Plant silicon as a factor in medusahead (*Taeniatherum caput-medusae*) invasion

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Abstract

Medusahead [*Taeniatherum caput-medusae* (L.) Nevski] is one of the most detrimental invasive annual grasses impacting the sustainability and function of rangeland in the western United States. This annual grass possesses high concentrations of tissue silicon (Si) that may facilitate invasion through key plant characteristics such as increased plant fitness, structure, and antinutritive qualities. These characteristics may affect known invasive processes such as increased plant productivity, slow litter decomposition, and decreased herbivory, facilitating a positive feedback cycle of invasion. However, Si is not considered an essential element and is often overlooked as a factor of *T. caput-medusae* invasion. Thus, this article provides a synthesis of plant Si, *T. caput-medusae*, and the self-reinforcing feedback cycle of invasion. We also discuss how current control strategies address plant characteristics determined by Si and suggest research avenues that may aid in novel or improved control strategies that target the *T. caput-medusae*–silica relationship.

Introduction

Medusahead [*Taeniatherum caput-medusae* (L.) Nevski] is one of the most detrimental invasive plants impacting rangeland sustainability and livestock operations (Johnson and Davies 2012; Mangla et al. 2011; Nafus and Davies 2014); it decreases wildlife habitat and plant diversity and increases the frequency of fires (Davies 2011). Recently, the integration of multiple control strategies has reestablished desirable plant species (Davies and Boyd 2018; Schantz et al. 2019), but the cost and uncertainty of success still exists for land managers (James et al. 2015). Consequently, there is a critical need to assess the underlying causes of *T. caput-medusae* invasion and how these causes impact traditional control strategies and to develop management strategies that decrease success uncertainty. These challenging questions can be partially addressed through a conceptual model that considers how tissue silicon (Si) concentration influences *T. caput-medusae* plant characteristics and the invasive processes.

High tissue Si concentration is a vital attribute of *T. caput-medusae*, as it forms mineral silica complexes within stems and an epidermal silica varnish on the leaves, awns, and glumes (Bovey et al. 1961; Epstein 1999; Swenson et al. 1964). The varnish hinders digestive processes within the rumen of herbivores (Montes-Sánchez and Villalba 2017) and contributes to a defense mechanism that facilitates aversive grazing behavior (Coskun et al. 2019; Hunt et al. 2008; McNaughton et al. 1985). The same varnish also limits leaf litter decomposition, causing a persistent litter or thatch layer (Torell et al. 1961; Young 1992). Accumulated litter inhibits establishment of non–*T. caput-medusae* seedlings and increases fine fuels, facilitating a grass-fire positive feedback cycle (Davies and Nafus 2013; Kyser et al. 2007; Young et al. 1999). Finally, high tissue Si concentrations may increase *T. caput-medusae* productivity directly through enhanced plant fitness and indirectly through accumulated litter, which may improve *T. caput-medusae* germination and root development (Evans and Young 1970). Consequently, *T. caput-medusae* Si concentrations are likely linked to increasing both the relative and overall abundance of the weed in plant communities, decreasing native species diversity, and reducing net primary productivity, and contribute to the creation of positive feedbacks that favor persistence of exotic species at the expense of native species (Elgersma et al. 2012; Inderjit and Cahill 2015; Suding et al. 2013).

The conceptual model we propose portrays linkages between tissue Si concentrations and a self-reinforcing positive feedback cycle of *T. caput-medusae* invasion. These linkages may enhance a more mechanistic understanding of the invasive processes and potentially refine *T. caput-medusae* control and restoration effort opportunities (Figure 1). This model illustrates how tissue Si concentrations directly influence critical plant characteristics (e.g., fitness, structure, and chemical composition), which subsequently impact fundamental invasive processes
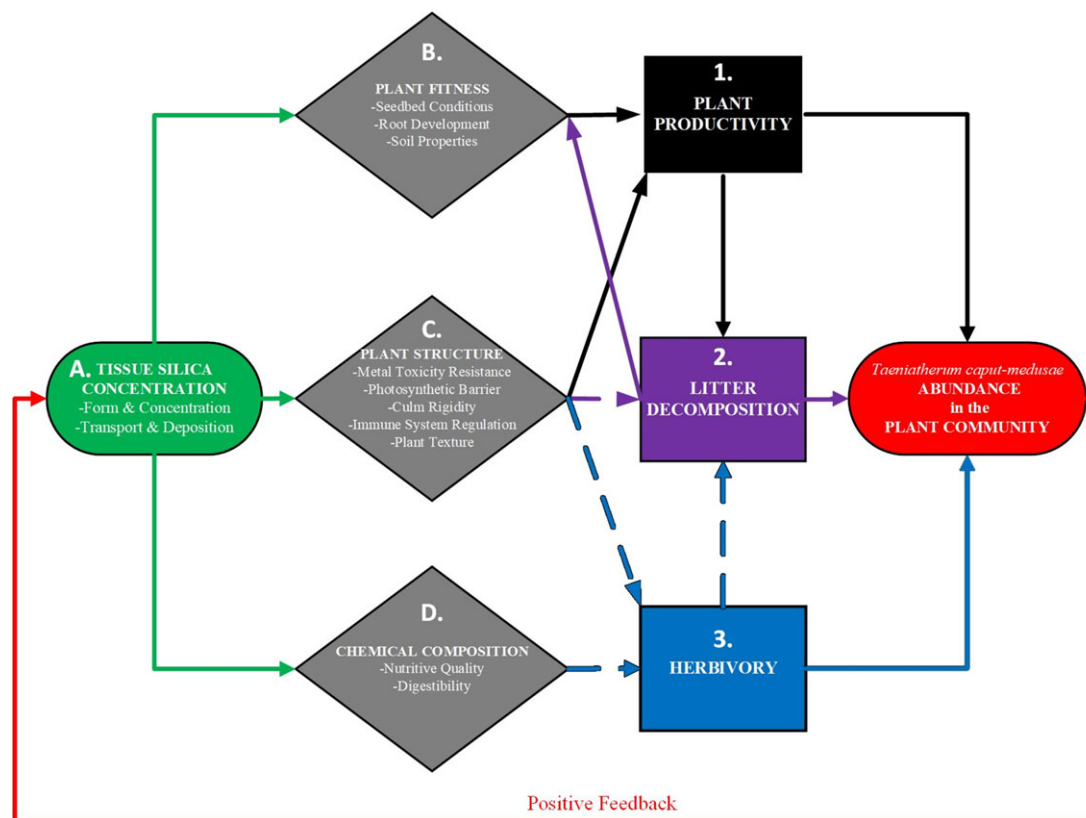
Figure 1. A model explaining the self-reinforcing positive cycle feedback of *Taeniatherum caput-medusae* invasion in relation to silicon (Si). Rhomboids represent plant characteristics; rectangles represent invasion processes; solid lines represent net positive effects and dashed lines net negative effects.

(e.g., plant productivity, litter decomposition, and herbivory). However, despite the connectivity between plant characteristics and invasive processes associated with *T. caput-medusae* abundance, close examination of the current knowledge base suggests that considerable uncertainty exists in how control strategies impact tissue Si concentrations.

Several categories of *T. caput-medusae* control (i.e., mechanical, cultural, and chemical) have been applied successfully to reduce and/or suppress the plant's abundance (Davies 2010; Kyser et al. 2007; Monaco et al. 2005; Stonecipher et al. 2016). However, tissue Si concentration is an underlying cause of invasion that is often overlooked, because Si is not considered an essential element of plant nutrition (Arnon and Stout 1939; Epstein 1999). Thus, the focus of this article will be to summarize the role of tissue Si in plants, identify *T. caput-medusae*'s characteristics and its invasive processes in relation to tissue Si using a conceptual model (Figure 1), address how control strategies address *T. caput-medusae* Si, and finally, suggest research avenues that may aid in novel or improved control strategies that target *T. caput-medusae*–silica relationships.

Silicon and Plants

Form and Concentration

Si is the second most abundant element found within the earth's crust (Epstein 1999), and the majority of plant Si exists as amorphous Si (i.e., phytoliths), which is insoluble in water. In contrast, its soluble form, orthosilicic acid, or simply silicic acid (Ma and Yamaji 2006), is the form taken up by plant roots and deposited

as the insoluble form, silica (Currie and Perry 2007; Epstein 1994, 1999). Often the literature does not distinguish between the two forms of Si, particularly with *T. caput-medusae*. Thus, unless soluble Si is directly stated herein, it is referring to the insoluble form, silica. Tissue silica varies widely among plant species (Hodson et al. 2005), and plants are generally classified as accumulators (1% to 10% silica on a dry matter basis) or nonaccumulators (<1%). Some monocots such as rice (*Oryza sativa* L.), sugarcane (*Saccharum officinarum* L.), and members of the Cyperaceae family (i.e., sedges) are considered hyperaccumulators, having greater than 10% silica in their tissues (Handreck and Jones 1967; Ma and Takahashi 2002; Neumann 2003). Consequently, many grasses are considered accumulators, but tissue silica varies widely depending on geographic location, phenological stage, and environmental conditions (McNaughton et al. 1985). For instance, tissue silica ranges between 1% and 4% in alpine tundra grasses, whereas African savanna grasses contain up to 20% (Johnston et al. 1968; McNaughton et al. 1985). Semiarid rangeland grasses are considered intermediate accumulators, with tissue silica ranging between 3% and 9% (Shewmaker et al. 1989), but *T. caput-medusae* stands out as a hyperaccumulator, with values ranging between 10% and 19% (Bovey et al. 1961; Epstein 1999; Swenson et al. 1964).

Transport and Deposition

The uptake of soluble Si varies based on species, genotype, and root structure, and its transport occurs via the transpiration stream (Ma and Yamaji 2006). Transport can be active, passive, and/or rejective (Ma et al. 2004; Mitani and Ma 2005; Takahashi et al. 1990).

For example, accumulation in grasses is believed to be a passive process, wherein these plants often display tissue silica concentrations reflective of soluble soil Si concentrations (Handreck and Jones 1967; Ma et al. 2001). In contrast, some dicots exhibit a rejective transport mechanism associated with a physical barrier in roots, allowing water and nutrient passage but limiting soluble Si uptake (Jones and Handreck 1969). Hyperaccumulators such as rice (Feng et al. 2011; Ma et al. 2007), barley (*Hordeum vulgare* L.) (Chiba et al. 2009), maize (*Zea mays* L.) (Mitani et al. 2008), wheat (*Triticum aestivum* L.) (Casey et al. 2004; Rains et al. 2006), and cucumber (*Cucumis sativus* L.) (Liang et al. 2005) display an active transport mechanism that facilitates soluble Si uptake and deposition (Chiba et al. 2009; Ma et al. 2006, 2007). In passive transport, soil moisture is one of the primary limiting factors of mineral uptake (Bloom et al. 1985; Hu and Schmidhalter 2005). In semiarid environments where soil moisture is limited, grass species display low to moderate levels of tissue Si concentrations (Shewmaker et al. 1989), likely due to passive transport. *Taeniatherum caput-medusae* has tissue silica concentrations similar to that of rice, although it is unknown whether it uses an active or passive transport mechanism. An active transport mechanism is more plausible, as concentrations of *T. caput-medusae* tissue silica are greater than those of other semiarid species (Bovey et al. 1961; Swenson et al. 1964).

As soluble Si is transported to various parts of a plant, it is dehydrated and polymerized into a di- or poly-silicic acid, which can be further polymerized within cellular structures to silica (Casey et al. 2004; Ma and Yamaji 2006; Mitani and Ma 2005). Cellular constituents such as hemicellulose, callose, pectin, and lignin have been shown to provide a framework for deposition (Guerriero et al. 2016). Tissue silica can also take on various forms, depending on deposition location, cell shape, and environmental conditions (Blackman 1971; Li et al. 2014). The location for silica deposition also varies greatly among plant species (Lewin and Reimann 1969; Lux et al. 2003). Tissue silica bodies have been observed in all major aboveground plant parts of *T. caput-medusae*, including sausage-shaped bodies beneath the epidermis of culms and a varnish-like structure on the awns as silicified barbs (Swenson et al. 1964).

Tissue Silicon and *Taeniatherum caput-medusae* Plant Characteristics

Plant Fitness

High tissue Si in *T. caput-medusae* may influence many factors associated with plant fitness that can be linked to plant productivity (Figure 1). For instance, tissue Si may increase root development, slow litter decomposition, alter soil conditions, and contribute to microsite conditions that favor *T. caput-medusae* germination. Overall, high tissue Si likely has a cascade of net positive effects on *T. caput-medusae* productivity and abundance within plant communities, which in turn strengthens the feedback cycle of invasion.

Seedbed Conditions

Successful seedling establishment in plants is often determined by the number of safe sites provided by the soil surface (Evans and Young 1970; Harper et al. 1965). Litter can create a favorable microenvironment for *T. caput-medusae* seeds that do not arrive at soil safe sites. For instance, as a consequence of high tissue Si concentrations, *T. caput-medusae* litter is slow to decompose (Figure 1), contributing to years of persistent decadent plant

material (Bovey et al. 1961; Young 1992). While many plant components such as lignin (Aerts 1997; Laishram and Yadava 1988; Stott et al. 1983), tannin-protein complexes (Palm 1988), and high C:N and C:P ratios (Goldman et al. 1987) reduce litter decomposition rates, Si is thought to be the primary contributor to slowed decay rates in *T. caput-medusae* (Torell et al. 1961; Young 1992). Evans and Young (1970) found that *T. caput-medusae* litter reduces seasonal and daily temperature fluctuations and water evaporation and increases humidity, which together contribute to a more favorable seedling microenvironment. The awns of *T. caput-medusae* seeds also get caught within the litter, limiting seed burial and intimate contact with the soil surface (Evans and Young 1970). For other plant species, this may pose a dire problem, as they require direct contact with a moisture-supplying substrate such as the soil, but *T. caput-medusae* seeds absorb moisture from the litter environment (i.e., they are hygroscopic) (Young 1992). In support of the favorable, self-induced seedbed conditions, *T. caput-medusae* was found to produce 47 times more seedlings within its litter environment than on bare ground conditions (Evans and Young 1970). This is not to say that *T. caput-medusae* cannot germinate without the presence of litter, but rather the accumulation of litter enhances *T. caput-medusae* establishment and persistence.

Root Development

Cheatgrass (*Bromus tectorum* L.) and *T. caput-medusae* roots develop at comparable rates and can grow to depths of 100 cm (Hironaka 1961). Both annual grasses primarily germinate in the autumn, continue slow root growth through the winter, and have greater root elongation into spring and summer than newly established native perennial grass species (Harris 1977; Hironaka 1961; Vasquez et al. 2008). Collectively, these unique root development traits enable *T. caput-medusae* and similar annual grasses to gain a competitive advantage over perennial plant species through greater resource acquisition (James et al. 2010; Vasquez et al. 2008; Young and Mangold 2008).

Taeniatherum caput-medusae diverges from other invasive annual grass species when it comes to root cell size and structure. For instance, Harris (1977) compared the root cellular composition of *T. caput-medusae*, *B. tectorum*, and a perennial grass through photomicrographs and showed that *T. caput-medusae* had thicker cell walls and overall larger root diameters than *B. tectorum*, but lower values than the perennial grass species. It was proposed that the thicker cellular root endodermis may allow for transpiration to occur even if the surrounding soil environment is drier, particularly in the upper soil horizons. When a Si-based fertilizer was applied to a variety of plant species (e.g., sorghum [*Sorghum bicolor* (L.) Moench], rice, wheat, and potatoes [*Solanum tuberosum* L.]), root endodermis cells were more rigid and efficient in water transpiration under moisture-lacking conditions (Chen et al. 2011; Crusciol et al. 2009; Gong et al. 2005; Hattori et al. 2003). In general, Si has been associated with increased plant tissue rigidity in several plant species (Ma et al. 2006; Namaganda et al. 2009; Raven 1983). Despite considerable information on Si and its beneficial role in other plants, there is very limited information pertaining to *T. caput-medusae* roots and how Si influences root development.

Soil Properties

Taeniatherum caput-medusae can be found on a variety of soil types, but more frequently in clayey soils as opposed to coarse-textured, sandy soils (Dahl and Tisdale 1975). Because clayey soils

are known for their high water-holding capacity and shrink–swell characteristics, which create large soil cracks and/or fissures when they dry, plant seedlings and their roots can experience increased desiccation as cracks develop (Young et al. 1999). However, *T. caput-medusae* roots are well adapted to this potential threat. For instance, if the primary root of *T. caput-medusae* is injured or dries out, an adventitious root emerges to replace the primary root (Young 1992). Vascular tissues have been found to be strengthened by Si accumulation and may be able to withstand the shrinkage-induced tissue stress from the drying of clayey soils (Hattori et al. 2003). With high tissue Si concentrations, *T. caput-medusae* likely responded more favorably (i.e., greater root growth) on clayey soils and large/infrequent watering treatments compared with other invasive annual grasses such as *B. tectorum* or ventenata [*Ventenata dubia* (Leers) Coss.] (Bansal et al. 2014).

Edaphic conditions, such as nutrient availability, may also be related to *T. caput-medusae* invasion. A transplant study between *T. caput-medusae* seeds from California and France showed that California soils produced larger plants than those from France (Blank and Sforza 2007). It was proposed that California soils have greater nutrient content than those from France. In a comparative growth study, nitrogen and phosphorus additions increased biomass production of *B. tectorum* more so than *T. caput-medusae* (Dakheel et al. 1993). In the same study, when soils were deficient in phosphorus, *B. tectorum* also outproduced *T. caput-medusae*. Similarly, *B. tectorum* produced more shoot mass than *T. caput-medusae* when grown in different nitrogen nutrient solutions (MacKown et al. 2009). Nevertheless, none of these studies reported soil or plant Si concentrations, likely due to the fact that Si is not considered an essential element of plant nutrition (Arnon and Stout 1939; Epstein 1972). Because Si has been shown to increase root and leaf elongation in hyperaccumulator plant species (i.e., sorghum and rice) (Hattori et al. 2003; Hossain et al. 2002), it is possible that the combination of Si dissolution in clayey soils (Tubaña and Heckman 2015) and the potentially high uptake capacity of soluble Si by *T. caput-medusae* may facilitate increased growth and offset the competitive superiority of *B. tectorum* described in the aforementioned studies.

Plant Structure

Tissue Si may influence many plant structural factors of *T. caput-medusae*, such as metal toxicity resistance, protection from ultraviolet-b (UV-B) radiation damage, increased culm rigidity, and upregulation of the innate immune system. These factors may directly decrease litter decomposition rate and herbivory, indirectly increase plant fitness and productivity, and contribute to the overall abundance of *T. caput-medusae* in the plant community (Figure 1).

Metal Toxicity Resistance
The accumulation of toxic metals can negatively impact plant fitness (Nagajyoti et al. 2010), and evidence suggests that tissue Si mitigates this toxicity through structural adaptations within the plant (Ma 2004). An apoplastic root membrane was shown to regulate the translocation of metals through plant cell walls (Emamverdian et al. 2018). Deposition of Si within the membrane was thought to decrease the porosity of the cell wall, consequently reducing the movement of toxic metals and salts into the plant (Coskun et al. 2019; Gong et al. 2006; Wu et al. 2013). Some toxic metals may pass through the membrane, but soluble Si can form mineral complexes to increase adsorption and reduce toxic metal

movement within plants (Keller et al. 2015; Wang et al. 2004; Ye et al. 2012). However, Adrees et al. (2015) suggested that changes in root structure were not the only mechanism of decreased toxic metal uptake. Modulation of the influx transporters by Si may also decrease toxic metal uptake. *Taeniatherum caput-medusae* was found to colonize waste mine sites high in toxic metals, although the aforementioned mechanisms of reduced metal toxicity were not addressed (Martínez-Ruiz et al. 2001; Reglero et al. 2008). Consequently, these mechanisms could reduce metal toxicity in *T. caput-medusae*, contributing to its invasion, but further exploration is needed.

Photosynthetic Barrier
Reductions in the atmospheric ozone layer have resulted in increased UV-B radiation reaching the earth's surface (Madronich et al. 1998). Increased UV-B radiation can damage leaves and reduce the photosynthetic capacity of plants (Kakani et al. 2003). Supplementing rice with soluble Si reduced UV-B damage through increased leaf rigidity and the production of phenolic compounds (Li et al. 2004; Tamai and Ma 2008). The presence of tissue Si within the cellular membranes also mitigated UV-B–induced reactive oxygen species, which are known to cause membrane damage, decrease enzyme activity, increase electrolyte leakage, and alter gene expression (Coskun et al. 2019; Shen et al. 2010). Despite these studies, the relationship between photosynthesis and tissue Si in *T. caput-medusae* has not been evaluated.

Culm Rigidity
Taeniatherum caput-medusae plants can reach a height of more than 60 cm, which is impressive, given that its culms are typically thin (e.g., <1-mm diameter) and inflorescences are relatively large and "wispy" (McKell et al. 1962), possibly making them susceptible to lodging and breakage (Savant et al. 1996). Culm integrity of *T. caput-medusae* is potentially enhanced due to the accumulation of silica, which increases the rigidity of the stem and leaves of certain plants (Ma et al. 2006; Namaganda et al. 2009). For instance, rice lodging was reduced with increasing tissue Si concentrations (Lee et al. 1990; Savant et al. 1996). However, no studies have examined the associations between culm rigidity in *T. caput-medusae*, tissue Si, and lodging.

Immune System Regulation
Wagner (1940) was the first to suggest that tissue Si increases plant defenses against stem-boring pathogens; this is known as the mechanical barrier hypothesis. However, studies in rice (Rodrigues et al. 2003, 2004) and wheat (Bélanger et al. 2003; Rémus-Borel et al. 2009) have shown that there is an upregulation of the innate immune system (e.g., chitinases, peroxidase, polyphenol oxidases, phytoalexins, and phenolic compounds) following predation rather than the aforementioned physical defense. Tissue Si is known to act as a modulator of these plant defenses. For instance, tissue Si–associated defenses increase the binding affinity of plant proteins within the defense signaling pathway, preventing these pathogenic enzymes from reaching their target (Datnoff et al. 2007; Fauteux et al. 2005). Recent work on pathogens and stem-boring insects demonstrated that these predators release effector proteins that interfere with the defense signaling pathway (Giraldo and Valent 2013; Mugford et al. 2016). Soluble Si deposition strengthens the apoplastic membrane and prevents the effector proteins from reaching their target (Holub and Cooper 2004; Nuernberger and Lipka 2005). Another postulation is that tissue Si allows for the redistribution of energy stores to upregulate

defense responses. For instance, Si-accumulating plants may replace energy-dependent processes involved in building structural carbohydrates for non–energy dependent ones (McNaughton et al. 1985; Van Soest 2006). Energy stores that would otherwise be used for growth and development of plant structural components are redistributed to the innate immune system (Coskun et al. 2019). Overall, the redistribution of energy stores and production of a tissue Si physical barrier allow for a stronger defense response upon predation. However, these theories on tissue Si and the upregulation of the innate immune response have not been explored in *T. caput-medusae*.

Plant Texture

Invertebrate insects (Massey et al. 2006), voles (Massey and Hartley 2006), rabbits (Cotterill et al. 2007), livestock (Massey et al. 2009; Shewmaker et al. 1989), small granivores, and birds (Longland 1994; Savage et al. 1969) all show decreased preference for Si-rich grasses. This avoidance may be a consequence of an undesirable oral texture. For instance, *T. caput-medusae* inflorescences have a large vertical awn attached to the seed, with shorter lateral spiked glumes (Miller et al. 1999). Microscopic examination of *T. caput-medusae* awns revealed that they contain a Si varnish with barbs (Swenson et al. 1964), which may contribute to the undesirable texture causing irritation to mouthparts (Massey and Hartley 2009). In addition, tissue Si in grasses has been associated with increased tooth wear (Baker et al. 1959), gastrointestinal urolithiasis (Bailey 1981), and esophageal tumors (O'Neill et al. 1982, 1980), possibly causing further *T. caput-medusae* avoidance.

Disarticulation of seeds from the seed head occurs from July to October, with the majority being dropped in August (Davies 2008), providing an opportunity for herbivory without the consequence of oral irritation. However, Si bodies are still present in the stem (Swenson et al. 1964), and likely in the spiked glume after seed disarticulation, and continue to provide an abrasive texture. In contrast, other annual grasses such as *B. tectorum* lack these short spiked glumes, and when seed drop occurs, the plants become susceptible to herbivory (Vallentine and Stevens 1994). Overall, the texture caused by *T. caput-medusae* tissue Si may deter herbivory of *T. caput-medusae*, facilitating a self-reinforcing positive feedback cycle.

Chemical Composition

Tissue Si concentrations have a direct effect on the nutrient content and digestibility of *T. caput-medusae* (Figure 1). These effects negatively impact herbivory and increase litter accumulation, which both directly and indirectly increase *T. caput-medusae* abundance within the plant community.

Nutritive Quality

Tissue nutrient concentrations and their association to plant secondary compounds or toxins largely influence the likelihood of a plant being consumed by an herbivore (Provenza et al. 2002). Bovey et al. (1961) showed that *T. caput-medusae* contains 10.4% crude protein (CP), 2.6% fat, 26.8% crude fiber, 6.1% lignin, and 13.9% ash during the vegetative phenological stage. Subsequently, rapid maturation causes a decline in CP and fat content, while fiber, lignin, and ash concentrations increase. Other more recent studies show similar trends for the nutritional composition of *T. caput-medusae* over time (Montes-Sánchez and Villalba 2017; Villalba and Burritt 2015). Plant ash is an indicator of tissue silica content, and silica in ash comprises values greater than 90% in rice plants (Charca et al. 2007; Yalçin and Sevinç 2001). These values can be lower, depending on plant species and tissue location (Lanning et al. 1980; Lanning and Eleuterius 1983). *Taeniatherum caput-medusae* ash comprises more than 70% tissue silica, whereas *B. tectorum* comprises 47% (Bovey et al. 1961). In the early phenological stages, *T. caput-medusae* has similar nutritional value to that of other desirable grass, and livestock grazing can be used as a method of control (Bovey et al. 1961; DiTomaso et al. 2008; Hamilton et al. 2015; Villalba and Burritt 2015). Because of its rapid maturation, decline in nutritional value, and high silica concentrations, the window of palatability is limited to 2 to 4 wk (Brownsey et al. 2017). After this period, consumption of *T. caput-medusae* is reduced, and grazing pressure on more nutritious plant species may occur and be deleterious (DiTomaso and Smith 2012; Sheley et al. 2008). Even if *T. caput-medusae* was palatable after seed drop, the nutritional quality of the plant is inadequate to sustain grazers. Domestic ungulates require a minimum of ~7.5% CP for body maintenance (National Research Council 2000, 2007a, 2007b), and supplementation is required for animals grazing most grasses at later phenological stages (Ganskopp and Bohnert 2001). Animal supplementation of nutrient-rich forages in combination with *T. caput-medusae* were shown to increase consumption of the troublesome grass (Hamilton et al. 2015; Montes-Sánchez et al. 2017; Stonecipher et al. 2016). Nevertheless, in these studies, *T. caput-medusae* consumption was low and would not likely discourage *T. caput-medusae* abundance within the plant community. Additionally, tissue Si was unaltered when fed to grazers, and thus the defense mechanism of the plant still existed, possibly limiting utilization of the chemical constituents within. Supplemental grazing of *T. caput-medusae* in the autumn also does not reduce the soil seedbank, as seed drop has already occurred, and may actually increase *T. caput-medusae* abundance in subsequent years (DiTomaso et al. 2008; Lusk et al. 1961). These studies indicate that similar to plant texture (discussed earlier), chemical composition alone does not explain the low intake and palatability of *T. caput-medusae*.

Digestibility

Tissue Si within plants has been proposed as a defense mechanism against herbivory (Hunt et al. 2008), similar to those induced by plant secondary compounds or toxins (Provenza et al. 2002). An epidermal silica varnish in *T. caput-medusae* acts as a physical barrier limiting the degradation of the cell wall by rumen microorganisms (Hunt et al. 2008; Montes-Sánchez and Villalba 2017). This barrier prevents utilization of the organic constituents beneath such a layer (Mayland and Shewmaker 2001; Van Soest 1994; Van Soest and Jones 1968). Support for this reduced digestion mechanism was shown by Montes-Sánchez and Villalba (2017), who reported declines in digestibility of *T. caput-medusae* with increments in the plant's particle size; with larger particles conserving the tissue Si barrier to a greater extent than particles of a smaller size. Although lignin content has been associated with decreased digestibility of certain plants, differences in *T. caput-medusae* digestion rates were not influenced by this factor, as alfalfa (*Medicago sativa* L.) and tall fescue (*Schedonorus arundinaceus* (Schreb.) Dumort., nom. cons.) hay had lignin concentrations similar to those present in *T. caput-medusae*. In addition, soluble Si limits enzymatic activity (Kind et al. 1954), thus decreasing plant digestibility in the rumen (Smith et al. 1971). Finally, for every percentile unit increase in tissue silica, there are between 1 and 3 percentile units of reduction in forage digestibility (Smith et al. 1971;

Van Soest and Jones 1968). In avian species, such as chukar partridges (*Alectoris graeca* Meisner), *B. tectorum* seeds were preferred over *T. caput-medusae* seeds (Savage et al. 1969), likely due to undesirable high tissue Si in *T. caput-medusae* and a concomitant lower digestibility, but other factors such as seed size may influence ingestion.

Traditional Control Strategies

Commonly used *T. caput-medusae* control strategies can be categorized into mechanical, cultural, and chemical. Each addresses certain aspects of the Si positive feedback cycle (Figure 1). Integrating multiple strategies is often more successful than using one strategy by itself (Davies 2010; Davies and Sheley 2011; Kyser et al. 2007; Monaco et al. 2005). This section will address individual strategies and their roles in the Si positive feedback cycle, potentially giving insight into why integrated control is often more successful.

Mechanical Control

Mowing

A window of opportunity for mowing *T. caput-medusae* was proposed, which was ~35 d from late vegetative to early reproductive phenological stage (Brownsey et al. 2017). The same study estimated that mowing before seed head emergence decreased *T. caput-medusae* seed production by ~50%. However, early spring mowing may miss younger plants and allow recovery of damaged plants, enabling *T. caput-medusae* to produce seeds and only temporarily reduce plant productivity. The optimal timing of mowing and control should be tailored to occur when the majority of plants are in the boot phenological stage, thus limiting seed production and additional late-maturing plants. Plant Si has been shown to increase plant tissue rigidity (Ma et al. 2006; Namaganda et al. 2009; Raven 1983) and potentially decrease microbial degradation, increasing litter accumulation (Torell et al. 1961; Young 1992). Mowing mulches the standing biomass and may artificially accelerate litter decomposition, but it may also create favorable microsites for *T. caput-medusae* seedlings (Evans and Young 1970). *Taeniatherum caput-medusae* seeds remain viable for up to 3 yr (Nelson and Wilson 1969); thus, repeated mowing treatments must be applied, which may lead to deleterious impacts on native plant species (Davies et al. 2012). The small window of opportunity for mowing may also be impractical for repeated application over large-scale infestations. Finally, *T. caput-medusae* infestations often occur on landscapes that are inaccessible to machinery due to slope and terrain, as well as being on uneven, rocky soils that can damage equipment (Young 1992). Overall, mowing may partially address the plant fitness and structural characteristics of *T. caput-medusae* within the Si positive feedback cycle (Figure 1), but it does not address the chemical composition of the plant.

Tillage

Tilling can break up litter, incorporating it into the soil, and create favorable seedbed conditions for revegetation efforts (Kaltenecker 1997). In addition, tilling can damage *T. caput-medusae* roots, bury germinable seeds, and reduce *T. caput-medusae* cover by ~50% (Kyser et al. 2007). These impacts on *T. caput-medusae* address both plant fitness and structure in the Si positive feedback cycle (Figure 1). It has been shown that *T. caput-medusae* seeds emerge poorly at depths greater than 5 cm (Young et al. 1969). However,

tillage may also increase erosion potential, facilitate soil moisture and organic matter losses, and have deleterious effects on native vegetation (Nafus and Davies 2014; Pierson et al. 2007). Soil disturbance has been shown to favor *T. caput-medusae* invasion through increased standing biomass and seed production in the subsequent year (Miller 1996). As with mowing, tillage may not be feasible, due to topographic features and surface obstacles that could damage equipment. Finally, tillage may negatively impact fragile biological crusts and interrupt nutrient cycling, all while providing a disturbance regime that favors additional undesirable exotic plant species (Kaltenecker 1997; Locke and Bryson 1997; Young 1992).

Cultural Control

Prescribed Fire

Prescribed fire can consume standing *T. caput-medusae* biomass, seeds, and litter (Kyser et al. 2008), while potentially interrupting aspects of the Si positive feedback cycle (Figure 1). Fire may also provide an opportunity for revegetation and additional treatments (Davies 2010; Davies et al. 2015). *Taeniatherum caput-medusae* matures 2 to 4 wk later than other annual grasses, including *B. tectorum* (Dahl and Tisdale 1975; Hironaka 1961; Young 1992), and retains its seeds within inflorescences until August (Davies 2008). Thus, timing a prescribed fire to coincide with viable seed retention can destroy these seeds. Coordinating the ideal timing and achieving suitable conditions for a prescribed fire may be difficult in the Intermountain Region of the western United States due to low air temperatures in the autumn/winter and insufficient amounts of combustible material in the spring and early summer (Kyser et al. 2008). Delaying prescribed fires to late summer or early autumn raises the risk of escape due to the contribution of other community vegetation to the overall fuel load. After seed drop, fires must reach temperatures greater than 250 C to consume seeds located on the soil surface (DiTomaso et al. 1999; Sweet et al. 2008). Slow-burning, high-temperature fires may result in unintended damage to desirable plant species, increasing the dominance of fire-adapted invasive annual grasses (Billings 1994; Whisenant 1990), possibly perpetuating the grass-fire feedback cycle (D'Antonio and Vitousek 1992). Uncontrolled fires have been shown to create opportunities for exotic plant establishment and contribute to air pollution and atmospheric CO_2 that impact the climate (Campbell and Cahill 1996; D'Antonio and Vitousek 1992; Peters and Bunting 1994; Young 1992). Fire also alters soil infiltration rates, soil porosity, soil hydraulic conductivity, and soil water storage capacity (Neary et al. 1999). Despite these difficulties and risks, under optimal timing and conditions, prescribed fire has been shown to successfully reduce *T. caput-medusae* populations in the California annual grasslands (Kyser et al. 2008; Meyer and Schiffman 1999).

Grazing

Livestock grazing has been shown to be one of the preferred methods of *T. caput-medusae* control due to its low cost and practicality (Hamilton et al. 2015; James et al. 2015; Johnson et al. 2011), positive effects on nutrient cycling (Davies et al. 2010; Hobbs 1996), and limited disturbance compared with other control methods (e.g., mowing, tillage, and fire). For instance, livestock grazing removes standing vegetation and litter, and the deposition of animal wastes (i.e., feces and urine), which are high in nitrogen (N), can directly influence soil N mineralization (Davies et al. 2010; Hobbs 1996). However, livestock consumption

of *T. caput-medusae* has a narrow time frame of palatability before seed head emergence; livestock tend to avoid the plant after this time (DiTomaso et al. 2008; Young 1992). Livestock avoidance may be due to high tissue Si concentration, which presents an abrasive oral texture (McNaughton et al. 1985) and limits rumen digestibility (Montes-Sánchez and Villalba 2017). The plant's structure and chemical composition may directly and indirectly increase *T. caput-medusae* abundance in the plant community (Figure 1) through reduced livestock consumption and repeated defoliation of other, more palatable grasses (Belsky and Gelbard 2000; Heady 1961; Hunt et al. 2008; Mueggler 1972). Grazing before seed head emergence has been shown to overcome these obstacles, but the window of opportunity is narrow (Brownsey et al. 2017) and high stocking rates when *T. caput-medusae* is most palatable may not be feasible (DiTomaso et al. 2008). Grazing has been shown to be successful in the California annual grasslands when proper timing and stocking rates are considered (DiTomaso et al. 2008; Lusk et al. 1961). In contrast, year-round grazing and early spring grazing saw increases in *T. caput-medusae* abundance (DiTomaso et al. 2008; Harrison et al. 2003). Overall, grazing can be used as a method of control to address the Si positive feedback cycle (Figure 1) if high-intensity grazing is timed to occur when *T. caput-medusae* is in the boot phenological stage.

Chemical Control

Herbicides are the primary form of chemical control of *T. caput-medusae* and have the potential to reduce plant fitness, alter plant structural components, and increase nutritive quality, consequently interrupting the Si positive feedback cycle (Figure 1). There are many herbicides labeled for the control of *T. caput-medusae*, including PRE, POST, broad-spectrum, grass-selective, and growth-regulator herbicides. Imazapic and rimsulfuron are two PRE herbicides that have been used to control *T. caput-medusae* (Davies 2010; Davies and Sheley 2011; Kyser et al. 2007, 2012b; Monaco et al. 2005; Sheley et al. 2007), but they are highly variable in their efficacy (Kyser et al. 2007, 2012b). This may in part be due to the accumulated litter inhibiting penetration of the herbicide to the soil surface (Kyser et al. 2007) or rapid degradation in warmer soils (Kyser et al. 2012b). A new herbicide, indazaflam, has been shown to effectively control annual grasses through its PRE residual capacity (Sebastian et al. 2016a, 2016b, 2017a, 2017b), but it is not yet labeled for areas grazed by livestock. This poses a problem, as most areas heavily infested with *T. caput-medusae* are also used for livestock production. Aminopyralid, a PRE growth-regulator herbicide, was shown to suppress *T. caput-medusae* seed production >95% in a greenhouse setting (Rinella et al. 2014), with similar success in the field (Rinella et al. 2018). Glyphosate, a broad-spectrum POST herbicide, has been used at low rates to decrease *T. caput-medusae* abundance by ~95% with limited damage to shrubs and other native vegetation in big sagebrush (*Artemisia tridentata* Nutt.)–scrub ecosystems (Kyser et al. 2012a). Glyphosate application before seed set may also temporarily decrease plant fitness by reducing seed production and viability and arresting root development (Figure 1). However, multiple applications are needed, as glyphosate is a foliar contact herbicide and does not directly influence the soil seedbank (Kyser et al. 2012a). Even with the potential of *T. caput-medusae* herbicide control, there are risks associated with herbicide application. For instance, spray drift due to wind, volatilization, and different herbicide formulations may cause nonuniform application and injury to non-target species (DiTomaso 1997). Repetitive herbicide

application selects for herbicide-tolerant plants and may decrease desirable plant species within the population (DiTomaso 1997). Chemical application is often temporary, with multiple applications needed, but has shown potential for *T. caput-medusae* control and interrupting the Si positive feedback cycle.

Research Needs

Although we know orthosilicic acid is the soluble form taken up by many plants (Ma and Yamaji 2006) and deposited as amorphous mineral silica in *T. caput-medusae* tissues (Bovey et al. 1961; Epstein 1999; Swenson et al. 1964), critical knowledge gaps exist. In particular, our understanding of how Si is transported through the soil to the root of *T. caput-medusae*, how roots respond to available Si, what mechanisms within the root are responsible for uptake, and how the Si is transported through the plant are largely unknown. In addition, addressing ways to constrain tissue Si deposition within *T. caput-medusae* may be key to interrupting the positive feedback cycle of invasion and facilitate control of *T. caput-medusae*. Consequently, there are critical research needs in relation to plant Si and *T. caput-medusae* that may lead to alternative methods of control and more successful management strategies.

The Soil

The normal range of soluble Si in soil is between 0.6 to 1.0 mM but can be higher or lower depending on soil weathering processes (Epstein 1994). When soluble Si concentrations exceed 2 mM, the Si polymerizes into a gel and becomes unavailable for plant uptake (Ma et al. 2001). Rice and an *Equisetum* species began to wilt and leaves became necrotic when grown in deficient soluble Si conditions (Chen and Lewin 1969; Yoshida et al. 1962). Reduced growth and production yields were also observed in Gramineae species when grown in similar deficient conditions (Vlamis and Williams 1967). Thus, soil concentrations of soluble Si play a fundamental role in plant uptake and fitness for these species.

Understanding the role of soil soluble Si in *T. caput-medusae*–invaded landscapes could help in improving and/or developing better control strategies. Similar to the aforementioned Si hyperaccumulators, Si-deficient soils may reduce *T. caput-medusae* fitness (Figure 1). Nevertheless, it is unknown how low soil values of soluble Si impact *T. caput-medusae*. If the soil soluble Si deficiency can reduce *T. caput-medusae* fitness, novel studies could develop control strategies that decrease available soil Si. Because soluble Si polymerizes at concentrations greater than 2 mM (Ma et al. 2001), future studies could help develop strategies that target reductions or increases in soil soluble Si concentrations, limiting uptake and consequently decreasing *T. caput-medusae* fitness.

The Root

Fitness of rice plants has been associated with the ability to take up soluble Si through the root (Takahashi et al. 1990) and uptake regulation by the *Ls1* gene (Ma et al. 2004). Modification of the active transport mechanisms in rice has led to increased plant production and disease resistance (Ma et al. 2006). If increased plant fitness can be achieved by identifying the uptake mechanism of soluble Si in rice, it is reasonable to conclude that identifying the transport mechanism in *T. caput-medusae* might enable modifications to be made to reduce *T. caput-medusae* fitness. Nevertheless, the practicality of applying these modifications to *T. caput-medusae*

in highly variable ecological system will require considerable research before implementation.

Chemical application, rather than genetic modification, may provide a more viable means of interrupting the uptake mechanism. For instance, in a laboratory setting, the active transporter in rice was inhibited through the use of metabolic inhibitors such as NaCN and 2,4-dinitrophenol at low temperatures (Ma et al. 2004). Although these chemicals would be hazardous if applied in a landscape-type setting, this research sets the stage for exploring environmentally friendly chemicals that could have similar beneficial results. While previous methods of restricting Si uptake rely on an active transport mechanism, if a passive transport mechanism exists, the addition of specific soil minerals may provide a form of competitive adsorption, reducing soluble Si uptake into the plant. However, identifying the uptake mechanism is critical before exploring soluble Si inhibition techniques.

When compared with roots of other grasses, the roots of *T. caput-medusae* were found to have thicker cell walls and overall larger root diameters than an annual grass, but values were lower than those of a perennial grass species (Harris 1977). A thicker root endodermis may allow for transpiration to occur even if the surrounding soil environment is drier, particularly in the upper soil horizons; however (Harris 1977), root Si concentrations were not reported. Evaluating root Si concentrations may give insight into why *T. caput-medusae* is superior in acquiring soil resources and tolerating soil environmental fluctuations (e.g., drought, temperature extremes). If root tissue Si plays a role in *T. caput-medusae* fitness, opportunities for research become available for discovering how deposition of soluble Si occurs in roots. This may lead to control strategies that manipulate soluble Si deposition processes within roots, decrease *T. caput-medusae* fitness, and reduce invasive superiority. Overall, little is known about *T. caput-medusae* roots in relation to Si uptake and tissue silica concentrations; thus, further examination is needed.

The Shoot

Little information is available about soluble Si transport and deposition as amorphous silica within tissues. Manipulation and reduction of Si deposition would be key to increased herbivore preference and digestibility and would make the plant texture less abrasive for herbivores. For instance, sublethal doses of a glyphosate-containing herbicide with a surfactant were shown to reduce tissue silica concentrations and increase tillering in quackgrass [*Elymus repens* (L.) Gould] (Coupland and Caseley 1975). Similarly, low rates of glyphosate increased the nutritional quality of annual ryegrass (*Lolium ridigum* Gaudin) (Armstrong et al. 1992; Gatford et al. 1999) and increased cattle preference for glyphosate-treated fescue pastures (Kisseberth et al. 1986). However, tissue Si concentrations were not reported in these last three studies. Understanding how glyphosate alters the soluble Si deposition process and increases nutritional composition may give insight into other chemical treatments with similar results.

Aspects of plant structure (e.g., toxicity resistance, photosynthetic barrier, culm rigidity, immune system response) are possibly linked to *T. caput-medusae* tissue Si, but these aspects need further study. For instance, toxic metal accumulation in plants may affect plant productivity (Adrees et al. 2015; Nagajyoti et al. 2010), increased UV-B radiation could damage leaves and reduce the photosynthetic capacity of plants (Kakani et al. 2003), low tissue Si can increase susceptibility of culms to breakage in rice (Lee et al. 1990; Savant et al. 1996), and a weak immune system response

to predation has detrimental consequences to fitness (Holub and Cooper 2004; Nuernberger and Lipka 2005), whereas tissue Si mitigates these constraints. These principles and processes are known for crops; however, they are unexplored for *T. caput-medusae*. Elucidation of the influence of Si on *T. caput-medusae* fitness could lead to more efficient and/or novel control strategies for *T. caput-medusae*, interrupting its invasive superiority.

Conclusion

Taeniatherum caput-medusae is a superior invasive annual grass overtaking rangeland ecosystems and leading to drastic changes in ecosystem services. While control strategies exist for invasive annual grasses, these strategies do not take into consideration the role of high tissue Si in *T. caput-medusae* invasion. High tissue concentration of Si in *T. caput-medusae* creates a self-reinforcing feedback cycle that contributes to its invasive success and difficulty of control. The proposed conceptual model in this article summarizes *T. caput-medusae* characteristics associated with Si content (e.g., plant fitness, structure, and chemical composition) and the invasive processes associated with these characteristics (e.g., plant productivity, litter decomposition, and herbivory). These characteristics and processes help to identify critical research needs that can be used to develop improved and/or novel management practices of control, strengthening current strategies. Interrupting the Si positive feedback cycle of *T. caput-medusae* invasion should be considered when researching and developing future management strategies.

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