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FRAWLEY ET AL.: ETHNOBOTANICAL STUDY OF ELYMUS

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24 **An ethnobotanical study of the genus *Elymus***

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30 **Abstract**

31 Grains of domesticated grasses (Poaceae) have long been a global food source and
32 constitute the bulk of calories in the human diet. Recent efforts to establish more sustainable
33 agricultural systems have focused in part on the development of herbaceous, perennial crops.
34 Perennial plants have extensive root systems that stabilize soil and absorb water and nutrients at
35 greater rates than their annual counterparts; consequently, perennial grasses are important
36 potential candidates for grain domestication. While most contemporary grass domesticates
37 consumed by humans are annual plants, there are over 7,000 perennial grass species that remain
38 largely unexplored for domestication purposes. Documenting ethnobotanical uses of wild
39 perennial grasses could aid in the evaluation of candidate species for *de novo* crop development.
40 The objectives of this study are 1) to provide an ethnobotanical survey of the grass genus
41 *Elymus*; and 2) to investigate floret size variation in species used by people. *Elymus* includes
42 approximately 150 perennial species distributed in temperate and subtropical regions, of which at
43 least 21 taxa have recorded nutritional, medicinal, and/or material uses. *Elymus* species used for
44 food by humans warrant pre-breeding and future analyses to assess potential utility in perennial
45 agricultural systems.

46 **Key Words**

47 *Elymus*, ethnobotany, fruit morphology, perennial agriculture, domestication, Poaceae.

48

49 **Introduction**

50 It is estimated that between 20% to 50% of the nearly 400,000 extant plant species in the
51 world may be edible to humans (Füleký 2009; Warren 2015); however, only 6,000 of these have
52 been cultivated for human consumption (FAO 2019). Cereals, members of the grass family
53 (Poaceae), include several widely cultivated species, such as barley (*Hordeum vulgare* L.), maize
54 (*Zea mays* L.), oats (*Avena sativa* L.), rice (*Oryza sativa* L.), rye (*Secale cereale* L.), sorghum
55 (*Sorghum bicolor* L. Moench), sugarcane (*Saccharum officinarum* L.), and wheat (*Triticum*
56 *aestivum* L.), among others (NGS 2008). Cereals are a staple of the human diet and comprise 50
57 percent of global caloric intake (Awika 2011; Warren 2015). Maize, rice, wheat, and sugarcane
58 account for over half of the total crop production worldwide (FAO 2019), indicating their
59 importance in the global food system and the relatively small number of grass species used in
60 modern agriculture (e.g., Khoury et al. 2014).

61 Cereal domestication began at least 12,000 years ago and resulted in morphological and
62 genetic changes in cultivated plants relative to their wild progenitors (Glémin and Bataillon
63 2009; Olsen 2013a; Olsen 2013b). For example, domesticated grass species exhibit a reduction
64 in axillary branching, synchronization of maturation, and easy threshing (Zohary et al. 2012).
65 Further, domesticated grasses have larger seeds that require reduced stratification and display
66 decreased dormancy, shattering, and reduced or absent awns (Glémin and Bataillon 2009, Harlan
67 et al. 1973; Harlan 1992). These characteristics contribute to more uniform harvest time, plants
68 that can be grown in denser stands, increased seedling vigor, and more efficient harvesting
69 (Glémin and Bataillon 2009). Subsequent crop improvement programs have focused largely on

70 enhanced grain production and nutritional qualities of domesticated grasses, resulting in
71 important alterations to a variety of seed traits, among other characteristics.

72 Grass species involved in early domestication processes were almost exclusively annuals
73 (NGS 2008), perhaps due to their high seed output (Cox 2009), adaptation to early agricultural
74 lands (DeHaan and Van Tassel 2014), and/or response to early selection efforts targeting
75 synchronized maturation (Glémin and Bataillon 2009). However, ecological impacts of
76 agricultural systems based on annual plants, including ongoing soil erosion and soil degradation
77 (e.g. Montgomery 2007) have turned attention to the potential role of herbaceous, perennial
78 species in contemporary agricultural systems. Perennials have deep root systems and longer
79 growing seasons resulting in reduced erosion risk and greater plant productivity over time
80 (Glover et al. 2010). Additionally, perennial species may be better adapted to temperature
81 increases driven by climate change, as they are less affected by changes in the uppermost soil
82 layer (Cox et al. 2006). As such, perennial crops may have an important role to play in the
83 development of more sustainable agricultural systems (Bommarco et al. 2013; Cassman 1999;
84 Ciotir et al. 2016; Ciotir et al. 2019; Cox et al. 2002; Doré et al. 2011; FAO 2009; Glover et al.
85 2010; Tittonell 2014).

86 Despite their potential utility, very few perennial grasses have been domesticated (Van
87 Tassel et al. 2010). Several hypotheses have been proposed to explain the near absence of
88 perennial, herbaceous crops. For example, some have suggested that their conservative resource
89 allocation to reproductive structures relative to vegetative structures hinders response to selection
90 for increased seed; others have proposed that herbaceous perennial plants exhibit reduced
91 competitive ability in agricultural habitats compared to annual species (DeHaan et al. 2010;
92 DeHaan and Van Tassel 2014). However, expanding understanding of agro-ecology, combined

93 with new tools and analytical approaches, is driving increasing interest in pre-breeding of wild,
94 herbaceous, perennial species. Several herbaceous, perennial species are currently under
95 development, including perennial rice, sorghum, and wheat, among others (e.g., Cox et al. 2018;
96 DeHaan et al. 2016; Huang et al. 2018).

97 There are two primary ways in which perennial grass crops can be developed (DeHaan
98 and Van Tassel, 2014). First, annual crops can be hybridized with their perennial wild relatives.
99 This serves to introgress annual traits (like high yield, abiotic stress tolerance) into a perennial
100 background (e.g. perennial wheat (*Triticum aestivum* x *Thinopyrum intermedium*) (DeHaan et al.
101 2018; Hayes et al. 2018) or vice versa. A second means of developing perennial grass crops is
102 through *de novo* domestication of wild species, as is underway, for example, with the wild wheat
103 relative Kernza (*T. intermedium* (Host) Barkworth & D.R. Dewey) at the Land Institute (Salina,
104 KS). However, one of the current challenges for *de novo* domestication is the identification of
105 wild species for inclusion in pre-breeding programs (Ciotir et al. 2019).

106 When investigating wild plant species with potential utility in perennial agricultural
107 systems it is valuable to consider historical and contemporary ethnobotanical uses, as well as
108 their fundamental morphological features and geographic distributions. Ethnobotanical and other
109 data on plant diversity and use, including records of plant form preserved in herbarium
110 specimens, are often housed in botanical gardens and museums (Miller et al. 2015). These
111 records offer a unique opportunity to explore agriculturally relevant questions about potential
112 candidates for domestication. For example, within a particular genus of grasses, how many
113 species are perennial? How many species have been used by people, what parts of the plant have
114 been used, and for what purposes?

115 *Elymus* L. (wild rye) is an appealing genus for perennial grain domestication because of

116 its compact and determinate inflorescence structure, capacity to self-pollinate, and current use as
117 forage, among other characteristics. Several *Elymus* species have been developed as forage
118 cultivars (e.g. blue wildrye (*E. glaucus* Buckley), thickspike wheatgrass (*E. lanceolatus* Scrib. &
119 J.G. S.M), Canada wild rye (*E. canadensis* L.), slender wheatgrass (*E. trachycaulus* Link), Snake
120 River wheatgrass (*E. wawawaiensis* J. Carlson & Buckley) and Virginia wildrye (*E. virginicus*
121 L.) (Aubry et al. 2005; Lloyd-Reilley 2010; Tilley et al. 2011). To date, multiple *Elymus* species
122 have been hybridized in a variety of pre-breeding initiatives. For example, there are at least
123 seventeen *Elymus*-wheat hybrids (Cox et al. 2002) that have been developed for drought and salt
124 tolerance (i.e. *Elymus mollis* Trin. x *Triticum durum* Desf.; Fatih 1983) and scab resistance (i.e.
125 *E. trachycaulus* x *T. aestivum* L., *E. tsukushiensis* Honda x *T. aestivum*; Kole 2011; Wang et al.
126 1999). Other *Elymus* hybrids include *Elymus hoffmannii* R.B. Jensen & R.H. Assay, an advanced
127 generation hybrid between quackgrass (*E. repens* L.) and bluebunch wheatgrass
128 (*Pseudoroegneria spicata* (Pursh) Á. Löve) with drought and salinity tolerance (St. John 2010).
129 This work indicates *Elymus* is amenable to breeding processes and that some species within the
130 genus may hold promise for perennial grain crop development.

131 In this study we investigate *Elymus* to provide information that might facilitate evaluation
132 of species for use in *de novo* domestication processes. The specific objectives of this study were
133 to: 1) conduct an ethnobotanical survey of the genus *Elymus*; and 2) investigate floret size in
134 species used by people. These data provide valuable information about *Elymus* use and floret
135 size variation, and underscore how ethnobotanical studies can aid agricultural processes through
136 the evaluation of wild species and their potential applications in pre-breeding processes.

137

138 **Methods**

139 ***Study System***

140 *Elymus* includes approximately 150 wild, herbaceous, perennial species distributed across
141 North Temperate regions (Barkworth 2007; Lu 1993), including 39 species that occur in North
142 America (32 of which are native; Barkworth 2007). *Elymus* caryopses (grains) are typically
143 oblong to oblong-linear and adherent to the lemma and palea with hairy apices (Barkworth 2007;
144 Chen and Zhu 2006; Lu 1993). Inflorescences are erect spikes with one to three spikelets at each
145 node. Spikelets are ordinarily sessile with one to 11 florets. The lower florets are typically
146 functional, and the distal florets are often reduced (Barkworth 2007; Chen and Zhu 2006;
147 Kellogg 2015). Species that occur in western and northern North America have solitary spikelets,
148 whereas those found east of the Rocky Mountains have multiple spikelets per node (Barkworth
149 2007).

150

151 ***Inclusion of Leymus***

152 Since the initial description of *Elymus* by Linnaeus, its taxonomy has varied under
153 different taxonomic treatments (Helfgott and Mason-Gamer 2004; Lu 1993). Of particular
154 interest to this study is the genus *Leymus* Hochst., whose species have often been included in
155 circumscriptions of *Elymus*. Three *Leymus* species presented in this survey, *L. cinereus* (Scribn.
156 & Merr.) Á. Löve, *L. condensatus* (J. Presl) Á. Löve, and *L. triticoides* (Buckley) Pilg., were
157 originally described as *Elymus* species by previous authors (*E. cinereus* Scribn. & Merr., *L.*
158 *condensatus* J. Presl, and *E. triticoides* Buckley), but are now considered synonyms for *Leymus*.
159 We included these species in our results because some ethnobotanical descriptions surveyed here
160 treat them as *Elymus*, and all three were used extensively by indigenous communities in the
161 American southwest.

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Ethnobotanical analysis of Elymus

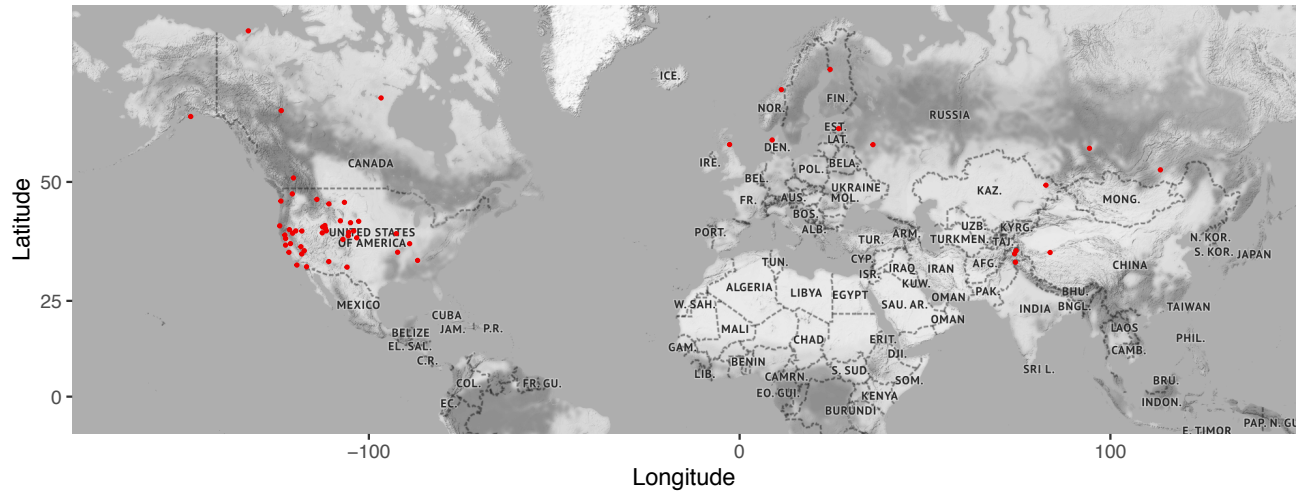
We performed a literature review to investigate recorded uses of *Elymus* species. We surveyed 121 print resources accessed at the Peter H. Raven Library at the Missouri Botanical Garden library. We reviewed 1) general ethnobotanical studies carried out in regions in which *Elymus* is known to occur; 2) ethnobotanical studies focused specifically on cultures of native communities located in these regions; and 3) global assessments of edible plants. We surveyed two online ethnobotany databases, *Native American Ethnobotany Database* (<http://naeb.brit.org/>) and *Plants for a Future* (<https://pfaf.org/>), and two online scientific databases, *JSTOR* (<http://www.jstor.org>) and *Web of Science* (<http://www.webofknowledge.com/WOS>) for relevant information about *Elymus*. We collected data on historical use by indigenous communities, human and animal edibility, cultivation history, and the uses of different plant parts. Results were recorded in the Perennial Agriculture Project Global Inventory online database (<http://www.tropicos.org/Project/PAPGI>). We also collected data on geographic distributions from specimen data at the Missouri Botanical Garden herbarium and from the Global Biodiversity Information Facility (www.gbif.org). Ethnobotanical uses were categorized as food, forage, medicine, and/or material. The food category included species that were consumed by humans; the forage category identified species cultivated for growth in pastures and for consumption by livestock; the medicine category designated species that were used in ceremonial decoctions or had therapeutic or healing utilities; finally, the material group covered species used as tools, housewares, and in construction, as well as other applications as raw materials.

185 ***Measurements of floret traits from herbarium specimens***

186 Grain morphology is an important target of selection in grass species undergoing
187 domestication for human consumption (Glemín and Batallion 2009). While many wild species
188 have relatively small, long, thin grains, selection during domestication generally favors larger,
189 rounder grains (Gegas 2010; Okamoto 2012; Stougaard and Xue, 2004). We were interested in
190 surveying grain size variation in species with documented ethnobotanical uses. We hypothesized
191 that *Elymus* species used for human consumption may display larger grain sizes than those used
192 for other purposes. A definition of the “pure seed unit” for crop conditioning is the floret: the
193 reproductive structure including the lemma, palea, and caryopsis (grain), and excluding the awn
194 when the awn length is longer than that of the entire floret (Gregg and Billups 2010). There is a
195 positive correlation between floret cavity size (volume) and grain growth, including grain size
196 and weight (Millet and Pinthus 1984; Millet 1986).

197 We calculated floret area for *Elymus* species with documented histories of use to examine
198 relationships between floret size, ethnobotanical use, and collection location. Our ethnobotanical
199 analysis identified 21 species with ethnobotanical uses (see results below). For each of these 21
200 species, we selected *Elymus* specimens from the herbarium at the Missouri Botanical Garden
201 based on their collection location, targeting specimens that had been collected in a country or
202 state where *Elymus* use by indigenous communities had been documented (Figure 1). If there
203 was no indigenous community specifically identified for a taxon, we selected a specimen from
204 the species known native range. For example, because *E. canadensis* was used historically in
205 Utah and Colorado, sampled specimens came from these states (Table 1).

Herbarium Specimen Collection Locations



206

207 **Figure 1.** Geographic locations of collection sites for all specimens measured across 21 *Elymus*
 208 species. Collection site determined from herbarium specimen label.

Species	Use Distribution	Native Range
<i>E. arenarius</i> (L.)	Eurasia (NOR)	Eurasia
<i>E. canadensis</i> (L.)	North America (UT, CO)	North America
<i>E. caninus</i> (L.)	Eurasia (RUS, CHN)	Temperate Asia
<i>E. elongatus</i> (Host.)	North America (USA, CAN)	Eurasia
<i>E. elymoides</i> (Raf.)	North America (CA)	North America, Temperate Asia
<i>E. fibrosus</i> (Schrenk)	Eurasia (RUS)	Temperate Asia
<i>E. glaucus</i> (Buckley)	North America (CA, NM, BC)	North America, Temperate Asia
<i>E. hystrix</i> (Moench)	North America (FL)	North America
<i>E. lanceolatus</i> (Scribn. & J.G. Sm.)	North America (USA, CAN)	North America, Temperate Asia
<i>E. mollis</i> (Trin.)	North America (AK, BC, WA)	North America, Eurasia
<i>E. multisetus</i> (J.G. Sm.)	North America (CA)	North America
<i>E. mutabilis</i> (Drobow)	Eurasia (RUS)	Eurasia
<i>E. repens</i> (L.)	North America (USA, CAN); Eurasia (FIN, SWE, RUS, TUR, BIH, IRL)	Eurasia
<i>E. semicostatus</i> (Nees ex Steud.)	North America (USA); Eurasia (JPN)	Asia
<i>E. sibiricus</i> (L.)	North America (UT); Eurasia (RUS)	North America, Eurasia
<i>E. smithii</i> (Rydb.)	North America (USA, CAN)	North America
<i>E. spicatus</i> (Pursh)	North America (USA)	North America
<i>E. trachycaulus</i> (Link)	North America (USA, CAN); Eurasia (RUS)	North America, Eurasia
<i>L. cinereus</i> (Scribn. & Merr.)	North America (AB, BC, MT, UT, CA)	North America
<i>L. condensatus</i> (J. Presl)	North America (UT, CA)	North America
<i>L. triticoides</i> (Buckley)	North America (CA)	North America

209

210 **Table 1.** Native ranges and location of ethnobotanical use for 21 *Elymus* species.

211
212 To investigate inter- and intra-specific variation in floret area in species used by people
213 we sampled three herbarium specimens per species and harvested eight florets from each
214 specimen, with the exception of *E. semicostatus* Nees ex Steud., for which only two herbarium
215 specimens existed. For every specimen, we recorded the location of collection, accession and
216 collection number, collection date, collector, and latitude and longitude when available
217 (Appendix 1). We removed the glumes to reveal the caryopsis enclosed by the adherent palea
218 and the lemma. We imaged florets in high resolution (iPhone XR, DPI 326) at the Missouri
219 Botanical Garden herbarium and measured area in ImageJ (v. 1.50i). We returned plant material
220 to the fragment packet on the herbarium sheet following imaging. We cropped each image to
221 encompass only the seeds, then converted the image to binary to analyze particles for individual
222 and average floret area (mm²). Raw data for floret area is available in Appendix 2. We fit linear
223 models in R (v. 1.0.143, RStudio Team 2015) and SAS (v. 9.4, SAS Institute 2017) to investigate
224 three main questions: 1) does individual floret area differ between species and among replicates
225 within a species, 2) do average floret areas vary with ethnobotanical uses in a given region, and
226 3) is there an association between average floret area and latitude and longitude? While *Elymus*
227 *hystrix* Moench was described in the literature as being used medicinally, its specific application
228 (maize seed germination: Table 2) was not consistent with the other species' medicinal uses.
229 Therefore we removed *E. hystrix* when testing for an effect of medicinal usage on floret size.

Species	Indigenous Communities	Plant Part Used	Food Uses	Medicinal Uses	Forage Uses	Material Uses	References
<i>E. arenarius</i> (L.)	Unspecified	Unspecified	Unspecified	Unspecified	Unspecified	Twisting ropes and making brooms.	Hooker 1839; Moerman 1998.
<i>E. canadensis</i> (L.)	Gosiute (G), Iroquois (I), Kiowa (K), Ute (U), Paiute (P)	Seeds, roots, and foliage	Gathered (G, U), ground into flour, used to make bread, cereals, rye casserole.	Compound decoction of roots taken for the kidneys (I).	Fodder (K); forage for deer, antelope, and buffalo (P); cultivated as a pasture grass (P).	Unspecified	Facciola 1990; Kindscher 1987; Kunkel 1984; Moerman 1998; Tanaka 1976; Yanovsky 1936.
<i>E. caninus</i> (L.)	Unspecified	Unspecified	Unspecified	Unspecified	Forage grass.	Unspecified	Hanelt 2001.
<i>E. elongatus</i> (Host.)	Unspecified	Unspecified	Unspecified	Unspecified	Hay and pasture crop.	Unspecified	Hanelt 2001.
<i>E. elymoides</i> (Raf.)	Navajo (N), Ramah (R), Potter Valley Pomo (PVP)	Seeds	As pinole, considered second best quality after wild oats (PVP).	Unspecified	Young plants used for sheep and horse feed (N, R).	Unspecified	Moerman 1998; Welch 2013.
<i>E. fibrosus</i> (Schrenk)	Unspecified	Unspecified	Unspecified	Unspecified	Minor forage crop.	Unspecified	Clayton et al. 2006; Hanelt 2001.
<i>E. glaucus</i> (Buckley)	Karok (KA), Keres (KE), Gitksan (GI)	Seeds	As porridge (seeds parched, pounded into a flour, and mixed with water into a paste), cooked, or ground into bread flour (KA).	To settle quarrels between families or individuals (KA).	Forage for deer, antelope, and buffalo; potential pasture and forage crop.	Used in socks and stuffing inside moccasins, as baby bedding, and to cover ground where people sat around fire (GI).	Couplan 1998; Ebeling 1986; Hanelt 2001; Moerman 1998; Schenck 1952; Smith 1997; Smith Jr. 2014; Tanaka 1976; Yanovsky 1936.
<i>E. hystrix</i> (Moench)	Iroquois	Unspecified	Unspecified	Ceremonial: decoction for corn seeds (I).	Unspecified	Unspecified	Austin 2004.
<i>E. lanceolatus</i> (Scribn. & J.G. Sm.)	Unspecified	Unspecified	Unspecified	Unspecified	Cultivated as forage grass and pasture crop.	Unspecified	Hanelt 2001.
<i>E. mollis</i> (Trin.)	Nitinaht (NI), Makah (M), Haida (H), Nunivak Eskimo (NE)	Seeds, stems, leaves, and roots	Seeds eaten.	Roots twisted together to form rope, rubbed on the bodies of young men for strength (NI); basal portion of stem chewed for incontinence (M).	Unspecified	Tough leaves used for sewing (NI), plants gathered, split, dyed, and used in basketry and mats (H, NE).	Couplan 1998; Turner et al. 1983; Turner 2010; Lantis 1946.
<i>E. multisetus</i> (J.G. Sm.)	Kawaiisu (KW)	Seeds	Pounded into a porridge/mush (KW).	Unspecified	Unspecified	Unspecified	Moerman 1998; Smith Jr. 2014.
<i>E. mutabilis</i> (Drobow)	Unspecified	Unspecified	Unspecified	Unspecified	Frost-resistant forage grass.	Unspecified	Hanelt 2001.
<i>E. repens</i> (L.)	Apache (A), White Mountain (WM), Cherokee (CHE), Gosiute, Iroquois, Okanagan-Colville (OC), Lukomir Highlanders (LH)	Seeds, stems, rhizomes, roots, shoots, and leaves	Roots dried, ground into meal, and substituted for bread; rhizomes dried and ground, roasted for coffee, or boiled into a syrup for beer; seeds, tips of rhizomes, leaves and shoots eaten raw; seed mashed (A; WM; G).	Orthopedic and urinary aid (CHE; I); decoction used to wash swollen legs and infusion taken for gravel, incontinence, and bedwetting (CHE); roots infused to make kidney and genitourinary treatment; rhizomes to treat kidney, liver, and urinary problems; worm expellant (I); to treat poor eyesight, chest pain, fever, syphilis, jaundice, and swollen and rheumatic limbs; other medicinal uses (LH).	Fodder and forage plant for hay (A; WM), N. American cultivar 'Newhy' promising forage hybrid (<i>E. repens</i> x <i>E. spicatus</i>).	Used under and over food in pit cooking (OC).	Allen and Hatfield 2004; Elliot 2009; Ferrier et al. 2015; Hanelt 2001; Jackson 2014; MacKinnon et al. 2009; Moerman 1998; Sargin 2013.
<i>E. semicostatus</i> (Nees ex Steud.)	Unspecified	Unspecified	Unspecified	Unspecified	Drought-resistant pasture grass.	Unspecified	Clayton et al. 2006; Hanelt 2001.
<i>E. sibiricus</i> (L.)	Gosiute	Seeds	Yes (G).	Unspecified	Infrequently cultivated as forage grass.	Unspecified	Chamberlin 1911; Clayton et al. 2006; Hanelt 2001; Moerman 1998.
<i>E. smithii</i> (Rydb.)	Unspecified	Unspecified	Unspecified	Unspecified	Cultivated for hay and pasture.	Unspecified	Clayton et al. 2006; Hanelt 2001.
<i>E. spicatus</i> (Pursh)	Unspecified	Unspecified	Unspecified	Unspecified	Forage grass for natural pastures.	Unspecified	Clayton et al. 2006; Hanelt 2001.
<i>E. trachycaulus</i> (Link)	Unspecified	Seeds	Unspecified	Unspecified	Cultivated mostly in grass mixtures as forage and pasture plant.	Unspecified	Clayton et al. 2006; Hanelt 2001; Smith Jr. 2014.
<i>L. cinereus</i> (Scribn. & Merr.) Á. Löve	Paiute, Thompson (T), Blackfoot (B)	Seeds, stems, leaves, and culm	Seeds eaten (P).	Unspecified	Hay for livestock (T).	Stems used for basket imbrication; leaves used to line graves; culms used as "fish spreaders" or for cleaning; grass used as bedding (T).	Ebeling 1986; Johnston 1970; Turner et al. 1996; Smith Jr. 2014.
<i>L. condensatus</i> (J. Presl) Á. Löve	Cahuilla (C), Gosiute, Paiute, Chumash (CH).	Stems, seeds	Seeds, whole plant eaten (G; P)	Unspecified	Unspecified	Stems used in arrowmaking (C; CH), roof thatching (C), brush handles, knives, and tobacco pipes. Used in house construction, clothes, and tools (CH).	Bean and Saubel 1972; Couplan 1998; Ebeling 1986; Kindscher 1987; Moerman 1998; Smith Jr. 2014; Timbrook 1984.
<i>L. triticoides</i> (Buckley) Pilg.	Paiute, Kawaiisu, Potter Valley Pomo	Seeds	Seeds pounded and cooked to form a thick mush (KW); pinole (PVP).	Unspecified	Unspecified	Unspecified	Ebeling 1986; Couplan 1998; Smith 1997; Smith Jr. 2014; Welch 2013; Zigmund 1981.

230

231 **Table 2.** Compilation of documented ethnobotanical records for 21 *Elymus* species.

232 “Unspecified” denotes where an indigenous community, plant part, or ethnobotanical use was

233 not documented for a given species in the literature we consulted.

234 **Results**

235 ***Ethnobotanical analysis of Elymus***

236 Of the ca. 150 known *Elymus* species, we identified 21 taxa that have documented
237 ethnobotanical uses by people in North America and/or Eurasia (Table 2). Fifteen species are
238 used as forage, 12 are used for food, six provide for raw materials for use in the home, and five
239 are used medicinally. We identified at least 25 different indigenous communities that use *Elymus*
240 in some capacity. Five Native American communities use more than one species from the genus:
241 Gosiute (four species), Paiute (four), Kawaiisu (two), Potter Valley Pomo (two), and Iroquois
242 (two). Additionally, eight taxa in our study are used by more than one indigenous group (*E.*
243 *canadensis*, *E. elymoides* Raf., *E. glaucus*, *E. mollis*, *E. repens*, *L. cinereus*, *L. condensatus*, and
244 *L. triticoides*. Forage uses are mainly as fodder, hay, and pasture grass. Food uses primarily
245 involve the seed, eaten raw (i.e. *E. repens*), as porridge or mash (i.e. *E. glaucus*, *E. multisetus*
246 J.G. Sm., *E. repens*), or as ‘pinole,’ a coarse flour made from ground seeds (i.e. *E. elymoides*).
247 Material uses are broad and encompassed many plant parts (culms, leaves, roots, and stems),
248 most frequently as components of houseware (i.e. basketry, broom handles). Medicinal uses are
249 equally diverse, with species being used in decoctions, infusions, and washes.

250

251 ***Elymus species used for forage***

252 The most common ethnobotanical use of *Elymus* in our study is forage. Fifteen *Elymus*
253 species are used for forage by at least one of seven indigenous communities across western
254 North America (Table 2). Forage uses are primarily for pasture grass, hay for livestock, and
255 fodder for antelope, buffalo deer, horses, and sheep. Seven species are used exclusively as forage
256 (there were no ethnobotanical records of use for food, medicine, or material for the species),

257 whereas eight of the *Elymus* species used for forage are also human edible (Table 2). Many
258 *Elymus* species used as forage have specific environmental tolerances. For example, *E. elongatus*
259 Host. is used as a saline and alkaline tolerant pasture grass in western North America; *E.*
260 *canadensis* and *E. smithii* Rydb. are used for revegetation and reseeding of disturbed rangelands,
261 prairies, and saline soils of the Great Plains; and *E. lanceolatus* aids soil stabilization in the
262 intermountain region of the United States and Canada (Hanelt 2001). Two additional pasture
263 grass species (*E. mutabilis* Drobow and *E. semicostatus*) are cultivated for their frost and drought
264 resistance, respectively (Hanelt 2001). Finally, *E. elymoides* is edible to sheep and horses early in
265 the season and is used for this purpose by at least two southwestern Native American
266 communities, the Navajo and Ramah (Barkworth 2007; Moerman 1998).

267

268 ***Elymus* species used for human consumption**

269 Ten *Elymus* species are consumed by people in some form, and we identified six
270 indigenous communities that used *Elymus* for this purpose (Table 2). *Elymus* species eaten by
271 humans are: *E. canadensis*, *E. elymoides*, *E. glaucus*, *E. mollis*, *E. multisetus*, *E. repens*, *E.*
272 *sibiricus* L., *L. cinerius*, *L. condensatus*, and *L. triticoides*. For some species there is no
273 comprehensive description of preparation method (i.e. *E. mollis*). Several others illuminate
274 important details on food use; for example, seeds, roots, rhizomes, and leaves of *E. repens* are
275 consumed, either eaten raw, roasted, as a mash, or in a flour. Likewise, seeds of *E. glaucus*, *E.*
276 *multisetus*, and *L. triticoides* are parched, ground, and mixed with water to form a type of
277 porridge. Pinole is also a common preparation method for seed, and it is used as a flour in breads
278 (*E. canadensis*, *E. elymoides*, *E. glaucus*, *L. triticoides*), cereals, and casseroles (*E. canadensis*).
279 Notably, *E. elymoides* is considered “second in quality for [pinole]” following wild oats (Welch

280 2013).

281

282 *Elymus species used for medicines and materials*

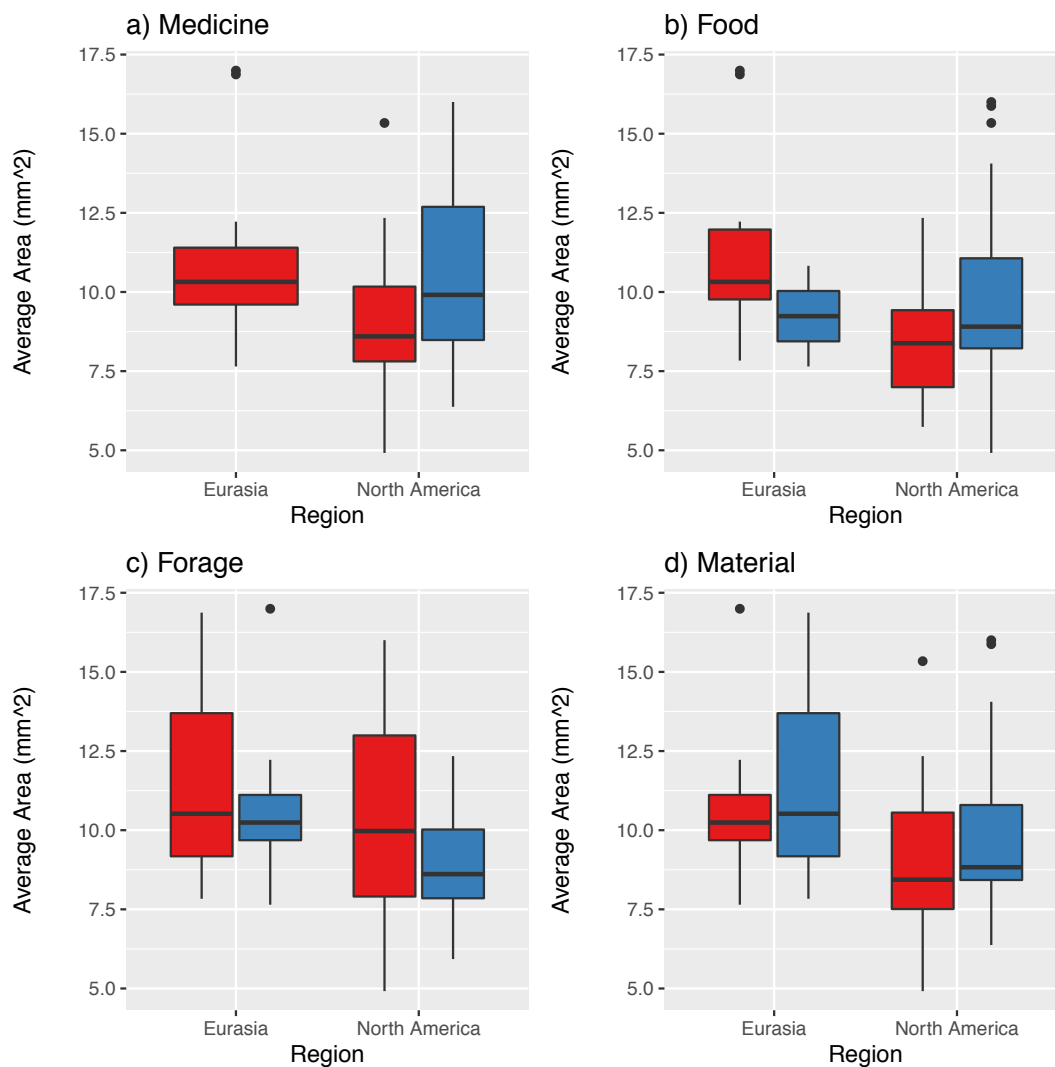
283 *Elymus* medicinal uses vary widely. Three taxa are used to treat renal and incontinence
284 issues as a diuretic, and two are applied topically to treat swollen limbs (Table 2). *Elymus*
285 *glaucus* is described by the Karok community as a medicine to help “settle quarrels” between
286 individuals or families (Moerman 1998; Schenk and Gifford 1952). In other medicinal
287 applications, roots and stems are either eaten, applied directly, or developed into infusions and
288 washes. *Elymus hystrix* is described as a “ceremonial medicine” by the Iroquois, and functions as
289 part of a decoction for maize seeds to enhance germination. The treatment is considered to
290 contribute to seed vitality and “protection” prior to planting (Austin 2004; Waugh 1916). Six
291 taxa have material applications (Table 2). Plants are formed into parts of household objects, such
292 as brooms, baskets, arrows, pipes, bedding, brush handles, knives, and mats, among other tools,
293 or into parts of the house, such as in roof thatching. For example, North American Thompson
294 River Indians imbricate stems of *L. cinereus* into baskets (Turner 1996), and *E. arenarius* L. is
295 formed into in ropes and brooms in parts of Eurasia (Hooker 1839). We found that roots, stems,
296 leaves, and culms of *Elymus* are all employed in material ways.

297

298 *Floret area measurements*

299 Floret area was measured for 21 *Elymus* species with documented use histories (see
300 above). Floret area varies significantly across *Elymus* species ($F_{20} = 13.37$, $P < 0.0001$), as well
301 as among individuals within species ($F_{21} = 10.60$, $P < 0.0001$). Using species’ means, we fit
302 linear models to assess if average floret area differed by location (i.e. North America vs. Eurasia)

303 and within each of the four ethnobotanical categories (i.e. documented use vs. unspecified)
304 (Table 2). For medicine, floret area does not differ by region ($F_1 = 3.63$, $P > 0.05$; Figure 2).
305 However, average floret area is significantly greater for species with medicinal uses compared to
306 species without documented medicinal uses in North America ($F_1 = 4.75$, $P = 0.03$; Figure 2a).
307 In contrast, for food, forage, and material categories, floret area does not differ significantly by
308 region (Food: $F_1 = 4.01$, $P > 0.05$; Forage: $F_1 = 3.93$, $P > 0.05$; Material: $F_1 = 3.87$, $P > 0.05$).
309 Additionally, no differences in floret area are observed when we compare average floret area for
310 species used for food, forage, and material to those without documented usage in each category,
311 (Food: $F_1 = 2.33$, $P > 0.05$; Forage: $F_1 = 1.71$, $P > 0.05$; Material; $F_1 = 1.24$, $P > 0.05$). In
312 summary, average floret area does not differ significantly across geographic regions and among
313 documented ethnobotanical uses, with the exception of species used for medicine in North
314 America. Florets of species used medicinally were larger than florets of species not used
315 medicinally in this region.



316

317 **Figure 2.** Comparison of average floret area by use (medicine, food, forage, and material) and
318 region (North America, Eurasia). Blue denotes a documented use within that ethnobotanical
319 category. Red denotes no documented use within that ethnobotanical category. Significant
320 differences ($F_1 = 4.75$, $P = 0.03$) found only for medicinal uses in North America (2a).

321

322 To further investigate drivers of variation in average floret area across specimens, we
323 tested for associations between average floret area, latitude, and longitude within region (i.e.
324 North America vs. Eurasia). In North America, average floret area increases from east to west (t

325 = -2.41, $P = 0.02$), but is not variable across latitudes ($t = 1.52$, $P = 0.14$). In Eurasia, there is no
326 significant relationship between average floret area and latitude ($t = 0.20$, $P = 0.85$) or longitude
327 ($t = 0.17$, $P = 0.87$); however, this may be an artifact of lower sampling in Eurasia in this study.

328

329 **Discussion**

330 Growing concerns about ecological impacts of agricultural systems based on annual
331 plants has turned attention to the potential of perennial, herbaceous species in contemporary food
332 systems. Through their large, persistent root systems, among other traits, perennial, herbaceous
333 plants offer ecological services including reduced erosion and increased absorption of water.
334 However, because of a dearth of herbaceous perennial crops, identifying potential candidates for
335 the ecological intensification of agriculture remains a challenge (Bommarco 2013).
336 Ethnobotanical records play an important role in this process by providing practical information
337 about wild plant use and morphology. *Elymus* is a genus of interest for pre-breeding and
338 domestication processes because of its rich ethnobotanical record, documented edibility, and
339 reproductive morphology. In addition, its history of hybridization suggests that members of the
340 genus may be intercrossed to develop new agricultural cultivars with beneficial trait
341 combinations. While there is no indication that native users of this group selected species with
342 larger floret areas for consumption, forage, or as material, significant variation in floret area
343 exists among and within species. Grain morphology is a valuable target of selection for
344 domestication in perennial grasses, and standing phenotypic variation in this group could serve
345 as a foundation for future breeding initiatives. Moreover, variation in use of *Elymus* species
346 illuminates the potential for broad application of this genus.

347

348 ***Ethnobotanical analyses as a foundation for agricultural innovation***

349 Ethnobotanical records are a vital source of information on plant diversity, use,
350 distribution, form, and function. In particular, ethnobotanical records can inform agricultural
351 processes by examining how plants have been manipulated or altered for human use (Casas et al.
352 1996). Further, these studies document which species were chosen for economic and cultural
353 purposes (Ford 2000). Additionally, ethnobotanical resources provide insight on geographic
354 distributions, environmental tolerances, toxicities, preparation methods, and human preferences
355 for certain features (flavors, shapes, textures, colors, etc.) of wild food plants (Casas et al. 1996).
356 These records thereby help identify species with agricultural potential, and provide pertinent
357 information on plant morphology and edibility in an agricultural context (Ciotir et al. 2019;
358 Minnis 2000; Plucknett and Smith 1986).

359 Our dataset identified 21 species of *Elymus* with known food, forage, medicine, and
360 material uses globally, and attributed these uses to at least 25 different indigenous communities.
361 The most frequent use of *Elymus* is as forage or fodder, further highlighting perennial members
362 of Triticeae as globally important sources of forage grass (Kole 2011). We identified ten species
363 of *Elymus* that are used for food (*E. canadensis*, *E. elymoides*, *E. glaucus*, *E. mollis*, *E.*
364 *multisetus*, *E. repens*, *E. sibiricus*, *L. cinerius*, *L. condensatus* and *L. triticoides*). Of these, the
365 seed is most frequently consumed, though in two instances (e.g. *E. repens* and *L. condensatus*)
366 there are food uses for the entire plant, including the roots and rhizomes (Table 2). The
367 preparation methods for seed are straightforward (i.e. ground and mixed with water as a mash, or
368 finely pounded into flour), suggesting that their edibility is not contingent on rigorous
369 processing. Further, food products prepared with *Elymus* are similar to many modern grain
370 products, and include bread, flour, and cereal. We suggest further investigation of these ten

371 species for their potential contribution to the ecological intensification of agriculture. Lastly, the
372 documentation of medicinal and material uses suggests that *Elymus* taxa are multifunctional, and
373 perhaps the whole plant can be employed post-production or at the end of their lifespan (i.e. as
374 hay for livestock or in thatching).

375 A previous ethnobotanical study of annual and perennial wild grass genera substantiated
376 their importance as a food source for Native American communities, including species from
377 *Oryzopsis*, *Sporobolus*, and *Panicum* and highlighted their potential to elucidate cereal
378 domestication processes (Doebley 1984). Similarly, ethnobotanical studies of other wild foods
379 have resulted in recommendations for their agricultural improvement, such as in grain chenopods
380 (Partap and Kapoor 1985). Other studies suggest improved collections of wild plants to
381 encourage their cultivation, such as in wild onion (*Allium*) (Bye 1985). Thus, in addition to
382 identifying potential crops, ethnobotanical studies can result in a variety of suggestions for pre-
383 breeding and domestication efforts in wild food plants.

384 *Elymus* is a cosmopolitan genus, and the 21 species in this study with documented
385 ethnobotanical uses have widely distributed native ranges, occurring across temperate North
386 America and Eurasia. While we identified documented uses for *Elymus* in several Eurasian
387 countries (Table 1), the depth of ethnobotanical information about *Elymus* species used in North
388 America was much greater. This disparity could be accredited to the fact that we primarily used
389 resources at the Missouri Botanical Garden library, thereby biasing the details of our study to
390 North America and to resources in English. As such, there are other globally-distributed *Elymus*
391 species that could have been used in an ethnobotanical capacity and that may also have potential
392 for use in pre-breeding and domestication programs. For example, wild relatives of sunflower
393 (Heliantheae) with larger ranges may have environmental tolerances and other traits useful to

394 breeding initiatives (Kantar et al. 2015).

395

396 ***Variation in floret traits of Elymus species***

397 Seed traits (floret traits in *Elymus*) are an important feature of wild and domesticated
398 plants that may bear some indication of other agronomically and ecologically important features.
399 For example, wild taxa with larger seeds can have larger seedlings, faster rates of germination,
400 higher recruitment success, and greater reproductive output, though trade-offs in seed size and
401 seed number exist for some species (Giles 1990; Jakobsson and Eriksson 2000). Similarly,
402 during grain domestication, selection favors species and individuals with larger seeds, resulting
403 in greater seedling vigor, root and shoot biomass, and yield, though the correlation of seed size to
404 plant size at maturity is weaker (Milla and Matesanz 2017; Preece et al. 2015; Rees and Venable
405 2007; Stougaard and Xue 2004). Further, it has been found that the progenitors of cereal crops
406 have larger seeds than other wild grasses that have never undergone domestication (Preece et al.
407 2015). Given this information, we hypothesized that *Elymus* species with larger floret areas
408 would perhaps be more frequently used as a food source and be more desirable for human
409 consumption/domestication purposes. For the *Elymus* taxa examined in this study, we found
410 significant differences in floret area between species and among replicates of a species. This
411 suggests that there is substantial natural variation in floret area within *Elymus*, an economically
412 and agriculturally important trait with potential for selection and evolution through the pre-
413 breeding process. From a conservation perspective, these data underscore the importance of a
414 dynamic *in situ* and *ex situ* conservation management that targets multiple species within a
415 genus, and diverse populations in different geographic locations (e.g., Khoury et al. 2019).

416 We observed a significant relationship between floret area and medicinal use in North

417 American *Elymus* species. We cannot ensure that the specimens measured accurately reflect the
418 plants used by indigenous communities in the last three centuries. However, some studies
419 exploring seeds traits of medicinal plants assess seed size in relation to oil content (i.e. *Moringa*,
420 Mani et al. 2007; *Pentaclethra*, Asoegwu et al. 2006). The medicinal uses of vegetative plant
421 parts (i.e. roots) of *Elymus* exist, yet seeds were rarely described in a medicinal context (Table
422 2); therefore, the benefit of a larger floret area for medicinal applications should be further
423 investigated. For example, what properties of *Elymus* grains matter in medicinal applications
424 (oils, carbohydrates)? Are the grains ground, infused, or eaten directly in a medicinal context?
425 Future work could use voucher specimens from ethnobotanical studies to track the relationship
426 between medicinal use and floret area. Further, this study and others like it emphasize the
427 importance of plant use histories in conservation management, as different cultural communities
428 have unique and varied uses for the same species or closely related species; or, they have used
429 different species for similar purposes (e.g., Albuquerque et al. 2009)

430 Despite the wide variation in floret size within and among *Elymus* species, we did not
431 observe a significant relationship between average floret area, region, and documented
432 ethnobotanical use for the remaining three categories examined here (food, forage, and material).
433 It is conceivable that use of *Elymus* species for forage and material would not necessarily lead to
434 changes in seed size, as the primary structures being used (e.g., stems, leaves) may have been the
435 targets of selection. Data for these components of the plant were not collected in this study;
436 consequently, we are unable to assess whether or not forage and material uses led to changes in
437 these traits. Regarding food uses, archaeological analyses of taxa previously used for food have
438 demonstrated differences in seed size and other traits over time (Langlie et al. 2014; Mueller
439 2017), providing evidence for selection and domestication. The lack of association between

440 floret size and use of *Elymus* for food in our dataset indicates that floret area was not associated
441 with utilization or consumption by indigenous communities. Detailed analyses of other traits,
442 including inflorescence size, plant height, historical abundance, may provide insights into
443 selection during at their time of use. Nonetheless, nearly all of the collections sampled in this
444 study were from the 20th century, and floret areas may have varied more significantly at the time
445 and place of use. Further, comparative analyses of the *Elymus* species with documented use
446 histories with other *Elymus* species for which no use history is known, might shed light on how
447 floret traits in *Elymus* species have changed through their interaction with humans. Floret and
448 grain traits remain important for *de novo* domestication in grasses and should be examined more
449 extensively in *Elymus* as well as other taxa of interest.

450
451 **Conclusions**
452

453 Morphological and genetic variation in cultivated plants, their wild progenitors, and other
454 wild species provides the foundation for plant domestication and breeding efforts. In response to
455 concerns about long-term sustainability of our current agricultural system, attention is focusing
456 in part on *de novo* domestication of wild species (Ciotir et al. 2016; Ciotir et al. 2019; Kole
457 2011). As such, *Elymus* and many other genera of herbaceous perennials, merits increased
458 attention to its research, development, and conservation. These efforts include improving the
459 availability of *Elymus* germplasm in biorepositories globally in conjunction with expanding the
460 collection of ethnobotanical histories throughout the genus. Additionally, we suggest more
461 comprehensive morphological and molecular studies of taxa with documented food uses to more
462 precisely identify promising candidates for agriculture. Similarly, we see value in *in-situ*
463 conservation for genetically, phenotypically, and culturally valuable populations (i.e. at sites of
464 indigenous use), as well as in-ground plantings to assess survivability in a controlled

465 environment. Ultimately, a variety of *Elymus* species show promise for the ecological
466 intensification of agriculture.

467

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474

475 **Author Contributions**

476 AJM, BM, CC, ESF, and MJR conceived of the study. BM, CC, and ESF collected the data. ESF
477 and MJR performed data analyses. AJM, BM, and ESF took the lead in writing the manuscript
478 and all authors contributed to manuscript editing.

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811 **Table Captions**

812 **Table 1 caption:** Native ranges and location of ethnobotanical use for 21 *Elymus* species.

813 **Table 2 caption:** Compilation of documented ethnobotanical records for 21 *Elymus* species.

814 “Unspecified” denotes where an indigenous community, plant part, or ethnobotanical use was
815 not documented for a given species in the literature we consulted.

816

817 **Figure Captions**

818 **Figure 1 caption:** Geographic locations of collection sites for all specimens measured across 21
819 *Elymus* species. Collection site determined from herbarium specimen label.

820 **Figure 2 caption:** Comparison of average floret area by use (medicine, food, forage, and
821 material) and region (North America, Eurasia). Blue denotes a documented use within that
822 ethnobotanical category. Red denotes no documented use within that ethnobotanical category.
823 Significant differences ($F_1 = 4.75$, $P = 0.03$) found only for medicinal uses in North America
824 (2a).

825

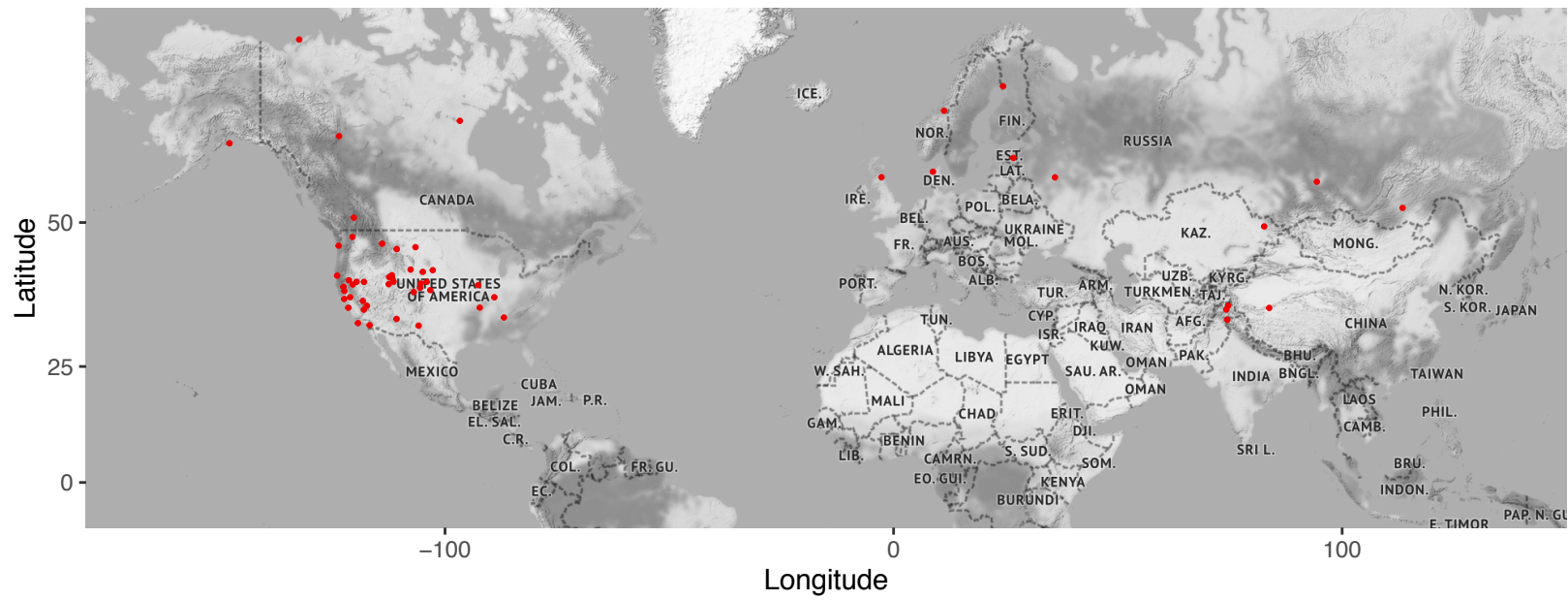
826 **Appendix Captions**

827 **Appendix 1 caption:** Herbarium specimen information from which florets were harvested for
828 area measurements. * = Specific latitudes and longitudes were not available at time of collection,

829 so coordinates were estimated in Google Earth for general analyses in R based off of detailed
830 geographic information provided on the specimen.

831 **Appendix 2 caption:** Individual floret area measurements for 21 *Elymus* species and replicates.

Herbarium Specimen Collection Locations



Species	Use Distribution	Native Range
<i>E. arenarius</i> (L.)	Eurasia (NOR)	Eurasia
<i>E. canadensis</i> (L.)	North America (UT, CO)	North America
<i>E. caninus</i> (L.)	Eurasia (RUS, CHN)	Temperate Asia
<i>E. elongatus</i> (Host.)	North America (USA, CAN)	Eurasia
<i>E. elymoides</i> (Raf.)	North America (CA)	North America, Temperate Asia
<i>E. fibrosus</i> (Schrenk)	Eurasia (RUS)	Temperate Asia
<i>E. glaucus</i> (Buckley)	North America (CA, NM, BC)	North America, Temperate Asia
<i>E. hystrix</i> (Moench)	North America (FL)	North America
<i>E. lanceolatus</i> (Scribn. & J.G. Sm.)	North America (USA, CAN)	North America, Temperate Asia
<i>E. mollis</i> (Trin.)	North America (AK, BC, WA)	North America, Eurasia
<i>E. multisetus</i> (J.G. Sm.)	North America (CA)	North America
<i>E. mutabilis</i> (Drobow)	Eurasia (RUS)	Eurasia
<i>E. repens</i> (L.)	North America (USA, CAN); Eurasia (FIN, SWE, RUS, TUR, BIH, IRL)	Eurasia
<i>E. semicostatus</i> (Nees ex Steud.)	North America (USA); Eurasia (JPN)	Asia
<i>E. sibiricus</i> (L.)	North America (UT); Eurasia (RUS)	North America, Eurasia
<i>E. smithii</i> (Rydb.)	North America (USA, CAN)	North America
<i>E. spicatus</i> (Pursh)	North America (USA)	North America
<i>E. trachycaulus</i> (Link)	North America (USA, CAN); Eurasia (RUS)	North America, Eurasia
<i>L. cinereus</i> (Scribn. & Merr.)	North America (AB, BC, MT, UT, CA)	North America
<i>L. condensatus</i> (J. Presl)	North America (UT, CA)	North America
<i>L. triticoides</i> (Buckley)	North America (CA)	North America

Species	Indigenous Communities	Plant Part Used	Food Uses	Medicinal Uses	Forage Uses	Material Uses	References
<i>E. arenarius</i> (L.)	Unspecified	Unspecified	Unspecified	Unspecified	Unspecified	Twisting ropes and making brooms.	Hooker 1839; Moerman 1998.
<i>E. canadensis</i> (L.)	Gosiute (G), Iroquois (I), Kiowa (K), Ute (U), Paiute (P)	Seeds, roots, and foliage	Gathered (G , U), ground into flour, used to make bread, cereals, rye casserole.	Compound decoction of roots taken for the kidneys (I).	Fodder (K); forage for deer, antelope, and buffalo (P); cultivated as a pasture grass (P).	Unspecified	Facciola 1990; Kindscher 1987; Kunkel 1984; Moerman 1998; Tanaka 1976; Yanovsky 1936.
<i>E. caninus</i> (L.)	Unspecified	Unspecified	Unspecified	Unspecified	Forage grass.	Unspecified	Hanelt 2001.
<i>E. elongatus</i> (Host.)	Unspecified	Unspecified	Unspecified	Unspecified	Hay and pasture crop.	Unspecified	Hanelt 2001.
<i>E. elymoides</i> (Raf.)	Navajo (N), Ramah (R), Potter Valley Pomo (PVP)	Seeds	As pinole, considered second best quality after wild oats (PVP).	Unspecified	Young plants used for sheep and horse feed (N , R).	Unspecified	Moerman 1998; Welch 2013.
<i>E. fibrosus</i> (Schrenk)	Unspecified	Unspecified	Unspecified	Unspecified	Minor forage crop.	Unspecified	Clayton et al. 2006; Hanelt 2001.
<i>E. glaucus</i> (Buckley)	Karok (KA), Keres (KE), Gitksan (GI)	Seeds	As porridge (seeds parched, pounded into a flour, and mixed with water into a	To settle quarrels between families or individuals (KA).	Forage for deer, antelope, and buffalo; potential pasture and forage crop.	Used in socks and stuffing inside moccasins, as baby bedding, and to cover ground where	Couplan 1998; Ebeling 1986; Hanelt 2001; Moerman 1998; Schenck 1952; Smith 1997; Smith Jr. 2014;

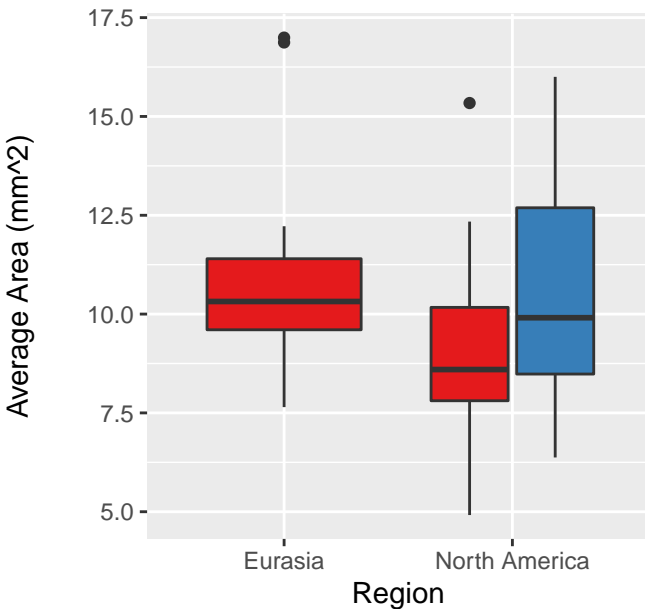
			paste), cooked, or ground into bread flour (KA).			people sat around fire (GI).	Tanaka 1976; Yanovsky 1936.
<i>E. hystrix</i> (Moench)	Iroquois	Unspecified	Unspecified	Ceremonial: decoction for corn seeds (I).	Unspecified	Unspecified	Austin 2004.
<i>E. lanceolatus</i> (Scribn. & J.G. Sm.)	Unspecified	Unspecified	Unspecified	Unspecified	Cultivated as forage grass and pasture crop.	Unspecified	Hanelt 2001.
<i>E. mollis</i> (Trin.)	Nitinaht (NI), Makah (M), Haida (H), Nunivak Eskimo (NE)	Seeds, stems, leaves, and roots	Seeds eaten.	Roots twisted together to form rope, rubbed on the bodies of young men for strength (NI); basal portion of stem chewed for incontinenc e (M).	Unspecified	Tough leaves used for sewing (NI), plants gathered, split, dyed, and used in basketry and mats (H ; NE).	Couplan 1998; Turner et al. 1983; Turner 2010; Lantis 1946.
<i>E. multisetus</i> (J.G. Sm.)	Kawaiisu (KW)	Seeds	Pounded into a porridge/mush (KW).	Unspecified	Unspecified	Unspecified	Moerman 1998; Smith Jr. 2014.
<i>E. mutabilis</i>	Unspecified	Unspecified	Unspecified	Unspecified	Frost-	Unspecified	Hanelt 2001.

(Drobow)					resistant forage grass.		
<i>E. repens</i> (L.)	Apache (A), White Mountain (WM), Cherokee (CHE), Gosiute, Iroquois, Okanagan-Colville (OC), Lukomir Highlanders (LH)	Seeds, stems, rhizomes, roots, shoots, and leaves	Roots dried, ground into meal, and substituted for bread; rhizomes dried and ground, roasted for coffee, or boiled into a syrup for beer; seeds, tips of rhizomes, leaves and shoots eaten raw; seed mashed (A ; WM ; G).	Orthopedic and urinary aid (CHE ; I); decoction used to wash swollen legs and infusion taken for gravel, incontinence, and bedwetting (CHE); roots infused to make kidney and genitourinary treatment; rhizomes to treat kidney, liver, and urinary problems; worm expellant (I); to treat poor eyesight,	Fodder and forage plant for hay (A ; WM), N. American cultivar 'Newwhy' promising forage hybrid (<i>E. repens</i> x <i>E. spicatus</i>).	Used under and over food in pit cooking (OC).	Allen and Hatfield 2004; Elliot 2009; Ferrier et al. 2015; Hanelt 2001; Jackson 2014; MacKinnon et al. 2009; Moerman 1998; Sargin 2013.

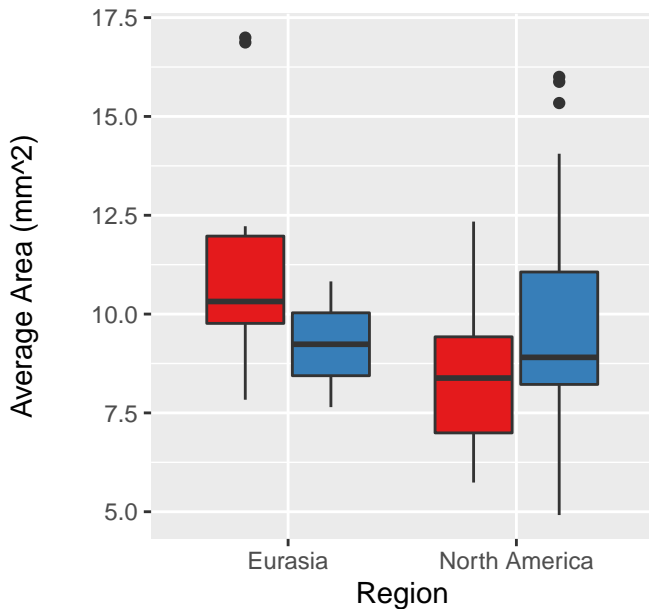
				chest pain, fever, syphilis, jaundice, and swollen and rheumatic limbs; other medicinal uses (LH).			
<i>E. semicostatus</i> (Nees ex Steud.)	Unspecified	Unspecified	Unspecified	Unspecified	Drought-resistant pasture grass.	Unspecified	Clayton et al. 2006; Hanelt 2001.
<i>E. sibiricus</i> (L.)	Gosiute	Seeds	Yes (G).	Unspecified	Infrequently cultivated as forage grass.	Unspecified	Chamberlin 1911; Clayton et al. 2006; Hanelt 2001; Moerman 1998.
<i>E. smithii</i> (Rydb.)	Unspecified	Unspecified	Unspecified	Unspecified	Cultivated for hay and pasture.	Unspecified	Clayton et al. 2006; Hanelt 2001.
<i>E. spicatus</i> (Pursh)	Unspecified	Unspecified	Unspecified	Unspecified	Forage grass for natural pastures.	Unspecified	Clayton et al. 2006; Hanelt 2001.
<i>E. trachycaulus</i> (Link)	Unspecified	Seeds	Unspecified	Unspecified	Cultivated mostly in grass mixtures as forage and pasture plant.	Unspecified	Clayton et al. 2006; Hanelt 2001; Smith Jr. 2014.
<i>L. cinereus</i>	Paiute,	Seeds, stems,	Seeds eaten	Unspecified	Hay for	Stems used for	Ebeling 1986;

(Scribn. & Merr.) Á. Löve	Thompson (T), Blackfoot (B)	leaves, and culm	(P).		livestock (T).	basket imbrication; leaves used to line graves; culms used as "fish spreaders" or for cleaning; grass used as bedding (T).	Johnston 1970; Turner et al. 1996; Smith Jr. 2014.
<i>L. condensatus</i> (J. Presl) Á. Löve	Cahuilla (C), Gosiute, Paiute, Chumash (CH).	Stems, seeds	Seeds, whole plant eaten (G; P)	Unspecified	Unspecified	Stems used in arrowmaking (C; CH), roof thatching (C), brush handles, knives, and tobacco pipes. Used in house construction, clothes, and tools (CH).	Bean and Saubel 1972; Couplan 1998; Ebeling 1986; Kindscher 1987; Moerman 1998; Smith Jr. 2014; Timbrook 1984.
<i>L. triticoides</i> (Buckley) Pilg.	Paiute, Kawaiisu, Potter Valley Pomo	Seeds	Seeds pounded and cooked to form a thick mush (KW); pinole (PVP).	Unspecified	Unspecified	Unspecified	Ebeling 1986; Couplan 1998; Smith 1997; Smith Jr. 2014; Welch 2013; Zigmund 1981.

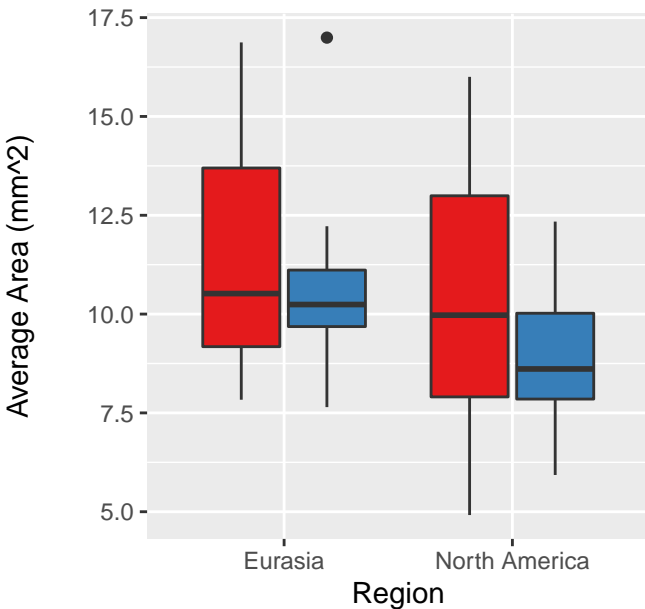
a) Medicine



b) Food



c) Forage



d) Material

