypes may already be favored in more northern seed zones and this is expected to continue with further climate change (Hu et al., 2017; Etterson et al., 2020), though experimental evidence does not always support the idea that planting ecotypes from warmer and drier climates increases their success (Bucharova 2017). Beyond the moving of populations, as climate changes, some species will no longer be adapted to their historical range and may experience a distribution shift (Schlaepfer et al., 2015), a reality that is affecting planning in the forestry community (Dumroese et al., 2015). In the short-term, ensuring that seeded native species are well-adapted to the local environment, including the conditions of the restoration, will increase the probability of successful restoration, but managers and scientists should collaborate on testing the efficacy of "prestoration" in sagebrush ecosystems (Butterfield et al., 2017).

Even with appropriately adapted plant materials, successful establishment of native perennial vegetation in the hotter and drier sagebrush communities is likely to be a challenge (Knutson et al., 2014; Pilliod et al., 2017). This is not surprising as most successful seeding projects in rangelands, including both native and introduced seedings, occur in average to above-average precipitation years (Hardegree et al., 2016). In addition, most of our native perennial species do not compete well with exotic annual grasses, particularly at the seedling stage (Asay et al., 2003). This is associated with the fact that many native species in the sagebrush ecosystem have evolved over millennia within an environment favoring traits that enhance persistence under abiotically variable conditions (e.g., perennial life histories with substantial investment in below ground biomass to maximize resource capture) vs. traits that produce rapid establishment (e.g., high production of viable seeds that reliably and rapidly germinate, emerge, and establish). Thus, the need of contemporary restoration practitioners to have reliable and rapid perennial seedling establishment in annual grass-prone rangelands is contrary to the evolutionary development of many of our native species. Therefore, increased inputs such as weed control, high seeding rates, supplemental water, or transplanting juvenile plants may be needed to establish native species in the driest, most invaded sites. Approaching the restoration of challenging areas with a focus towards creating smaller "islands" of diverse, native vegetation within a matrix of invaded areas may be the most realistic option (Hulvey et al., 2017). Strategically locating these high-input restoration efforts in areas with geographic features that tend to be natural refugia during wildfire (Meddens et al., 2018; Martinez et al., 2019) would create potentially valuable resources for wildlife (Steenvoorden et al., 2019) as well as serve as a long-term source of native plants that could re-establish if future conditions shift to favor perennial life-history strategies.

Selection of native species and populations with increased likelihood of establishing and persisting in hotter and drier environments would improve restoration. Early seral species such as annuals may be better at establishing quickly in disturbed areas (Uselman et al., 2014), and including these species in restoration mixes may lead to greater success. Furthermore, within wild plant populations, there is considerable variability in plant characteristics, and there is evidence that some seed sources may be particularly good at establishing in highly invaded, dry sites (Leger et al., 2019). Selecting or breeding for traits that have proven beneficial in natural environments, compared to those selected for agricultural production of seed, could improve restoration success (Kulpa and Leger 2013). Plant breeding and selection should also focus

on improving native species' competitiveness with exotic annual grasses so they can be a more viable option to restore exotic annual grasslands. This could include selecting populations that have persisted in exotic annual grasslands, as they can show evidence of adapting to exotic annual grass competition (Leger 2008; Goergen et al., 2011). While identifying adaptive characteristics and valuable populations requires a great deal of support to be successful, applying these concepts to selecting specific seed sources is likely to be fruitful (e.g. Leger et al., 2020).

Advancements in seed enhancement technologies tailored to overcome specific barriers to native plant establishment can increase the probability of restoration success (Madsen et al., 2016a). Seed enhancement technologies can be used to improve seed soil contact (Madsen et al., 2016b) and overcome ecological barriers such as crusting soil surfaces (Madsen et al., 2012a) and hydrophobic soil surfaces (Madsen et al., 2012b), delay germination to prevent winter freezing mortality of young seedlings (Richardson et al., 2019), or speed up germination to capitalize on desirable environmental conditions (Madsen et al., 2018). Seed enhancement technologies have also shown promise when used in conjunction with exotic annual grass control. Small amounts of activated carbon around seeds have proven effective at neutralizing pre-emergent herbicides in the immediate area around seeds and thus allows desired species to be seeded at the same time annual grasses are controlled (Davies et al., 2017; Davies 2018; Clenet et al. 2019, 2020). This affords seeded species an opportunity to establish without competition from exotic annual grass, thereby greatly increasing the probability of establishing a perennial-dominated community. Although seed enhancement technologies have great potential for improving native species restoration, significant investments are needed to refine them and make them commercially available and economically viable.

Finally, restoring native vegetation could also be improved by developing restoration plans that include strategies and funds for adaptively implementing additional treatments, in case initial efforts fail. For example, seeding native species in multiple years can increase the probability of seeding coinciding with environmental conditions favorable for establishment (Davies et al., 2018b). Research could help these endeavors by determining the probability of restoration success across environmental gradients. Knowing the likelihood of success prior to treatment application would allow restoration practitioners to envision and plan for the logistical and financial resources needed for restoration success at a time coincident with funding availability (e.g. post-fire).

Incorporating the aforementioned suggestions into restoration efforts will improve the probability of reestablishing perennial-dominated communities in the sagebrush ecosystem and also other degraded rangelands throughout the world. Success will not be guaranteed, but the likelihood of success can be much greater than its current level. However, the scale of the exotic annual grass problem is so extensive that many locations will probably not be restored because of fiscal constraints. Furthermore, the probability of success in some locations is so low because of harsh site environmental characteristics that large-scale restoration efforts should probably not be attempted without innovative methods that demonstrated success at smaller scales.

6. Living with exotic annual grasslands – lessons from California grasslands

Unlike the sagebrush ecosystem, which has an expanding annual grass invasion (Smith et al., 2021), California grasslands have long been almost fully converted to annual grasses. As such, California may provide a useful counterpoint for determining when and how to live with exotic annual grasses in the sagebrush ecosystem. Exotic annual grasses, particularly cheatgrass, were introduced to the sagebrush ecosystem in the mid-1800s but did not invade extensively until a combination of overgrazing and drought drove their spread in the early 1900s (Svejcar

et al., 2017). In contrast, the exotic annual grass invasion in California began much earlier and has been characterized by multiple invasion waves. Exotic Mediterranean plant species initially replaced native California vegetation in the 1700s and 1800s. This first invasion wave consisted of higher quality forage species such as wild oats (*Avena sp.*) and filaree (*Erodium sp.*) introduced by Spanish settlers (Bartolome et al., 2007; D'Antonio et al., 2007). A combination of drought and over-grazing in the mid-1800s is associated with a second and third wave of invasion consisting of less-palatable exotic annual grasses including bromes (*Bromus sp.*) and foxtails (*Hordeum sp.*)(Jackson 1985). Currently, California is experiencing a fourth invasion of exotic annuals grasses such as medusahead, which can be the first exotic annual grasses to invade sagebrush communities. California's longer history of invasion may provide insights into how to manage the contemporary sagebrush ecosystem in the Great Basin and surrounding areas that is at risk of exotic annual grass invasion or already invaded.

The initial exotic annual grass invasion in California occurred so early that there is a limited understanding of which native species initially dominated the system. As such, management goals in California are often based on contemporary values rather than returning to a historical state (Stein et al., 2014). The majority of California grasslands are managed for forage, with goals aimed at maintaining production during drought and minimizing the impact of less desirable invasive species. At the same time, pockets of California grasslands such as serpentine grasslands support high native plant species diversity, and management goals in these areas are frequently focused on conservation. Given the widespread contemporary changes in the sagebrush ecosystem, management may similarly benefit from goals developed by explicitly identifying and discussing desired use and value of particular land areas, rather than focusing entirely on historical reference communities. The rise of participatory cooperatives and working groups throughout the Great Basin and surrounding areas indicates a path forward for this process. An exclusive focus on restoring historical communities may cause us to overlook management actions that could increase the ecosystem service value of already converted annual grasslands in the sagebrush ecosystem.

A second lesson from California is that the environmental and spatial context is important for determining when to manage for native perennial species and when to learn to live with annuals (Hobbs et al., 2014). In California, as in the sagebrush ecosystem, perennial grass populations are more likely to successfully compete with annuals in cooler, wetter sites, but unlikely to be as competitive in hotter, drier sites (Corbin and D'Antonio 2004), indicating that perennial restoration in California is unlikely to be successful past a rainfall threshold. Similarly, ongoing nitrogen deposition has favored annual grasses in some areas of California, and past a certain nitrogen threshold exotic annual grasses will always outcompete perennial bunchgrasses (Fenn et al., 2010; Larios et al., 2017). Finally, fire disturbance is frequent in California, and perennial grasslands can quickly convert to exotic annual dominance post-fire if surrounded by an exotic annual seed source (Larios et al., 2013). Consequently, even under environmental conditions that support perennial bunchgrasses, efforts to restore or maintain perennials are often stymied by the landscape context.

All of these considerations – climate, nutrients, disturbance, and spatial context – equally apply when identifying when and where to restore or revegetate exotic annual grass-dominated areas of the sagebrush ecosystem. The likelihood of restoration success in the sagebrush ecosystem diminishes as environmental conditions become hotter and drier (Kimball et al., 2015). These areas also have lower resilience to fire disturbance, furthering the risk that they will return to exotic annual grass dominance (Chambers et al., 2014). Finally, this risk is compounded when the surrounding landscape is dominated by exotic annual grasses; attempts to restore a 1000 ha within a 100,000-ha exotic annual grassland that burns every decade or less would be a Sisyphean task. This has been evident in areas of the Hanford Reach National Monument in Washington where planted sagebrush seedlings were subsequently

killed by wildfire (Dettweiler-Robinson et al., 2013). In regions with wide-spread degradation and conversion to exotic annual grasslands, it may not be possible to find locally adapted native species because exotic annual grasses have largely displaced them and, therefore, success would be unlikely. Areas that have to be broadcast seeded because of topography or logistical challenges are also much less likely to result in successful establishment of seeded vegetation than areas that can be drill seeded, assuming other influencing factors are similar (Nelson et al., 1970). Thus, not all areas possess a similar probability of being restored to perennial-dominance.

The best use of limited restoration resources is to focus on areas where success is somewhat probable, given site conditions, available seeds, and technological options available. Research is clearly needed to help determine where efforts should and should not be expended, considering the tools available. This could assist in prioritizing areas based on the probability of successfully establishing perennial vegetation that will persist as well as help develop realistic expectations. Until research has filled this critical knowledge gap, local expertise should be used to determine which annual grass-invaded landscapes can be converted to perennial-dominated communities, and which are economically infeasible or not realistic without additional advancements.

There are substantial areas of exotic annual grass-invasion that are unlikely to be successfully converted to perennial-dominated communities under current conditions. These areas are currently in stable states, and they need to have management objectives and goals that take into consideration the characteristics and traits of these annual plant communities. We propose referring to these communities as Intermountain West Annual Grasslands to aid in recognizing that these communities need different management than perennial communities. Most importantly, resource managers will need to recognize that grazing and management plans for maintaining perennial-dominance are unlikely to achieve objectives and goals in exotic annual grasslands. As in the California Annual Grasslands, the recognition that some areas have fully converted to annual grasslands should lead to the development of new management methods designed to maximize the value and ecosystem services obtained from these areas, despite their converted state.

Indeed, a third lesson from California is that management can significantly alter the ecosystem service value of annual grasslands, even when it cannot return them to perennial dominance (Stein et al., 2014). In the sagebrush ecosystem, grazing prescriptions are often focused on maintaining habitat for sagebrush-associated wildlife (Miller and Eddleman 2000; Davies et al., 2011); aligning with our focus on preventing annual grass spread. However, the habitat value of annual grass-dominated areas is already low, and developing alternative grazing practices for areas where annual dominance is entrenched may enhance other services. Unlike sagebrush communities, especially those at risk of exotic annual grass dominance, exotic annual grass communities are tolerant of intense grazing pressure (Norton et al., 2007; HilleRisLambers et al., 2010). Thus, it may be appropriate to graze these exotic annual grasslands more heavily and frequently, allowing greater forage consumption and aiding in the reduction of fine fuels. To date, research into grazing management for Intermountain West Annual Grasslands has received almost no attention. In contrast, extensive research on grazing management in California Annual Grasslands has identified practices to enhance forage production and stability, increase plant and avian diversity, and reduce the spread of noxious weeds (e.g. Hayes and Holl 2003; Stahlheber and D'Antonio 2013; Gennet et al., 2017; Brambila et al., 2020). Similar research is needed to determine grazing management strategies that encourage more diversity and desired community composition, improve forage quality, maintain soil health, and meet fine fuel management objectives in exotic-dominated grasslands in the sagebrush ecosystem. There could be unexpected benefits to surrounding perennial communities from this type of management, including focusing grazing use in converted lands, providing habitat for late-season perennial plants (such as drought- and grazing-tolerant forbs), and allowing for innovative ways to increase the potential habitat value of annual grasslands for pollinators, birds, and other wildlife.

7. Conclusions

Exotic annual grasses have caused unprecedented degradation of the sagebrush ecosystem. Preventing exotic annual grass dominance should be a high priority, since it is challenging to reestablish perennial vegetation once an exotic annual grassland has developed. Maintaining perennial vegetation, especially perennial grasses, is key to limiting exotic annual grasses. In areas that have been substantially invaded, breaking the annual grass-fire cycle should be a management objective. When natural recovery will be insufficient, seeding perennial vegetation after disturbances should be used to prevent exotic annual grass invasion in areas where that seeding is likely to be successful. Native species should be seeded whenever possible, but the likelihood of success with natives and the cost and availability of adapted native seeds will determine when and where. When and where natives are unlikely to be successful, judicious seeding of introduced bunchgrasses can be a valuable tool to stem the negative impacts of exotic annual grass invasion and potentially limit their spread. Seeding introduced perennial bunchgrasses is a better choice than allowing these communities to become exotic annual grass-dominated. However, native species that can co-occur with these introduced bunchgrasses should also be seeded or re-introduced when feasible, and creating islands of native species with intensive restoration methods could maintain landscape level diversity in otherwise non-native systems. Furthermore, introduced grasslands should be managed to encourage co-occurring native species, especially ones with limited overlapping resource use with crested wheatgrass. Efforts to improve native vegetation establishment and persistence are needed to expand their use and increase their efficiency. This involves using plant materials that are adapted to local environmental conditions, including competition from exotic annual grasses. Improved plant breeding and selection as well as seed enhancement technologies can also increase the probability of success with native species. However, even with these efforts, there are likely to be extensive expanses of exotic annual grasslands that cannot be feasibly restored. Recognizing these areas are now exotic annual grasslands and focusing restoration resources on areas where success is more probable will be important. Intermountain West Annual Grasslands need to be managed differently than perennial-dominated communities because their response to management and potential vegetation composition are vastly different. Clearly, research is needed to improve our management of exotic annual grasslands, particularly the effects of different types of grazing management on composition, fuel accumulations, habitat value, and forage. We are going to have to adapt to living with exotic annual grasses in the sagebrush ecosystem (Fig. 2) and develop novel ways to increase the value of these grasslands, as they are not going away in our lifetimes. Although we focused on exotic annual grasslands in the sagebrush ecosystem, the strategy of adapting to live with exotic plants can likely be applied to other wide-spread invasive species such as mesquite (*Prosopis* sp.) in Australia and Africa and molasses grass (*Melinis minutiflora* Beauv.) in the tropics. In particular, this would include determining realistic management and restoration goals for invaded ecosystems and investigating methods for enhancing ecosystem services derived from these ecosystems.

Declaration of competing interest

We have not conflict of interest to declare.

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