

REVIEW



Diverse ecological functions and the convergent evolution of grass awns

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Abstract

The awn of grasses is a long, conspicuous outgrowth of the floral bracts in a grass spikelet. It is known to impact agricultural yield, but we know little about its broader ecological function, nor the selective forces that lead to its evolution. Grass awns are phenotypically diverse across the extant ~12,000 species of Poaceae. Awns have been lost and gained repeatedly over evolutionary time, between and within lineages, suggesting that they could be under selection and might provide adaptive benefit in some environments. Despite the phylogenetic context, we know of no studies that have tested whether the origin of awns correlates with putative selective forces on their form and function. Presence or absence of awns is not plastic; rather, heritability is high. The awns of grasses often are suggested as adaptations for dispersal, and most experimental work has been aimed at testing this hypothesis. Proposed dispersal functions include soil burial, epizoochory, and aerial orientation. Awns may also protect the seed from drought, herbivores, or fire by helping it become buried in soil. We do not fully understand the fitness or nutrient costs of awn production, but in some species awns function in photosynthesis, providing carbon to the seed. Here we show that awns likely provide an adaptive advantage, but argue that studies on awn function have lacked critical phylogenetic information to demonstrate adaptive convergent evolution, are taxonomically biased, and often lack clear alternative hypotheses.

KEYWORDS

adaptation, agriculture, evolutionary ecology, exaptation, florivory, geniculate, grass ecology, herbivore defence, herbivory prevention, Poaceae, spikelet

GRASSES, GRASS FLOWERS, AND AWNS

Poaceae (the grass family) are an agriculturally important, ecologically diverse, and species-rich plant family. The ~12,000 species of Poaceae (Soreng et al., 2017) collectively cover approximately 31–43% of global land surface in almost all habitat types, including open, dry savannah, dry woodlands, and wet tropical rainforests (Gibson, 2009; Lehmann et al., 2019).

The flowers of grasses are tiny, with each one subtended by a (relatively) large bract, the lemma; together, the flower itself plus the lemma are known as a floret (Schrager-Lavelle

et al., 2017). An individual floret comprises a uniovular gynoecium (female reproductive parts) and three to six stamens (pollen-producing organs). The structures in the position of petals are known as lodicules, which typically become turgid at anthesis to force the floret open and then shrivel afterward. Outside the lodicules are two grass-specific structures, the palea and the lemma (Figure 1). The palea has historically been interpreted as a bract or prophyll, although increasing evidence suggests that it represents highly modified adaxial outer tepals and, as such, is part of the flower (Kellogg, 2015; Schrager-Lavelle et al., 2017). The lemma generally encloses the other organs. One or more florets are then aggregated into a larger structure, the

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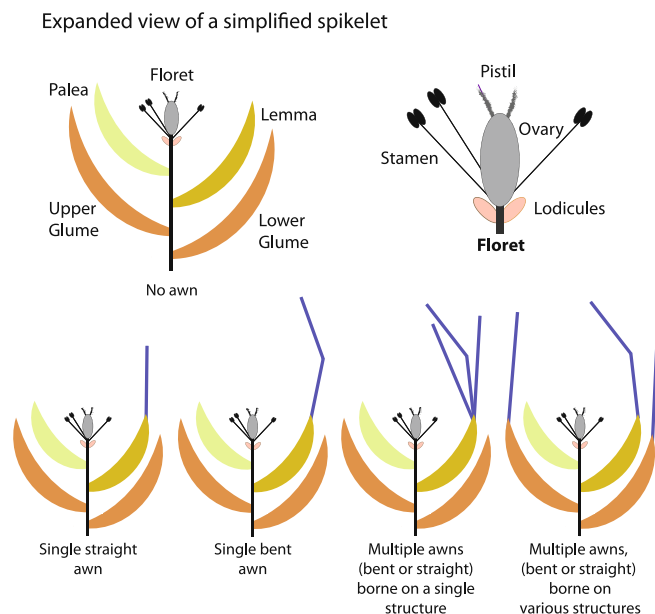


FIGURE 1 Simplified diagram of a grass spikelet to illustrate the position of nonfloral structures. The four example spikelets show positions where awns commonly develop and the possible variations in number and form. Awns can develop from lemma or glumes or more rarely paleas. The type of awn can be mixed within a single spikelet, e.g., bent and straight.

spikelet, which is subtended by bracts (usually two) known as glumes (Figure 1).

In many grasses, the lemma, one or both glumes, or occasionally the palea, may end in a sharp point, or bear a short, pointed extension (a mucro), or bear a longer extension known as an awn (Figure 1) (Gould and Shaw, 1983; Kellogg, 2000). The distinction between a mucro and awn is arbitrary; for this review, we define any structure over 1 mm long as an awn. The awn is most commonly an extension of the mid-vein and is usually apical, but in some species forms on the abaxial side of the lemma. It is generally vascularized and usually tapers to a sharp tip. In some species, additional awns form from lateral veins, with their position, number, and morphology being species-specific (Clayton et al., 2006–2021; Cavanagh et al., 2019). The awn may be straight, curved, once- or twice-geniculate (bent like a knee because of a reverse twist), coiled, or even (in a few taxa) branched.

Despite the ubiquity of awns, their function is not fully known. Here, we optimize awn presence and structure over a previously published phylogeny, showing that awns have been repeatedly and independently gained and lost in grass evolution. We then review literature showing that awns are (1) generally fixed as present or absent within a species, (2) are costly to produce, and (3) may have roles in carbon capture, seed dispersal, seed defence, and seed burial. Taken together, these observations suggest that awns could confer a selective advantage. We also note that existing data are sparse and taxonomically biased. Finally, we conclude with suggestions for future research.

AWNS ARE REPEATEDLY GAINED FROM AN AWNLESS ANCESTRAL STATE

To provide a phylogenetic context for the remainder of this review, we mapped presence/absence of awns on the grass plastome phylogeny of Saarela et al. (2018), which is well supported and includes all grass subfamilies. For each species in the phylogeny, we retrieved awn data from descriptions in GrassBase (Clayton et al., 2006–2021) and augmented this information where necessary with our own observations of herbarium specimens at GBIF.org (2021) (Appendix S1). We optimized awn presence/absence using maximum likelihood in the *ace* function as part of the R package phytools (Revell, 2012; R Core Team, 2022). We compared Equal Rates (ER) and All Rates Different (ARD) models. For the questions addressed here, the models produced similar results so only the ER results are shown. With this sample of species, we found that awns appear to have been gained at least 12 times in the history of Poaceae, but once gained may often be lost (Figure 2; Appendix S2).

We noted whether awns were borne on the lemma, palea, glumes, or some combination (Appendix S1). Glume awns usually evolve in groups that have already developed lemma awns (Figure 3), but appear independent of ancestral lemma awns in at least three instances (marked with arrows on the figure). Thus, the lemma awn is not an evolutionary or genetic prerequisite for the evolution of glume awns, and glume awns may be a response to independent and distinct selection in those lineages. For this sample of species, palea awns have only a single origin, in Oryzeae (rice tribe), although a broader species sample might well uncover more instances. Lemma awns are common within the Oryzeae, and our analysis suggests they were likely present in the ancestors of the group.

We mapped awn morphology on the phylogeny (Figure 4), using the awn shape character states straight, curved (falcate) and geniculate, following Cavanagh et al. (2019), except that we combined once- and twice-geniculate into the single category of geniculate. Geniculate and straight awns are most common, with only a few awn types not fitting into either category (branched and coiled). Rarely, the two types co-occur on a single spikelet; in which case, the geniculate awn is generally the central awn on the lemma, and the straight awns are either lateral on the lemma or form on paleas or glumes (Figure 1). Geniculate awns are rarely evolutionarily derived from straight awns. Of the six groups bearing geniculate awns, only two (noted with arrows on the figure and both in the large subfamily Pooideae) convincingly suggest ancestral awns were straight (Figure 4). The reverse appears even rarer, with geniculate awns not leading to straight awns anywhere in the phylogeny. Two unique awn morphologies appear in *Aristida* and *Streptochaeta*, coiled and branched, respectively. We do not know whether the coiled awns of *Streptochaeta* represent early awn evolution or a unique derived state in that tribe (Figure 4). However, *Aristida* appears to represent an independent evolution of

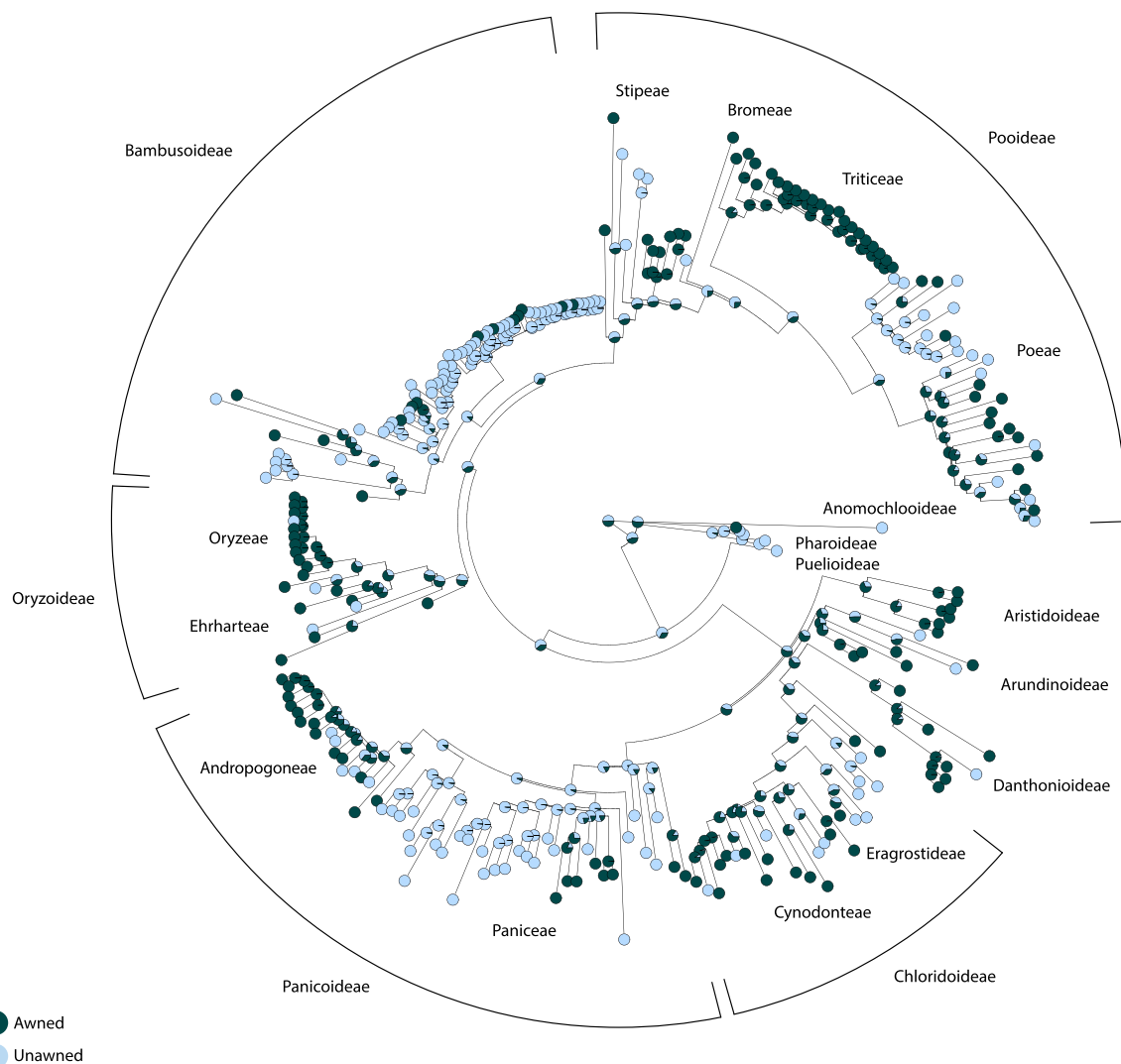


FIGURE 2 Presence or absence of awns in Poaceae regardless of developmental origin (e.g., glume or lemma) optimized on a phylogeny from Saarela et al. (2018). Outer names indicate subfamily classification; inner names indicate tribe level classifications. Dark green: awned species or genera; blue: no awn. An awn is defined as present if it is ≥ 1 mm long. Full species names are in Appendix S2.

branched awns, unique to that group and any other known extant awns (Figure 4).

Repeated gains and losses (i.e., convergent evolution) often suggest that a trait has been subject to natural selection (Losos, 2011; Stayton, 2015). The limited phylogenetic analyses here provide evidence that the selective forces acting on awn position and awn type may vary and provide context for the functional data described below. A phylogenetic analysis with a larger sample of taxa and a broader range of models will ultimately be needed, but the evidence of multiple origins and convergent morphology appears robust.

Awn presence is not a plastic response

Presence or absence of awns appears to be insensitive to environmental conditions and is largely fixed for a given

genotype. Greenhouse-grown plants do not lose or gain awns when moved indoors or outdoors, and awn characters are stable when plants are grown in different environments (K. B. Petersen and E. A. Kellogg, personal observations). Species descriptions also indicate that awn presence or absence is fixed within the species, although a few polymorphic species have been recorded (Clayton et al., 2006–2021). In wild *Hyparrhenia diplandra* and domesticated *Sorghum bicolor*, *Oryza sativa*, *Triticum aestivum*, and *Hordeum vulgare*, awn traits were highly heritable (Garnier and Dajoz, 2001; Zhang et al., 2015; Magwa et al., 2016; Sanad et al., 2019; Wang et al., 2019 [Preprint]), with broad sense heritability of awn presence over 40% and awn length 63–98%, depending on the species, environment, and degree of stress. Awn length of *H. diplandra* varied slightly with and between populations, but presence of awns is fixed. Furthermore, awn length appears to be under polygenic control, with multiple genes

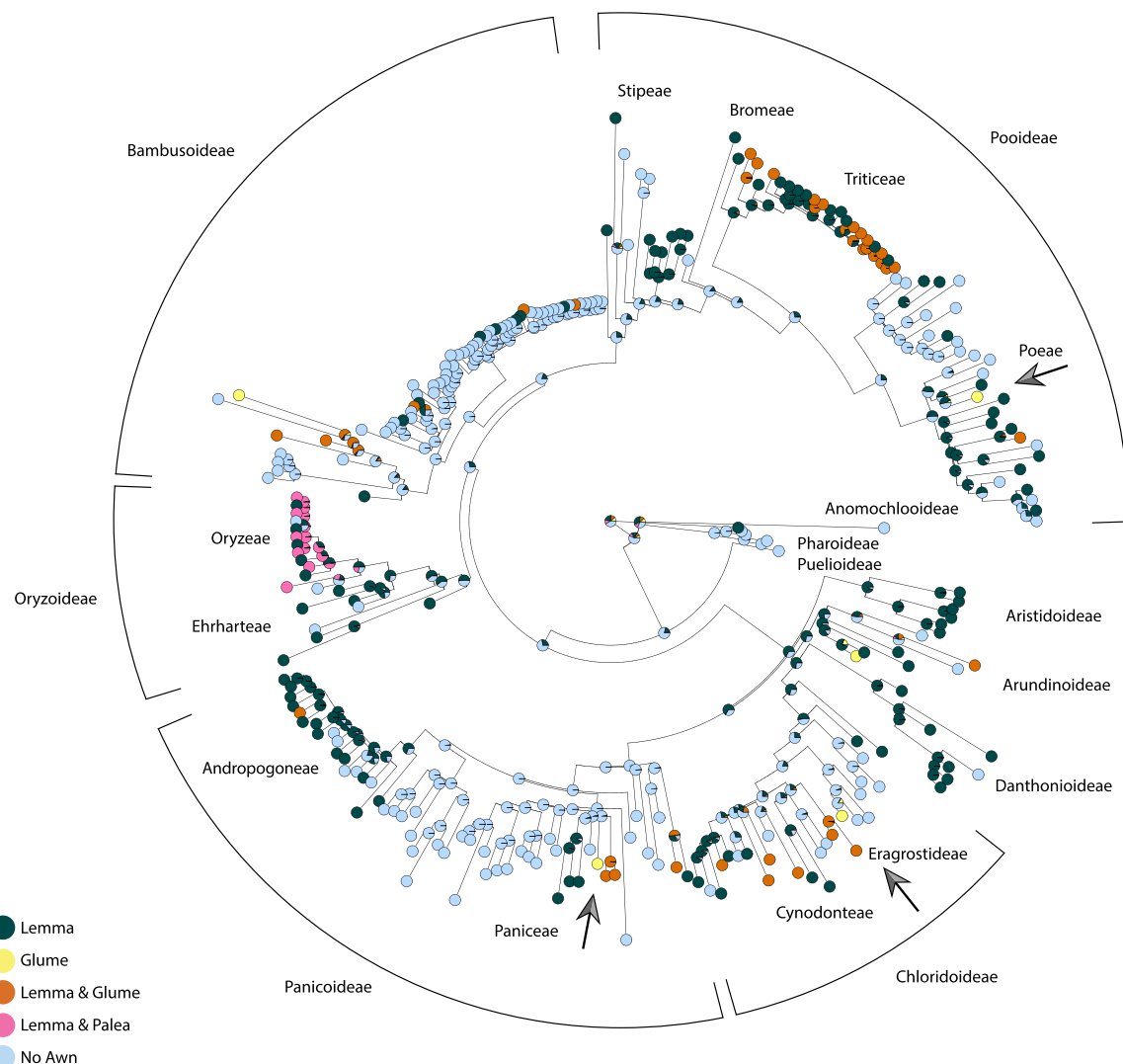


FIGURE 3 Morphological origin of awns on the spikelet, optimized on a phylogeny from Saarela et al. (2018). Outer names indicate subfamily classification; inner names indicate tribe level classifications. Light blue: species or genera without awns; dark green: lemma awn; yellow: glume awn, pink: palea awn, orange: both lemma and glume awns. Arrows specify taxa in which glume awns appear to have evolved independently of any other awn.

controlling length but not abolishing awns completely (Liu et al., 2007; Toriba et al., 2010; Yuo et al., 2012; Hua et al., 2015; Bessho-Uehara et al., 2016; Jin et al., 2016).

POSSIBLE FUNCTIONS OF AWNS

Awns capture carbon but are costly to produce

The growth and presence of an awn on a spikelet has a cost, although it is unclear if costs are carbon-driven or the result of other nutrient limitations. A negative relationship between awn presence and seed number has clearly been shown in some cultivated species (*Oryza sativa*, *O. sativa* subsp. *japonica* × *O. sativa* subsp. *indica*, *Triticum aestivum*, *Hordeum vulgare*) (Gu et al., 2015; Rebetzke et al., 2016; Liller et al., 2017; De Leon et al., 2020), and in wild species (*Oryza rufipogon* and *Elymus sibiricus*) (Gu et al., 2015;

Ntakirutimana et al., 2019). In wild Siberian wildrye (*Elymus sibiricus*), awn length is negatively correlated with florets per inflorescence, percentage seed set, and total seeds per inflorescence (Ntakirutimana et al., 2019). However, even though fewer seeds and flowers are produced with the production of larger awns, the seeds were significantly larger. We hypothesize that the development of awns represents a shift in reproductive life strategy, from production of many small seeds to fewer large well-provisioned seeds.

Awns are not necessarily a nutrient sink. Awns of some grasses may photosynthesize, offsetting carbon costs and provisioning seeds (Atkins and Finney, 1957; Grundbacher, 1963; Faris, 1974; Olugbemi, 1978; Tambussi et al., 2007). Photosynthetic awns are common among species in the tribe Triticeae and in subfamily Oryzoideae (Grundbacher, 1963; Tambussi et al., 2007). In both groups, experiments that block photosynthesis (e.g., by covering the awn or removing it) reduce yield; conversely, tracing

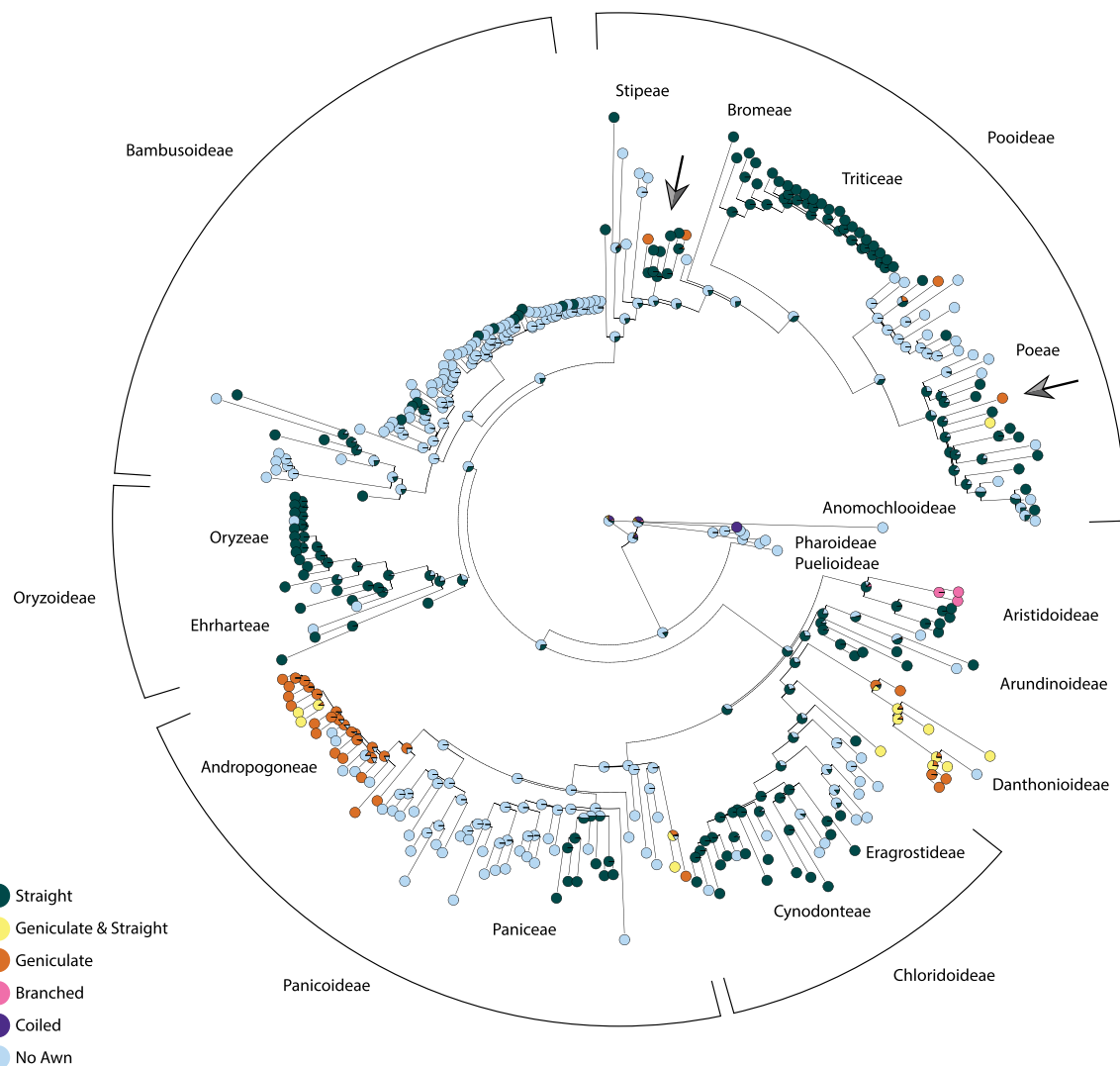


FIGURE 4 Type of awns optimized on a phylogeny from Saarela et al. (2018). Outer names indicate subfamily classification; inner names indicate tribe level classifications. Light blue: species or genera without awns, orange: geniculate (twisted and bent) awns, dark green: straight awns, yellow: mixed geniculate and straight awns, pink: others (branched or coiled). Arrows specify places where geniculate awns have evolved in lineages of straight awns.

labelled carbon shows movement of photosynthate from the awn to the seed (reviewed by Grundbacher [1963] and Tambussi et al. [2007]).

Not all awns photosynthesize, however (Moskalenko, 1930; Grundbacher, 1963; AuBuchon-Elder et al., 2020). In particular, awns on seed-bearing spikelets in Andropogoneae (Panicoideae) show no evidence of carbon assimilation (AuBuchon-Elder et al., 2020). Seed-bearing spikelets in that tribe are paired with awnless sterile spikelets, which assimilate carbon that is then transferred to the seed. In this tribe then, awn function in photosynthesis appears to be replaced by the sterile spikelet.

The carbon provided to developing seeds from awns (and neighboring underdeveloped spikelets, where present) suggests that awns are an adaptation to provide carbon to the seed. If a cost to produce awns exists, it may be offset by selective advantage of a larger seed.

Awns as aids in dispersal

The awns of grasses may function in dispersal in three ways: hygroscopically active awns move in response to changes in moisture, moving the diaspore (the seed and all other dispersed spikelet structures) into or across the soil, awns position the diaspore in the air and to enhance germination on landing, and awns attach to animals (epizoochory). The three are not mutually exclusive, and none is universal. Evidence for epizoochory remains the weakest, with static awns positioning in the air column and hygroscopic awn movement having better experimental support.

The distinctive hygroscopic movement of awns was noticed as early as in the 19th century (Quekett, 1844, p. 25):

“There is another act performed by the aid of moisture and dryness which approaches

somewhat near to locomotion: this occurs in ... the parts surrounding the fruit of *Avena fatua*, commonly known as the “animated oat,” where, by the twisting by dryness and untwisting by moisture of the awn, change of place is the result.”

Hygroscopic awns take up moisture from the air and then dry out. Each time the awn gets wet, it straightens, but as it dries, it twists and moves the diaspore. The underlying cellular structures that drive this motion were investigated in the 19th century by Zimmermann (1879), Hildebrand (1873), and briefly summarized by Murbach (1900) for species of *Avena* and *Stipa*. Curiously, this aspect of grass awns has not been studied since, although recent studies in Geraniaceae (Evangelista et al., 2011; Jung et al., 2014) are likely relevant. Many such twisted awns also exhibit a reverse twist, such that the lower (proximal) part of the awn twists one direction and the upper (distal) part twists the other. This bidirectional twist creates a flat section where the twist reverses, producing a pronounced bend or knee (hence the term geniculate). The physical forces involved in such reverse helices and their reversion point have been studied extensively in coiled tendrils (e.g., McMillen and Goriely [2002] Gerbode et al. [2012]) but not in grass awns.

Geniculate twisting is not the only known form of hygroscopic movement in grass awns. Elbaum et al. (2007) also showed that the long lemma awns from two adjacent florets of wheat actively propelled the seed into the soil. Cellulose in the awns is arranged such that different layers of cells expanded differently depending on ambient humidity conditions. The result of this expansion is that the awns move outward when drying and inward with increased humidity. The action of the awns causes the diaspore to push down into the soil, burying it deeper (Elbaum et al., 2007). The hygroscopic movement in wheat (Triticeae) may be an example of convergence in function for burial in awns. Whether the hygroscopic mechanism of wheat awns occurs in other species is unknown.

Hygroscopic awn movement, the role of passive inactive awns, burial ability, development, and their direct ecological importance have been investigated experimentally for ca. 75 species of Poaceae (Table 1) or 1% of the family (Peart, 1979, 1984; Peart and Clifford, 1987; Adams and Tainton, 1990; Ghermandi, 1995; Garnier and Dajoz, 2001; Schöning et al., 2004; Elbaum et al., 2007; Molano-Flores, 2012; Drizin, 2013; Cavanagh et al., 2021). The data are heavily biased toward Australian species, representing only a few tribes (notably Andropogoneae). Hygroscopic awns in particular may function in germination and establishment within communities of mixed grass species (Peart, 1984; Peart and Clifford, 1987; Cavanagh et al., 2021). However, function has generally been extrapolated from limited and taxonomically biased species sampling without considering phylogenetic relationships (Stebbins, 1971; van der Pijl, 1982).

Hygroscopic awns in some species aid burial and soil surface movement. Awn removal reduced successful germination 12-fold in *Danthonia penicillata* (= *Rytidosperma penicillatum*) (Simpson, 1952) or showed significantly less movement (Cavanagh et al., 2021). (Here and throughout this paper, we cite the species name used in the original paper followed by the currently accepted name in parentheses if it is different.) Using the methods of Simpson (1952), multiple investigators have tested burial ability by placing spikelets (with or without modified awns) of various species on soil and observed the subsequent soil-spikelet interaction (Peart, 1979, 1981; Adams and Tainton, 1990; Garnier and Dajoz, 2001; Elbaum et al., 2007; Cavanagh et al., 2021). In these studies, removal or modification of awns changes the proportion of spikelets buried, the germination rate, and overall movement distance. In diaspores bearing both a hygroscopic and passive straight awn, removal of one awn did not significantly affect the ability of spikelets to move to a microsite location, but a significantly lower proportion of spikelets became permanently lodged or buried (Peart, 1979). However, removal of awns produced inconsistent results in *Dichelachne micrantha* and *Themeda triandra*, suggesting the awn alone does not determine burial success (Peart, 1979; Adams and Tainton, 1990).

The depth of burial and distance moved by diaspores correlates with awn length ($r = 0.61$, $P < 0.001$), as shown by a large Australian study on 30 species representing five of the 12 grass subfamilies (Cavanagh et al., 2021). The deepest burial was achieved by diaspores with hygroscopically active awns, with *T. triandra*, *Bothriochloa macra*, and *Anthosachne scabra* being buried 12.4, 6.4, and 5.9 mm, respectively (Cavanagh et al., 2021). The species with the lowest frequency of burial was *Cynosurus echinatus*, which has a single straight inactive awn. In an unrelated study, diaspores of the African grass *Hyparrhenia diplandra* were also buried deeper if they had longer awns (Garnier and Dajoz, 2001). Notably, the starting conditions in burial experiments were often artificial, with diaspores pushed slightly into the soil at the start, removing the need for the diaspore to initiate its own burial.

Soil type and heterogeneity of the surface may be important for the function of large hygroscopic awns (Humphreys et al., 2011). For example, *T. triandra* diaspores move and are effectively buried in heterogeneous soils (Peart, 1979; Cavanagh et al., 2021), but bury themselves poorly in fine homogeneous soils (Adams and Tainton, 1990). In fine soils over 80% of de-awned diaspores were buried, but none of the awned diaspores achieved burial (Adams and Tainton, 1990). Slightly increasing the heterogeneity of the soil increased burial of awned *T. triandra* spikelets to 30% from zero. Introducing the large awned *T. triandra* diaspores to a soil surface with high heterogeneity led to an increase in burial depth, and adding solid objects to the soil surface was required for many species to achieve burial at all (Cavanagh et al., 2021). In northern Australia, heavily clay-based soils with many cracks have significantly more species with hygroscopically

TABLE 1 Species mentioned in this paper, reference, tribe, and subfamily. Species are sorted by tribe. The first species name listed is as written in cited literature (in at least one paper when an older name is listed). Synonyms are the currently accepted species names, following POWO (2021). Authority is for the accepted name, not synonyms.

Species and Authority	References	Tribe	Subfamily
<i>Andropogon gerardi</i> Vitman	Rosas et al. (2008)	Andropogoneae	Panicoideae
<i>Andropogon schirensis</i> Hochst. ex A. Rich.	AuBuchon-Elder et al. (2020)	Andropogoneae	Panicoideae
<i>Bothriochloa bladhii</i> (Retz.) S.T. Blake	Cavanagh et al. (2021)	Andropogoneae	Panicoideae
<i>Bothriochloa macra</i> (Steud.) S.T. Blake	Cavanagh et al. (2021)	Andropogoneae	Panicoideae
<i>Chrysopogon fallax</i> S.T. Blake	Cavanagh et al. (2021)	Andropogoneae	Panicoideae
<i>Cymbopogon refractus</i> (R.Br.) A. Camus	Peart (1984)	Andropogoneae	Panicoideae
<i>Dichanthium sericeum</i> (R.Br.) A. Camus	Peart (1979); Peart and Clifford (1987); Cavanagh et al. (2021)	Andropogoneae	Panicoideae
<i>Heteropogon contortus</i> (L.) P. Beauv. ex Roem. & Schult.	Peart (1979); Peart and Clifford (1987)	Andropogoneae	Panicoideae
<i>Hyparrhenia diplandra</i> (Hack.) Stapf	Garnier and Dajoz (2001)	Andropogoneae	Panicoideae
<i>Schizachyrium fragile</i> (R.Br.) A. Camus	Peart (1979)	Andropogoneae	Panicoideae
<i>Sorghum bicolor</i> (L.) Moench	Zhang et al. (2015); AuBuchon-Elder et al. (2020)	Andropogoneae	Panicoideae
<i>Themeda triandra</i> Forssk.	Agnew and Flux (1970); Peart (1979); Adams and Tainton (1990); AuBuchon-Elder et al. (2020); Cavanagh et al. (2021)	Andropogoneae	Panicoideae
<i>Aristida jerichoensis</i> (Domin) Henrard	Cavanagh et al. (2021)	Aristideae	Aristidoideae
<i>Aristida latifolia</i> Domin	Cavanagh et al. (2021)	Aristideae	Aristidoideae
<i>Aristida ramosa</i> R.Br.	Cavanagh et al. (2021)	Aristideae	Aristidoideae
<i>Aristida vagans</i> Cav.	Peart (1981, 1984)	Aristideae	Aristidoideae
<i>Bromus tectorum</i> L.	Kelrick et al. (1986); Ceradini and Chalfoun (2017); Lucero and Callaway (2018)	Bromeae	Pooideae
<i>Bouteloua curtipendula</i> (Michx.) Torr.	Laughlin (2003); Titulaer et al. (2018)	Cynodonteae	Chloridoideae
<i>Bouteloua gracilis</i>	Titulaer et al. (2018)	Cynodonteae	Chloridoideae
<i>Chloris truncata</i> R.Br.	Cavanagh et al. (2021)	Cynodonteae	Chloridoideae
<i>Enteropogon acicularis</i> (Lindl.) Lazarides	Cavanagh et al. (2021)	Cynodonteae	Chloridoideae
<i>Leptochloa dubia</i> syn. <i>Disakisperma dubium</i> (Kunth) P.M. Peterson & N. Snow	Titulaer et al. (2018)	Cynodonteae	Chloridoideae
<i>Leptothrium senegalense</i> (Kunth) Clayton	Agnew and Flux (1970)	Cynodonteae	Chloridoideae
<i>Tragus berteronianus</i> Schult.	Agnew and Flux (1970)	Cynodonteae	Chloridoideae
<i>Triodia danthonioides</i> (F. Muell.) Lazarides	Cavanagh et al. (2021)	Cynodonteae	Chloridoideae
<i>Triodia schinzii</i> (Henrard) Lazarides	Cavanagh et al. (2021)	Cynodonteae	Chloridoideae
<i>Danthonia penicillata</i> syn. <i>Rytidosperma penicillatum</i> (Labill.) Connor & Edgar	Simpson (1952)	Danthonieae	Danthonioideae
<i>Danthonia tenuior</i> syn. <i>Rytidosperma tenuius</i> (Steud.) O.E. Erikss., A. Hansen & Sunding	Peart (1979)	Danthonieae	Danthonioideae
<i>Rytidosperma caespitosum</i> (Gaudich.) Connor & Edgar	Humphreys et al. (2011); Cavanagh et al. (2021)	Danthonieae	Danthonioideae
<i>Rytidosperma oreophilum</i> H.P. Linder & N.G. Walsh	Cavanagh et al. (2021)	Danthonieae	Danthonioideae
<i>Rytidosperma pallidum</i> (R.Br.) A.M. Humphreys & H.P. Linder	Cavanagh et al. (2021)	Danthonieae	Danthonioideae

(Continues)

TABLE 1 (Continued)

Species and Authority	References	Tribe	Subfamily
<i>Microlaena stipoides</i> (Labill.) R.Br.	Peart (1981, 1984)	Ehrharteae	Oryzoideae
<i>Enneapogon nigricans</i> (R.Br.) P. Beauv.	Cavanagh et al. (2021)	Eragrostideae	Chloridoideae
<i>Eragrostis brownii</i> (Kunth) Nees	Peart (1984)	Eragrostideae	Chloridoideae
<i>Eragrostis lehmanniana</i> Nees	Titulaer et al. (2018)	Eragrostideae	Chloridoideae
<i>Harpachne schimperii</i> Hochst. ex A. Rich.	Agnew and Flux (1970); Hovstad et al. (2009)	Eragrostideae	Chloridoideae
<i>Oryza sativa</i> L.	Liu et al. (2007); Bessho-Uehara et al. (2016); Magwa et al. (2016)	Oryzeae	Oryzoideae
<i>Oryza rufipogon</i> Griff.	Gu et al. (2015)	Oryzeae	Oryzoideae
<i>Melinis repens</i> (Willd.) Zizka	Titulaer et al. (2018)	Paniceae	Panicoideae
<i>Panicum bisulcatum</i> Thunb.	Liang et al. (2019)	Paniceae	Panicoideae
<i>Pennisetum ciliare</i> syn. <i>Cenchrus ciliaris</i> L.	Titulaer et al. (2018)	Paniceae	Panicoideae
<i>Agrostis capillaris</i> L.	Hovstad et al. (2009)	Poeae	Pooideae
<i>Avena fatua</i> L.	Quekett (1844)	Poeae	Pooideae
<i>Cynosurus echinatus</i> L.	Cavanagh et al. (2021)	Poeae	Pooideae
<i>Deschampsia cespitosa</i> (L.) P.Beauv.	Hovstad et al. (2009)	Poeae	Pooideae
<i>Deyeuxia fauriei</i> (Hack.) Ohwi	Clayton et al. (2006–2021)	Poeae	Pooideae
<i>Dichelachne micrantha</i> (Cav.) Domin	Peart (1979)	Poeae	Pooideae
<i>Echinopogon ovatus</i> (G. Forst.) P. Beauv	Cavanagh et al. (2021)	Poeae	Pooideae
<i>Festuca idahoensis</i> Elmer	Lucero and Callaway (2018)	Poeae	Pooideae
<i>Festuca ovina</i> L.	Hovstad et al. (2009)	Poeae	Pooideae
<i>Sesleria korabensis</i> (Kümmerle & Jáv.) Deyl	Clayton et al. (2006–2021)	Poeae	Pooideae
<i>Austrostipa aristiglumis</i> (F. Muell.) S.W.L. Jacobs & J. Everett	Cavanagh et al. (2021)	Stipeae	Pooideae
<i>Austrostipa bigeniculata</i> (Hughes) S.W.L. Jacobs & J. Everett	Cavanagh et al. (2021)	Stipeae	Pooideae
<i>Austrostipa blackii</i> (C.E. Hubb.) S.W.L. Jacobs & J. Everett	Cavanagh et al. (2021)	Stipeae	Pooideae
<i>Austrostipa mollis</i> (R.Br.) S.W.L. Jacobs & J. Everett	Cavanagh et al. (2021)	Stipeae	Pooideae
<i>Austrostipa nitida</i> (Summerh. & C.E. Hubb.) S.W.L. Jacobs & J. Everett	Cavanagh et al. (2021)	Stipeae	Pooideae
<i>Austrostipa nivicola</i> (J.H. Willis) S.W.L. Jacobs & J. Everett	Cavanagh et al. (2021)	Stipeae	Pooideae
<i>Austrostipa nodosa</i> (S.T. Blake) S.W.L. Jacobs & J. Everett	Cavanagh et al. (2021)	Stipeae	Pooideae
<i>Austrostipa rudis</i> (Spreng.) S.W.L. Jacobs & J. Everett	Cavanagh et al. (2021)	Stipeae	Pooideae
<i>Austrostipa scabra</i> (Lindl.) S.W.L. Jacobs & J. Everett	Cavanagh et al. (2021)	Stipeae	Pooideae
<i>Hesperostipa spartea</i> (Trin.) Barkworth	Molano-Flores (2012)	Stipeae	Pooideae
<i>Nassella neesiana</i> (Trin. & Rupr.) Barkworth	Cavanagh et al. (2021)	Stipeae	Pooideae
<i>Oryzopsis hymenoides</i> , syn. <i>Achnatherum hymenoides</i> , syn. <i>Eriocoma hymenoides</i> (Roem. & Schult.) Rydb.	Kelrick et al. (1986); Lucero and Callaway (2018)	Stipeae	Pooideae
<i>Stipa parviflora</i> , syn. <i>Achnatherum parviflorum</i> (Desf.) M. Nobis	Schöning et al. (2004)	Stipeae	Pooideae

TABLE 1 (Continued)

Species and Authority	References	Tribe	Subfamily
<i>Stipa tenacissima</i> , syn. <i>Macrochloa tenacissima</i> (L.) Kunth	Schöning et al. (2004)	Stipeae	Pooideae
<i>Stipa verticillata</i> , syn. <i>Austrostipa verticillata</i> (Nees ex Spreng.) S.W.L. Jacobs & J. Everett	Peart (1979); Cavanagh et al. (2021)	Stipeae	Pooideae
<i>Stipa viridula</i> , syn. <i>Eriocoma lettermanii</i> (Vasey) Romasch.	Kelrick et al. (1986)	Stipeae	Pooideae
<i>Aegilops geniculata</i> Roth	Clayton et al. (2006–2021)	Triticeae	Pooideae
<i>Anthosachne scabra</i> (R. Br.) Nevski	Cavanagh et al. (2021)	Triticeae	Pooideae
<i>Elymus elymoides</i> (Raf.) Swezey	Lucero and Callaway (2018)	Triticeae	Pooideae
<i>Hordeum vulgare</i> L.	Faris (1974); Liller et al. (2017)	Triticeae	Pooideae
<i>Pascopyrum smithii</i> , syn. <i>Elymus smithii</i> (Rydb.) Gould	Kelrick et al. (1986)	Triticeae	Pooideae
<i>Pseudoroegneria spicata</i> (Pursh) Á. Löve	Lucero and Callaway (2018)	Triticeae	Pooideae
<i>Triticum aestivum</i> L.	Sanad et al. (2019); AuBuchon-Elder et al. (2020)	Triticeae	Pooideae
<i>Elymus sibiricus</i> L.	Ntakirutimana et al. (2019)	Triticeae	Pooideae

Notes: Plus 69 unspecified Australian species from Peart and Clifford (1987) (overlapping habitat with those described by Peart [1979, 1981, 1984]).

active, awned diaspores than unawned diaspores (Peart and Clifford, 1987). Conversely, sandier sites with fewer deep cracks had a significantly higher species abundance of unawned diaspores (Peart and Clifford, 1987). In another study, seed length, awn length and width, and seed biomass of the grass *Hesperostipa spartea* were significantly different between diaspores originating from loam and sandy soils (Molano-Flores, 2012), although all diaspores were significantly better at burying themselves in loam soils, regardless of diaspore origin. Diaspores originating in sandy soils were smaller and had significantly shorter awns, but buried themselves more deeply than the diaspores of loam origin. These results suggest an unclear and complex interaction between soil type, soil surface structure, and awn design (Humphreys et al., 2011).

Inactive passive awns do not appear to interact with the environment in the same way as hygroscopic awns, and frequency of diaspores with passive awns does not correlate with any particular soil type (Peart and Clifford, 1987). Straight awns are commonly passive-inactive, but there are exceptions such as wheat (Elbaum et al., 2007). Most phylogenetic origins of straight awns are independent of geniculate hygroscopic ones (Figure 4). The passive awns of grasses may function in positioning spikelets on the soil or in the air column. The spikelets of *Aristida vagans* and *Microlaena stipoides*, which have rigid passive awns, fall consistently with the callus (base of the spikelet where the radicle emerges) downward when dropped from height (Peart, 1981). Removal of awns significantly decreases callus-down landing and significantly decreases germination (Peart, 1981). Other studies on terminal velocity and falling orientation of diaspores found similar results, with hairs and

rigid awns guiding the diaspores to fall almost straight down (Rabinowitz and Rapp, 1981). Furthermore, observations suggest that diaspores of passive-awned species are often found in a standing position (Peart, 1984). However, there is no evidence to suggest that aerial orientation is a trait unique to straight, rigid awns.

Awns may also aid epizoochory, the transport of seed on the skin or fur of animals (Sorensen, 1986; Chambers and MacMahon, 1994; Tackenberg et al., 2006; Will et al., 2007; Costa et al., 2014; Quick et al., 2017). Epizoochory has been documented primarily on mammals and is rare in birds (Costa et al., 2014), but even the numbers of diaspores recorded on mammals are small, making the data anecdotal rather than statistical. Epizoochory undoubtedly occurs in grasses, but whether awn structures are selected specifically for this purpose is not clear. Some domesticated animals such as sheep (Mouissie et al., 2005) will carry any diaspores in the environment, and the unawned diaspores of *Agrostis capillaris* represent the most common grass on Galloway's cattle in Belgium (Couvreur et al., 2004). However, because sheep and cattle are rarely raised in environments where they are native, they cannot account for selection over evolutionary time.

In the few studies of wild mammals, diaspores of high-abundance grass species attach more often than those of low-abundance ones (Fischer et al., 1996; Couvreur et al., 2004; Hovstad et al., 2009). In a North American prairie, 622 diaspores of *Andropogon gerardi* (big bluestem), a dominant tallgrass prairie species, were found on 67 individual bison, with *Bromus* species the second most common grasses on the animals (331 diaspores on 65 individuals) (Rosas et al., 2008). Diaspores of both species are awned; awns of *A. gerardi* are

hygroscopically active, whereas those of *Bromus* are straight and presumably passive. Bison also dispersed *Bouteloua curtipendula* (Laughlin, 2003), whose diaspores bear several straight awns; bison fur retained more diaspores than did fur of elk, deer, coyote, rabbit, and fox (down to 20% retention). However, pushing a fox dummy (using a real fox coat) through a meadow led to notably different results in Norway (Hovstad et al., 2009). High retention rates were observed for *Deschampsia caespitosa* (hairy and awned), and *Festuca ovina* (short awned and few hairs) on the fox coat. Overall in this study's field site, 19 of the 29 local species diaspores attached to the fox coat to some extent (Hovstad et al., 2009). However, even with an impressive variety of grasses attached to the coats, natural behavior of the animals was not taken into account, nor did the study provide a clear indication of selection. The long-awned *T. triandra* where common in Kenya showed limited attachment to hares, even though grasses were the most common diaspore type on their coats (Agnew and Flux, 1970). The diaspores of *T. triandra* seemed to drill into the skin of the animal, and the natural outcome of this action is unclear, but appears to be an accidental consequence of hygroscopic function. The abundant hook-covered diaspore of *Tragus berteronianus* was commonly found attached to hare fur, but the very similar diaspore of *Latipes senegalensis* (= *Leptothrium senegalense*) was not found at all. The lack of attachment of morphologically similar diaspores suggests that animal behavior may play a big part in which diaspores attach, in addition to (or rather than) diaspore morphology.

Overall, the existing literature documenting epizoochory in Poaceae species lacks a clear testable hypothesis involving awns and does not present convincing evidence of awns' involvement in animal attachment.

Awns as a defense mechanism

Awns may provide protection from fire by enhancing burial or deterring herbivores. Fire is common in grass-dominated habitats (Mouillot and Field, 2005; Linder et al., 2018), but the ability of different grass lineages to survive fire varies markedly (Lehmann et al., 2019). Fire-driven awn adaptation has only received attention in the literature once, with evidence for fire interaction with awns coming primarily from Andropogoneae (Garnier and Dajoz, 2001). Andropogoneae make up 37% of all grassy vegetation and tolerate chronic fire regimes better than any other grass tribe with a return interval of only 2 years (Lehmann et al., 2019; Simpson et al., 2021). Soil is an effective insulator with depths of 50 mm or more significantly reducing dangerous temperatures for seeds (Bradstock and Auld, 1995). However, a considerable burial depth requirement might suggest that only longer awns are suitable for achieving sufficient insulation. Longer awns were correlated with burial depth in *Hyparrhenia diplandra* in a savanna on the Ivory Coast that burned every year, but because fire intensity is unpredictable, fire could sustain the variable awn sizes

within the population (35–70 mm) (Garnier and Dajoz, 2001). However, presence of awns does not seem to guarantee a germination advantage after a fire. In years preceding fire in Australia, awned species (awns 6–16 mm) were substantially more abundant than unawned species (Peart, 1984), but seedling abundance of awned species post fire dropped substantially, being replaced by unawned species (Peart, 1984). Alternatively, burial via hygroscopic awns may be too limited to provide an effective defence against fire, or possibly, a minimum size of awns is required to offer any protection from fire.

Herbivory from insects causes significant damage to reproductive structures of grasses in both natural (Bertness et al., 1987; Bertness and Shumway, 1992; Kelly and Sullivan, 1997) and agricultural environments (Naresh and Smith, 1984; Singh, 1987; Tindall et al., 2005; Awuni et al., 2015), with loss of reproductive output both before seed dispersal (Bertness et al., 1987; Singh, 1987; Bertness and Shumway, 1992; Kelly and Sullivan, 1997) and afterward (Reed et al., 2004; Schöning et al., 2004). While pre-dispersal herbivory on grains is substantial and well documented (Naresh and Smith, 1984; Singh, 1987; Tindall et al., 2005; Parsons and Munkvold, 2010; Awuni et al., 2015), there is no information whether awns help prevent such herbivory. Pre-dispersal herbivory is rarely studied in natural populations despite being a potentially important selective force (Bertness et al., 1987; Bertness and Shumway, 1992; Kelly and Sullivan, 1997). In an herbivore-exclusion study, Bertness et al. (1987) found up to 80% of ovules were lost before dispersal in natural populations of *Spartina patens* (= *Sporobolus pumilus*), *Spartina alterniflora* (= *Sporobolus alterniflorus*), and *Distichlis spicata*, three unawned North American grass species. Loss was likely because of predation by the grasshopper *Conocephalus spartinae*. To our knowledge, no one has tested whether such herbivory might be less extensive on spikelets with awns.

The role of awns in preventing post-dispersal herbivory is better documented. Like pre-dispersal loss, the loss of dispersed seeds to herbivores can be high (Capon and O'Connor, 1990; Reed et al., 2004; Schöning et al., 2004). Awns may deter herbivores by increasing the time they spend handling the seeds (Schöning et al., 2004; Titulaer et al., 2018). Seed preference of sparrows around Chihuahua, Mexico varied considerably among six species of grass: *Bouteloua gracilis*, *B. curtipendula*, *Leptochloa dubia* (= *Disakisperma dubium*), *Melinis repens*, *Eragrostis lehmanniana*, and *Pennisetum ciliare* (= *Cenchrus ciliaris*), comprising three native and three exotic grasses, respectively (Titulaer et al., 2018). *Cenchrus ciliaris* and *E. lehmanniana* were largely avoided by sparrows. The former has multiple bent, long bristles (awn-like and usually twice as long as any other structure) and was only exploited by one species of sparrow, while the latter is awnless; the low preference is attributed to its small size (difficulty of handling and low nutrient value). *Bouteloua gracilis* has six to nine awns (three per floret in a spikelet) but was consumed preferentially by the sparrows.

The awns of *B. gracilis*, unlike *C. ciliaris*, are short, rarely reaching past the end of the spikelet, and fewer in number. Proportionate length and numbers of awns could be important to predatory deterrence, although importantly, this study was observational rather than experimental, so the relationship between predation and awn structure remains speculative.

Herbivory by ants (*Messor* spp.) is reduced by large hygroscopic awns in *Stipa tenacissima* (= *Macrochloa tenacissima*) and *S. parviflora* (= *Achnatherum parviflorum*) (Schöning et al., 2004). Handling time of the *M. tenacissima* diaspore was significantly longer when the awn was intact than when it was removed ($P < 0.001$). Ants were significantly more likely to take diaspores of *A. parviflorum* with awns removed than with awns intact when provided a choice ($P < 0.001$). Hygroscopic awns may also allow diaspores to move or actively bury themselves before ants have the chance to consume them (Schöning et al., 2004). However, in another study in sagebrush desert in Wyoming, United States, ants showed little preferential removal of seeds, and only *Purshia tridentata* (awnless Rosaceae) was significantly preferred over *Bromus tectorum* (large awned Poaceae) and *Artemisia tridentata* (awnless Asteraceae) (Kelrick et al., 1986). Ants in other studies were observed abandoning seeds and returning to their nest (Willard and Crowell, 1965; Rissing, 1981; Kelrick et al., 1986). Thus, diaspores with awns and developed seeds may not have been always consumed by ants.

Awns of *Bromus tectorum* may increase handling time for small rodents and thus are more likely to be avoided (Kelrick et al., 1986; Ceradini and Chalfoun, 2017). In a comparison of four Poaceae in subfamily Pooideae (*Stipa viridula* [= *Eriocoma lettermanii*], *Pascopyrum smithii* [= *Elymus smithii*], *Oryzopsis hymenoides* [= *Eriocoma hymenoides*], and *Bromus tectorum*) and two other local plant species (*Purshia tridentata* and *Artemisia tridentata*) from Wyoming, the large-awned *B. tectorum* and unawned *E. smithii* were least preferred by small mammals along with the dicot *A. tridentata* (Kelrick et al., 1986). However, the fine awns of *E. lettermanii* did not appear to discourage herbivores.

Nutrient value of seeds has been considered a potential factor for herbivores, but the high nutritional value of *B. tectorum* does not appear to matter (Lucero and Callaway, 2018). Lucero and Callaway (2018) removed awns from *B. tectorum* and all other plants in their study (*Festuca idahoensis*, *Pseudoroegneria spicata*, *Elymus elymoides*, and *Achnatherum hymenoides* [= *Eriocoma hymenoides*]). Regardless of awn state, *B. tectorum* was always significantly less consumed by rodents than other seed, suggesting nutritional value alone cannot necessarily explain herbivore choice. In summary, the link between awns and herbivory prevention requires further investigation. In particular, a more experimental approach is needed along with experimental designs that consider the possibility that biochemical and nutritional differences among species are more important than presence or absence of awns.

MAJOR QUESTIONS AND NEEDS FOR FUTURE AWN RESEARCH

Expansion of phylogenetic sampling in analysis of awn trait evolution

A crucial step for understanding convergence is determining if observed traits are the result of convergence or simply phylogenetic relatedness. Our phylogenetic analyses indicate that major awn traits have arisen multiple times independently, suggesting that they are the result of convergent evolution and could be adaptive (Figures 2–4). Nonetheless, these analyses are a shallow examination of the diversity of Poaceae and complex questions of adaptation or exaptation cannot be confidently concluded from this or previous published studies. Incorporating an explicit phylogenetic structure for experimental design would be helpful for future studies. For example, although AuBuchon-Elder et al. (2020) focused largely on *Sorghum bicolor*, they compared it to several other distantly related species of Andropogoneae and showed that none had awns that supplied carbon to the grain. Because of the position of the species in the phylogeny, they could reasonably infer that their conclusions applied to most if not all awned Andropogoneae. Likewise, Tambussi et al. (2007) reported on awns in several species in Triticeae, all of which are an important source of carbon for the grain; based on their choice of species and the similarities among them, we can infer that awns in all members of the tribe are likely to function similarly. Thus, awn function differs in Triticeae and Andropogoneae, but whether that difference characterizes their respective subfamilies or can be extended to larger clades is unknown. Because most studies on awn function have been based on the assemblage of species in a local community, rather than on species chosen phylogenetically, such extrapolation awaits future studies.

Fitness and energetic costs of awns

Awns are clearly not beneficial in all habitats, and losses of awns are not uncommon across Poaceae (Clayton et al., 2006–2021; Humphreys et al., 2011; Teisher et al., 2017; McAllister et al., 2019). Repeated loss of awns in a lineage suggests a fitness and/or energetic cost associated with awn production and maintenance. However, the repeated evolution and persistence of awns suggest that they can offer significant fitness advantages in certain environments. Soil type may be an important factor for awn benefit (Peart and Clifford, 1987; Humphreys et al., 2011; Liang et al., 2019). The major questions that arise are: If awn production is limited by nutrient availability, which nutrient(s) are most important? If awns are costly to produce, what benefit did the original awns provide to the plant? Does awn production consistently cause a shift from producing many small seeds to fewer larger seeds, and if so, what are the

conditions under which this shift is advantageous? The results from Ntakirutimana et al. (2019) in *Elymus sibiricus* suggest a trade-off may occur, although more than a single study must exist for any generalisation across Poaceae to be possible. Nonetheless, from this available data, we hypothesize that the development of awns represents a shift in reproductive life strategy, from production of many small seeds to fewer large, well-provisioned seeds.

Genetic basis of awns and plasticity

Awn length and presence are highly heritable in species that have been investigated, suggesting much of the observed variation is genetic. Extensive population- and individual-level analyses are required to fully understand the controls of awn length within individuals and species. A few species produce awned, mixed, and unawned plants, but do not appear plastic in response (e.g., *Sorghum halepense* [Johnsongrass]; K. B. Petersen and E. A. Kellogg, personal observations). What advantage does a mixed awn system confer? These species present an opportunity to test whether yield and seed size are correlated with differences observed in other awned grasses. All studies of genetic control for awns that we know of to date have included only a handful of species and investigated only lemma awns (see recent review by Schrager-Lavelle et al. [2017]). A few studies have found that a single gene functions as a genetic switch, with one allele allowing awns to develop and the other allele preventing awn formation. Such genes include the rice gene *Awn-1* (*An-1*), which encodes a bHLH transcription factor that controls cell division at the tip of the lemma, thereby regulating the presence or absence of awns (Luo et al., 2013). Similarly, *OsETTIN2*, an auxin response gene, eliminates awns completely if silenced, depending on the genetic background (Toriba and Hirano, 2014). If the presence or absence of awns is regulated by a single gene, it is appropriate to treat it phylogenetically as a single qualitative binary trait as in Figure 2. It remains unclear whether genes that control awn production in paleas and glumes are the same as those in lemmas.

CONCLUSIONS

The diversity of extant Poaceae makes understanding their various ecological interactions an enormous task, although mapping the presence and absence of awns on a more comprehensive phylogeny should be relatively straightforward. The diversity in structure and the loss and reappearance of awns in different lineages has not inspired as much research as one would expect given the ubiquity and accessibility of the plants. Only a few species (e.g., *Themeda triandra*) have been included in more than one study to test dispersal mechanisms. However, these studies and others

ignore the complex evolutionary history and diversity of awns in other grass species. Assumptions of adaptive convergence are made between species that are both closely related and completely unrelated. Consideration of ancestral traits is critical in understanding whether traits are a result of adaptive convergence or simply exaptation of existing traits. Furthermore, the adaptive origin of awns has been relatively ignored, and focus has been placed on complex functions such as burial in hygroscopic geniculate awns. We are unconvinced that awns were originally selected for burial; rather they may still retain another less complex adaptation such as carbon fixation or herbivore deterrence. Despite the range of potential functions for awns, research has disproportionately focused on burial and spikelet movement, particularly in a limited sample of geniculate-awned plants. Evidence for epizoochory, herbivory, and pre-dispersal defense remains weak. Fire has been suggested to be a selection force acting on particular aspects of awns, but the evidence is mostly circumstantial and may only apply to some species of Andropogoneae. The fitness or nutrient cost of producing awns is poorly understood, although carbon assimilation is well documented in awns for two clades of Poaceae. Furthermore, there is no evidence to suggest awn characteristics are plastic in any grasses, supporting independent and distinct selection occurring in grass lineages to evolve awns. Functional convergence in species-rich families of angiosperms such as Poaceae (grasses) provides significant opportunity to explore adaptation and convergent evolution of floral structures.

AUTHOR CONTRIBUTIONS

K.B.P. produced initial structure, drafted the manuscript, did the data analyses and prepared the figures. E.A.K. developed the trait data set for the phylogenies. Both authors made extensive edits and revisions and prepared the document for final submission.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Awn traits assembled from GrassBase.

Appendix S2. Alternative version of Figure 2 with species visible on tree tips.

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