Hygroscopic awns of two prairie grasses, *Andropogon gerardii* and *Sorghastrum nutans*

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Abstract

The prairie grasses *Andropogon gerardii* and *Sorghastrum nutans* have seeds with awns that twist in response to changes in humidity. The humidity-sensitive, or hygroscopic, part of the awn twists, moving the bent, passive portion in an arc. This trait has been demonstrated to improve seedling recruitment in other grass species by dispersing the seeds to superior microsites. Hygroscopicity was defined as the time taken for the awn to complete one rotation. The goals were to 1. estimate heritability of hygroscopicity, 2. assess population-level differences in hygroscopicity, and 3. examine the relationship between hygroscopicity and seed movement. Two sets of seed were used. Seeds were collected in west-central Minnesota from individual maternal plants in remnant and restoration populations and were grown out to collect a second seed generation, used to assess heritability. To assess population differences and unidirectional movement, seeds were purchased from conservation seed suppliers from across the species' range. Time-lapse photography and humidity manipulation were used to characterize seed movement. I found a weak trend of heritability in *Andropogon* but not *Sorghastrum.* Northern populations of *Sorghastrum* spun more slowly than those of southern populations. There was no difference in rotation time among *Andropogon* populations. The awn did not propel most seeds of either species, though the seeds did move back and forth within a small area. The differences among populations suggest that there may be local adaptation, and care should be given when selecting seeds for restoration purposes.

Acknowledgments

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Table of contents

List of figures

Introduction

Many organisms have a wide range of adaptations to improve the dispersal and survival of their offspring in spite of biotic and abiotic impediments. For any trait to be adaptive, individuals within a population must exhibit variation, some variation of the trait must be heritable, and in each generation, some individuals with this trait must be more successful in their reproductive efforts (Darwin, 1859). Dispersal adaptations are as varied as the numerous impediments to survival they surmount.

Many plant species have seed appendages that improve seed dispersal. The seed and appendages together are referred to as a diaspore, though the term diaspore and seed will be used interchangeably in this paper. An awn is a bristle-like appendage found on some grass seeds. Awns can improve primary dispersal by catching the wind as the seed falls from the maternal plant (Rabinowitz and Rapp, 1981; Fowler, 1986). *Vulpia ciliata*, an awned grass found in England, disperses about six centimeters in the direction of the prevailing winds, but with human or animal disturbance, seeds can be dispersed three times further (Carey and Watkinson, 1993). In the case of disturbance, an awn could reorient the diaspore with the ground. Peart found the awns of *Aristida* spp. and *Enneapogon* spp. keep the seeds oriented downward as they reach the ground and that germination is greatly impaired if diaspores are dispersed with the awns removed (Peart, 1979). These are examples of passive awns, which are simply rigid structures attached to the seed. Conversely, active awns react to environmental stimuli, such as humidity.

A hygroscopic awn differs from a passive awn in that it has two distinct parts: a helical humidity-sensitive section proximal to the seed and at the end, a stiff straightened section at an angle to the hygroscopic part (Figure 1). As humidity changes, the hygroscopic portion of the awn twists and untwists, causing the distal end to rotate (Schöning et al., 2004; Wolgemuth, 2009). This movement has been suggested to promote secondary dispersal (Peart and Clifford, 1987; Stamp, 1989). A small spike in humidity, such as with a morning dew, infuses the awns with moisture. As the awns dry, they spin, thereby propelling the diaspores forward (Garnier and Dajoz, 2001; Kulic et al., 2009). This movement has evolved in several taxa, including multiple lineages in *Poaceae* (Peart, 1979; Oudtshoorn and Rooyen, 1999; Barker et al., 2001). Hygroscopic motion has been shown to facilitate seedling recruitment of *Erodium*, *Stipa*, and other taxa by moving the seed to desirable microsites, such as cracks in the soil (Peart, 1981; Stamp, 1989; Sindel et al., 1993; Garcia-Fayos and Gasque, 2006). Crevices in the soil provide an anchor point and moisture, and secondary dispersal helps seeds reach those sites when they fall elsewhere during primary dispersal events.

Tallgrass prairie has long been threatened by human activity. Road-building, settlement, and agricultural expansion have reduced the range of grasslands in North America; tallgrass prairies in North America now span a very fragmented three percent of their historical extent (Samson et al., 2004). A number of prairie grasses, including the dominant grasses *Andropogon gerardii* and *Sorghastrum nutans* produce seeds with hygroscopic awns. While this trait has been studied in other prairie species (Peart and Clifford, 1987; Stamp, 1989; Garnier and Dajoz, 2001; Schöning et al., 2004), little is known about this trait in *Andropogon* and *Sorghastrum*.

To investigate the heritability and utility of the hygroscopic awn in *Andropogon gerardii* and *Sorghastrum nutans*, I performed experiments on two sets of seed. *Andropogon* and *Sorghastrum* seeds were collected from populations in west-central Minnesota, which were later grown out and the offspring cohort collected to estimate heritability. To assess population-level differences and unidirectional movement, I purchased seed from five conservation seed suppliers from across the species' range. The overall purposes were to 1. estimate heritability of hygroscopic response among mother and offspring plants, 2. examine differences among hygroscopic responses of seeds from the edges of the species' natural range, and 3. investigate the ability of the seeds to travel along the ground.

Methods

Species description

Andropogon gerardii and *Sorghastrum nutans* (hereafter referred to by genus) are perennial warm-season grasses native to North America. Their range extends from the Rocky Mountains to the East Coast and from Texas through southern Canada. They are the dominant species in tallgrass prairies, where they are found in a dense matrix of grasses, forbs, and dead plant material (Kilde, 2000; USDA-NRCS, 2013). Plants grow one to three meters tall and form tussocks (Gleason and Cronquist, 1991). Growth begins in April or May, with flowering beginning in late July (Sedivec et al., 2009), though first-year plants can flower later (personal observation). Seeds develop from September into late October. Seeds do not disperse far from the maternal plant, falling almost straight downward (Sedivec et al., 2009). *Andropogon* seeds are borne on three or more spike-like projections while *Sorghastrum* seeds are in a dense plume. The diaspore, including the awn, is two to five centimeters long. Seed germination is typically in mid-spring, when temperatures are around 20 °C and humidity is relatively high (Baskin and Baskin, 2000). Because of the similarity in the two species' seed structure, the experiments were performed unaltered for each species.

Seed material acquisition

Two seed sources were used for this research. One set was collected in 2009 by M. Gallagher from individual maternal plants in fourteen prairie remnants and reserves in Douglas County MN. Seeds were collected between August 31 and September 26, 2009. Fifty individuals from each species were randomly selected for harvest. Collected seeds were placed into individually labeled coin envelopes and stored in a seed dryer at 14 °C and 15 % relative humidity (RH) (Gallagher, 2011). Seed from this collection was later germinated and grown so the offspring cohort of seeds could be collected.

I acquired the second set from conservation seed suppliers in five regions across the eastern United States: Prairie Moon, Minnesota; Stock Seed Farm, Nebraska; Ernst Conservation Seed, New York; Mellow Marsh Farms, North Carolina; Native American Seed, Texas. Seeds were purchased or donated as bulk seed. I acquired from several hundreds to several thousands of each species' seed from each location.

Estimating seed fullness

Due to the difficulty of visually assessing *Andropogon* and *Sorghastrum* seed fullness, I used weight as an indicator for fullness. Thirty seeds of each species were randomly selected and weighed. The diaspores were then dissected to determine fullness. Based on this trial, *Andropogon* weighing more than 0.0016 g (binomial GLM, deviance 32.5964 on 29 DF, $p < 0.001$) and *Sorghastrum* weighing more than 0.0019 g (binomial GLM, deviance 37.3628 on 28 DF, $p < 0.001$) were considered full.

Assessing hygroscopic response with time-lapse photography

To measure hygroscopicity, I designed and built a time-lapse photography setup to capture the motion of the awns. I defined hygroscopic response as the time elapsed for the awn to complete one full rotation, with the seed oriented to allow unrestricted motion. To photograph the seeds from above, I attached a series of gentle adhesive “Glue Dots” to ¼-inch balsa wood sticks (Glue Dots International, New Berlin, WI); the adhesive held the diaspores with the awns oriented upward and allowed me to remove diaspores without damage. I randomized the diaspores before placing them on the adhesive. To prepare the awns, I placed the diaspores and sticks into a 100 % RH aquarium overnight. The next day, I removed the sticks and seeds from the humid chamber. I then inverted a fish tank atop the seeds to protect them from incidental air currents. Awn movement was measured as humidity approached ambient humidity, which was 15

– 25 % RH. Relative humidity was measured with a digital hygrometer. I placed a Canon Digital Rebel XT camera (Tokyo) on top of the fish tank and connected it to a computer via USB (see Figure 2). I recorded time-lapse series using the gPhoto2 software, with photos taken every five to seven seconds for up to two hours. Photo intervals varied due to hardware and software limitations. I used ImageJ (NIH, Bethesda, MD) to locate and translate the starting positions of the awns into pixel coordinates, with which the starting points were marked on each image in GraphicsMagick (GraphicsMagick Group). I assessed the single rotation time of each specimen by stepping through the image series until the awn reached or passed the beginning marker. I identified the image files depicting the last frame of a single rotation and used the timestamps contained in the image EXIF metadata to calculate elapsed time.

1. Heritability

To examine broad-sense heritability, I used the seed collected from populations in Douglas Co, Minnesota. I randomly selected a total of fifty seed envelopes per species from twelve of fourteen available sites; *Andropogon* was not found in two sites and *Sorghastrum* was not found in two others. I haphazardly removed seeds from their coin envelopes, weighed them, and preferentially selected full seeds, as they were to be germinated. The selected diaspores were then assessed for hygroscopicity and sown into plug trays. I placed seeds in a growth chamber set to 20 °C at 80 % relative humidity (Baskin and Baskin, 2000) to germinate. Seedlings were planted together in Douglas Co, MN in early June 2011. Grasses were allowed to open pollinate. I watered the plot as needed, typically every three to four days, and fertilized the plot in mid-July with 5-5-5 NPK organic fertilizer. Seeds were collected in October 2011 and stored in individually labeled brown paper bags in a seed dryer at 14 °C and 15 % relative humidity. I randomly selected three seeds from each plant to measure hygroscopicity. I regressed offspring hygroscopicity against maternal hygroscopicity to estimate half-heritability. I performed an

ANCOVA to assess differences in hygroscopicity among individual maternal plants. I included collection site, site type (restoration or remnant), and maternal ID as explanatory factors.

2. *Population differences*

Population differences were assessed using the seed material acquired from the five seed suppliers. Twenty-eight diaspores were haphazardly selected from each species from each supplier, and were randomly placed on balsa sticks to assess their hygroscopic response, as above. I performed a one-way ANOVA of population on hygroscopicity to assess differences among populations.

3. Ground movement

For each species, I haphazardly chose twenty-eight diaspores from each of the five seed suppliers and placed them in a humid chamber overnight without placing them on balsa sticks. I placed the diaspores horizontally on a textured paper substrate in the photography setup and started time-lapse as above. I used desiccant silica gel to accelerate chamber drying due to a relatively high ambient humidity. I included a ruler in the photographs to provide scale. I marked starting and ending positions of the tip of the seed in ImageJ and calculated distance traveled with R. To measure awn length, I placed the same diaspores on a labeled sticky-note and placed them on a flatbed scanner. To get a good scan, I lowered the the top of the scanner to flatten the awns. This is a destructive process, and some awns were damaged during scanning. I included a ruler in the scans to calculate scale. I used ImageJ to measure the length of the awns. I performed an ANCOVA with distance traveled as the response and time to complete one rotation, seed source, and awn length as explanatory factors.

All statistical tests were performed with R 2.15. Each species was analyzed separately. I simplified all models using backwards elimination to choose the minimal adequate model (Crawley, 2012).

Results

Weight: Germination

Germination success was positively related to seed mass in *Andropogon* (GLM, deviance 377.84 on 436 degrees of freedom, $p < 0.001$) and *Sorghastrum* (GLM, deviance 105.05 on 484 degrees of freedom, $p < 0.001$). Of the 485 *Andropogon* and 495 *Sorghastrum* seeds planted, 81 and 35 seeds germinated, respectively, or 17 % and 7 %.

1. Heritability

There was little evidence of a relationship between maternal and offspring hygroscopicity in either species (*Andropogon:* $½H^2 = 0.14$, 95 % CI -0.15 – 0.50, $F = 1.95$ on 1 and 41 DF, $p = 0.17$; *Sorghastrum:* $½H^2 = 2.4$, 95 % CI -11 – 16.7, $F = 2.279$ on 1 and 5 DF, $p = 0.19$). Hygroscopic response differed among individual maternal plants for both *Andropogon* ($F = 1.83$ on 47 and 286 DF, $p = 0.002$, $r^2 = 0.23$) and *Sorghastrum* ($F = 2.36$ on 50 and 277 DF, $p < 0.001$, $r^2 = 0.30$). *Andropogon* and *Sorghastrum* awns completed one revolution in 6 and 4 minutes on average, respectively (Figure 3). There was no evidence that collection site or site type was related to hygroscopicity in either model (*Andropogon*: $p = 0.28$, *Sorghastrum*: $p = 0.12$).

2. Population differences

Hygroscopic response did not differ among the five populations of *Andropogon* ($F = 0.2751$ on 4 and 65 DF, $p = 0.9$, Figure 4). The awns of the Minnesota population took about 6 ± 4 minutes to complete a revolution while the North Carolina, Nebraska, New York, and Texas populations completed a revolution twice as fast (3 ± 1 minutes). Hygroscopic response did differ among populations of *Sorghastrum* ($r^2 = 0.16$, $F = 2.693$ on 4 and 58 DF, $p = 0.04$, Figure 4). Minnesota and New York awns completed a revolution slowly, at 7.5 ± 3 minutes and 8.5 ± 5 minutes, respectively, compared to the faster 4-5 minutes of the North Carolina, Nebraska, and Texas populations.

3. Ground movement

Diaspores for both species moved, from beginning of photography to end, less than 0.5 cm, save for a single individual in each species, each of which moved about 3 cm (Figure 5). Seeds did, however, move back and forth within a range of less than 1 cm over the duration of filming.

Hygroscopic response was not associated with distance moved along the ground for either *Andropogon* (F = 0.3093 on 1 and 22 DF, p = 0.58) or *Sorghastrum* (F = 0.3985 on 1 and 19 DF, p = 0.54). Origin location was not a significant explanatory variable in either model (*Andropogon* p = 0.55, *Sorghastrum* p = 0.46). Awn length is not a significant predictor of distance traveled for *Andropogon* (F = 0.4946 on 1 and 25 DF, p = 0.49) or *Sorghastrum* (F = 0.5901 on 1 and 23 DF, p = 0.45) (Figure 6).

Discussion

My findings suggest that hygroscopic awns may be an adaptive trait in *Andropogon* and *Sorghastrum*. My results demonstrated that hygroscopicity differs among individuals in both species and among populations of *Sorghastrum*. The evidence for heritability is weak, though this may be due to low sample sizes. I did not find evidence to support the hypothesis that hygroscopic movement can drive the seed along the ground.

Though I had low sample sizes, I found a suggestive trend of heritability in hygroscopicity in *Andropogon* but not *Sorghastrum*. The heritability estimate of *Sorghastrum* is 2.4, which is invalid, as the proportion of of total variation due to genetic variation cannot be greater than 1. This result is a statistical anomoly due to the low germination rate and survival of only eight *Sorghastrum* plants, rather than a biological phenomenon. *Andropogon* had a larger sample size than *Sorghastrum*, though only 18 maternal plants are represented; this is fewer than other heritability studies, which usually comprise many more replicates (Platenkamp and Shaw, 1993; Garnier and Dajoz, 2001). In their study of the hygroscopically-awned African savanna grass *Hyparrhenia diplandra,* Garnier and Dajoz found awn length to be highly heritable, $h^2 = 0.61$ (Garnier and Dajoz, 2001). In *Andropogon*, about 15 % of the variation in offspring hygroscopicity can be explained by maternal hygroscopicity. The other 85 % of the variation may be to a combination of factors, such maternal effects or issues with the experimental apparatus. Awns started spinning as soon as they left the humid environment, so the first ten seconds or so of hygroscopic movement was lost in all trials. The cameras would also occasionally stop responding, so one or two minutes of data were lost while the camera was restarted. Solving these issues in future studies, along with larger sample sizes, may show hygroscopic reaction to be heritable.

Hygroscopicity differed among five widely-separated populations of *Sorghastrum*, but not among similar *Andropogon* populations. This finding differs somewhat from Gustafson et al., who found a number of genetic and phenotypic differences in both *Andropogon gerardii* and *Sorghastrum nutans* populations in the US (Gustafson et al., 2005). I found that northern populations of *Sorghastrum* spin more slowly than those of the southern populations. Because the experimental humidity range is greater than is typically found in natural systems, differences in reaction to humidity may indicate adaptations to the prevailing local humidity environment, but may also be an unintentional effect of the cultivation practices of seed distributors, like the loss of dormancy in cultivated *Echinacea purpurea* (Qu et al., 2005). Variability in trait expression is common among widely-distributed populations (Joshi et al., 2001; Macel et al., 2007). Faster movement may indicate that the awns react to smaller changes in humidity than those exhibiting slower movement. A new experiment for local adaptation would need to be performed to test this hypothesis. Evidence for local adaptations indicates that for restoration purposes, local seed should be preferred (Joshi et al., 2001; Gustafson et al., 2005).

Surprisingly, neither species' diaspores moved more than about a centimeter from their starting points, but did move back and forth several times over the duration of filming. In a related trial, I again found that few diaspores were traveling, even on such substrates as sand, potting soil, or wire mesh over paper. A few seeds traveled farther, and over the course of several days it is possible that a diaspore may move greater distances, potentially moving it towards a desirable microsite. Propulsion and drilling have been documented in many hygroscopic species (Garnier and Dajoz, 2001; Schöning et al., 2004; Garcia-Fayos and Gasque, 2006; Kulic et al., 2009). In these species, the hygroscopic reaction causes the seed to travel. In some species, this movement allows seeds to reach more suitable microsites or bury themselves (Stamp, 1989; Garcia-Fayos and Gasque, 2006). *Stipa tenacissima* diaspores able to become buried in the soil through hygroscopic motion were more successful in escaping ant predation (Schöning et al., 2004). *Hyparrhenia diplandra* grows in a fire-prone prairie environment and is capable of self-burial through hygroscopic motion. The depth at which *H. diplandra* buries itself is positively correlated with the length of the awn. Those diaspores with longer awns would bury deeper than those with short awns, which allowed them to survive hotter fires (Garnier and Dajoz, 2001). My results, however, showed no such relationship between awn length and distance traveled. Instead, the length of the awn was not correlated with distance traveled in either *Andropogon* or *Sorghastrum.* Because *Andropogon* and *Sorghastrum* do not commonly travel along the ground, the hygroscopic awn may improve fitness in a different way. Primary dispersal could be improved if the awn helps orient the seed while it falls to the ground. Peart found evidence that the awns in some Australian grasses help orient the seed scar downwards while falling, which can improve water uptake during germination (Peart, 1979). The awn may also brace the seed against the force of the emerging radicle, as the radicle can push the seed off the ground, causing dessication and killing the seedling (Peart, 1979; Stamp, 1989). The hygroscopic awn may help the seed navigate the litter found in prairies and reach the soil. Further experiments could shed more light on the utility of hygroscopic awns to *Andropogon* and *Sorghastrum*.

In summary, I found differences among populations of *Sorghastrum* and a trend of heritability in *Andropogon.* While neither species' diaspores traveled unidirectionally, their movement may indicate that hygroscopicity affects seed dispersal or fitness in other ways. In light of the differences in hygroscopicity in *Sorghastrum,* and the evidence of awn utility in the literature, land managers should endeavor to use locally-sourced seeds. A study with a broader representation of plants from around the species range could provide better evidence of the heritability and population difference of hygroscopic motion. Similarly, further research is needed to investigate fitness of the awns.

Bibliography

BARKER, N., L. CLARK, J. DAVIS, M. DUVALL, G. GUALA, C. HSIAO, E. KELLOGG, ET AL. 2001. Phylogeny and subfamilial classification of the grasses (Poaceae). *Annals of the Missouri Botanical Garden* 88: 373–457.

BASKIN, C.C., AND J.M. BASKIN. 2000. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press.

CAREY, P.D., AND A.R. WATKINSON. 1993. The dispersal and fates of seeds of the winter annual grass Vulpia ciliata. *Journal of Ecology* 81: 759–767.

CRAWLEY, M.J. 2012. The R Book. Wiley.

DARWIN, C. 1859. The origin of species. 6th ed. John Murray, London.

FOWLER, N.L. 1986. Microsite Requirements for Germination and Establishment of Three Grass Species. *American Midland Naturalist* 115: 131.

GALLAGHER, M.K. 2011. Plant performance in prairie restorations: does seed source matter? Northwestern University.

GARCIA-FAYOS, P., AND M. GASQUE. 2006. Seed vs. microsite limitation for seedling emergence in the perennial grass Stipa tenacissima L. (Poaceae). *Acta Oecologica-International Journal of Ecology* 30: 276–282.

GARNIER, L.K.M., AND I. DAJOZ. 2001. Evolutionary significance of awn length variation in a clonal grass of fire-prone savannas. *Ecology* 82: 1720–1733.

GLEASON, H.A., AND G. CRONQUIST. 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. 2nd ed. The New York Botanical Garden, Bronx, NY.

GUSTAFSON, D.J., D.J. GIBSON, AND D.L. NICKRENT. 2005. Using local seeds in prairie restoration -- data support the paradigm. *Native Plants Journal* 6: 25–28.

JOSHI, J., B. SCHMID, M.C. CALDEIRA, P.G. DIMITRAKOPOULOS, J. GOOD, R. HARRIS, A. HECTOR, ET AL. 2001. Local adaptation enhances performance of common plant species. *Ecology Letters* 4: 536–544.

KILDE, R. 2000. Going native: A prairie restoration handbook for Minnesota landowners. Available at: http://www.dnr.state.mn.us/prairierestoration/index.html.

KULIC, I.M., M. MANI, H. MOHRBACH, R. THAOKAR, AND L. MAHADEVAN. 2009. Botanical ratchets. *Proceedings of the Royal Society B-Biological Sciences* 276: 2243–2247.

MACEL, M., C.S. LAWSON, S.R. MORTIMER, M. ŠMILAUEROVA, A. BISCHOFF, L. CRÉMIEUX, J. DOLEŽAL, ET AL. 2007. Climate vs. soil factors in local adaptation of two common plant species. *Ecology* 88: 424–433.

OUDTSHOORN, K. VAN R. VAN, AND M.W. VAN ROOYEN. 1999. Dispersal Biology of Desert Plants (Adaptations of Desert Organisms). Springer. Available at: http://books.google.com/books?id=bdTfBfsl-DcC [Accessed April 18, 2013].

PEART, M.H. 1979. Experiments on the biological significance of the morphology of seed-dispersal units in grasses. *Journal of Ecology* 67: 843–863.

PEART, M.H. 1981. Further experiments on the biological significance of the morphology of seed-dispersal units in grasses. *Journal of Ecology* 69: 425–436.

PEART, M.H., AND H.T. CLIFFORD. 1987. The influence of diaspore morphology and soil-surface properties on the distribution of grasses. *Journal of Ecology* 75: 569–576.

PLATENKAMP, G.A.J., AND R.G. SHAW. 1993. Environmental and Genetic Maternal Effects on Seed Characters in Nemophila menziesii. *Evolution* 47: 540.

QU, L., X. WANG, Y. CHEN, R. SCALZO, M.P. WIDRLECHNER, J.M. DAVIS, AND J.F. HANCOCK. 2005. Commercial Seed Lots Exhibit Reduced Seed Dormancy in Comparison to Wild Seed Lots of Echinacea purpurea. *HortScience* 40: 1843–1845.

RABINOWITZ, D., AND J.K. RAPP. 1981. Dispersal Abilities of Seven Sparse and Common Grasses from a Missouri Prairie. *American Journal of Botany* 68: 616.

SAMSON, F.B., F.L. KNOPF, AND W.R. OSTLIE. 2004. Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin* 32: 6–15.

SCHÖNING, C., X. ESPADALER, I. HENSEN, AND F. ROCES. 2004. Seed predation of the tussock-grass Stipa tenacissima L. by ants (Messor spp.) in southeastern Spain: the adaptive value of trypanocarpy. *Journal of Arid Environments* 56: 43–61.

SEDIVEC, K.K., D.A. TOBER, AND W.L. DUCKWITZ. 2009. Grasses for the Northern Plains: Growth Patterns, Forage Characteristics and Wildlife Values. Volume II-Warm-Season.

SINDEL, B., S. DAVIDSON, M. KILBY, AND R. GROVES. 1993. Germination and Establishment of Themeda triandra (Kangaroo Grass) as Affected by Soil and Seed Characteristics. *Australian Journal of Botany* 41: 105.

STAMP, N.E. 1989. Seed dispersal of 4 sympatric grassland annual species of Erodium. *Journal of Ecology* 77: 1005–1020.

USDA-NRCS. 2013. The PLANTS Database. *The PLANTS Database*. Available at: http://plants.usda.gov.

WOLGEMUTH, C.W. 2009. Plant biomechanics: Using shape to steal motion. *Current Biology* 19: R409–R410.

Figures

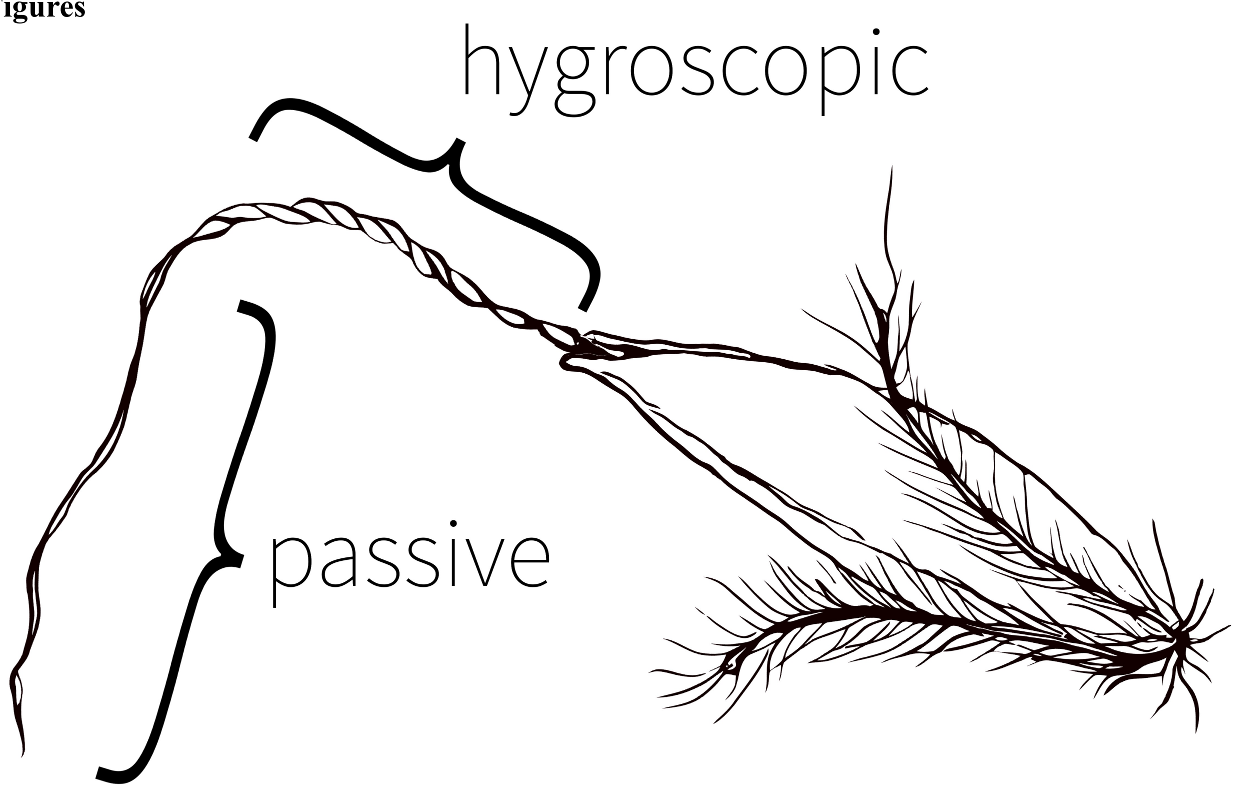

Figure 1. The diaspore of *Sorghastrum nutans* has a relatively long awn. The entire diaspore ranges from two to five centimeters long. The hygroscopic part of the awn reacts to humidity, causing the passive section to rotate relative to the seed. The morphology of the *Andropogon* diaspore is very similar.

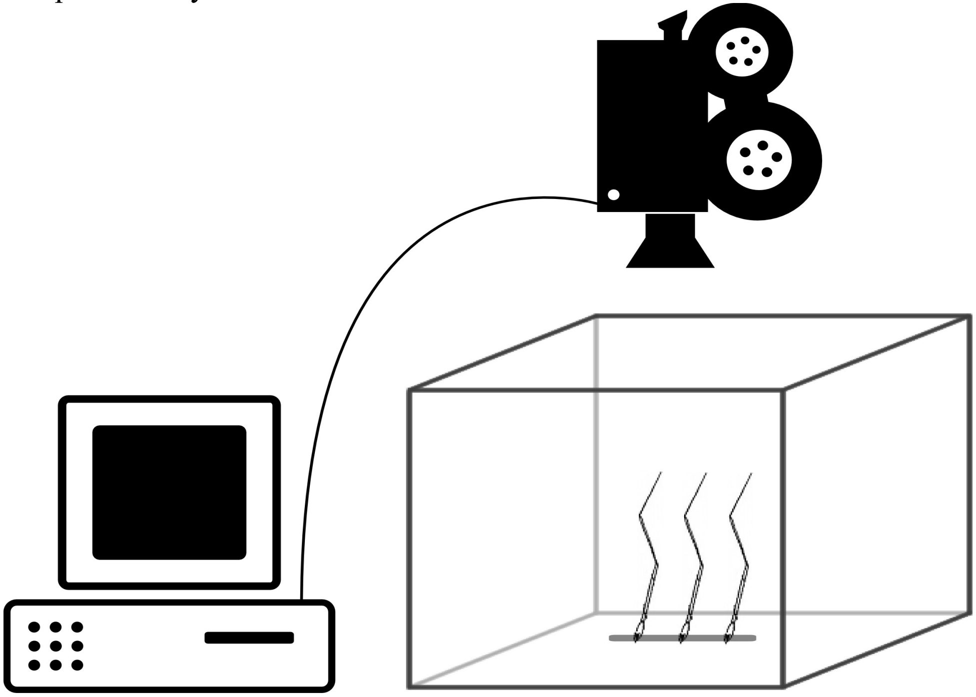

Figure 2. Simplified diagram of the photographic setup. Diaspores are placed on sticks with awns pointing upwards. The camera is placed atop the aquarium such that all the awns are in frame and the computer controls the camera and runs the time-lapse program.

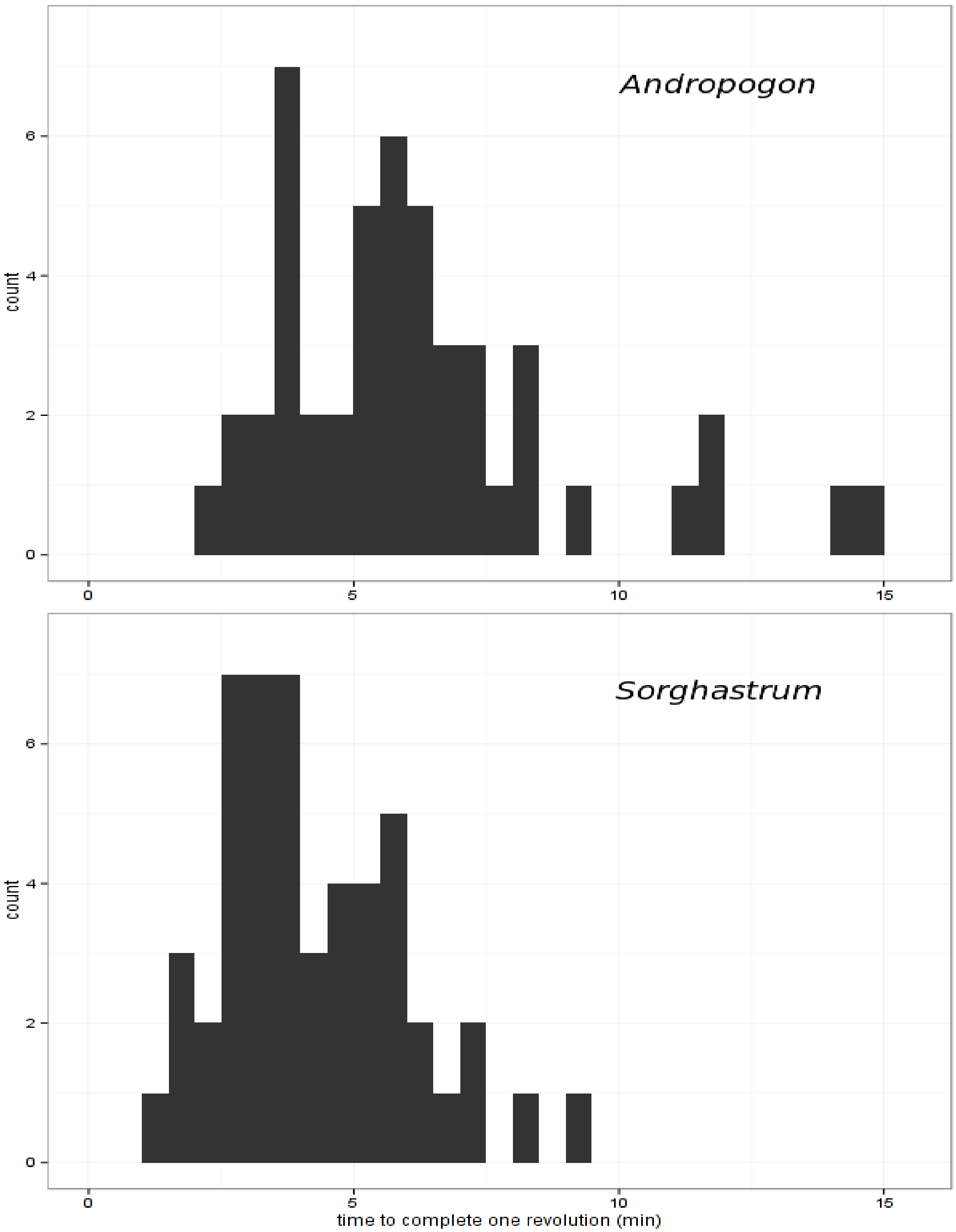

Figure 3. Histogram of the amount of time taken to complete one full revolution (min) by individual maternal lines. Hygroscopic response was averaged for the seeds of each individual and grouped into 30-second intervals. *Andropogon* n = 48, *Sorghastrum* n = 50.

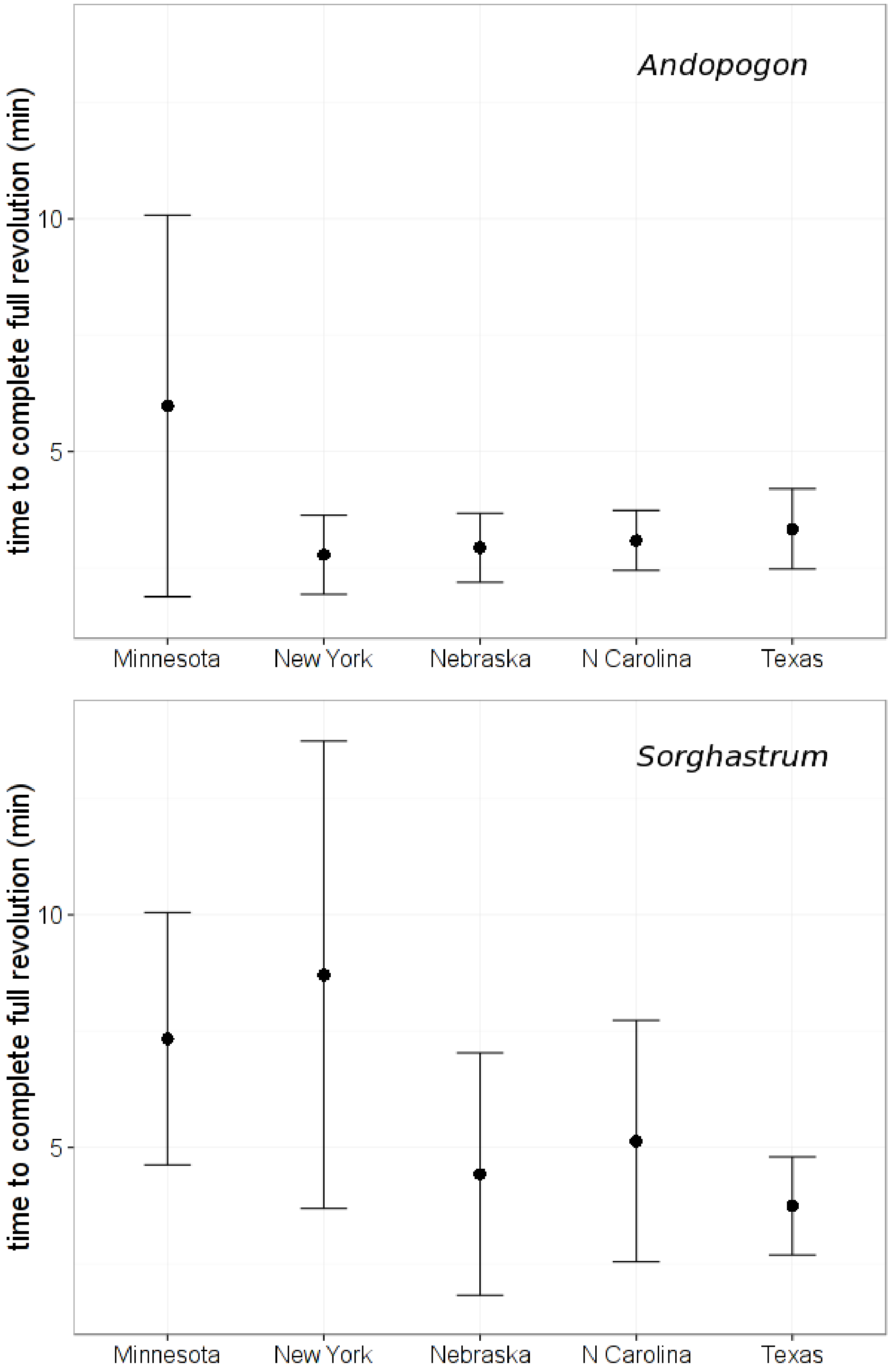

Figure 4. The average time for an awn to complete a full revolution by seed site of origin. Error bars are 95 % CI (100k bootstrap) Sites are arranged from north to south. Hygroscopic response did not differ among populations of *Andropogon* but did among *Sorghastrum.*

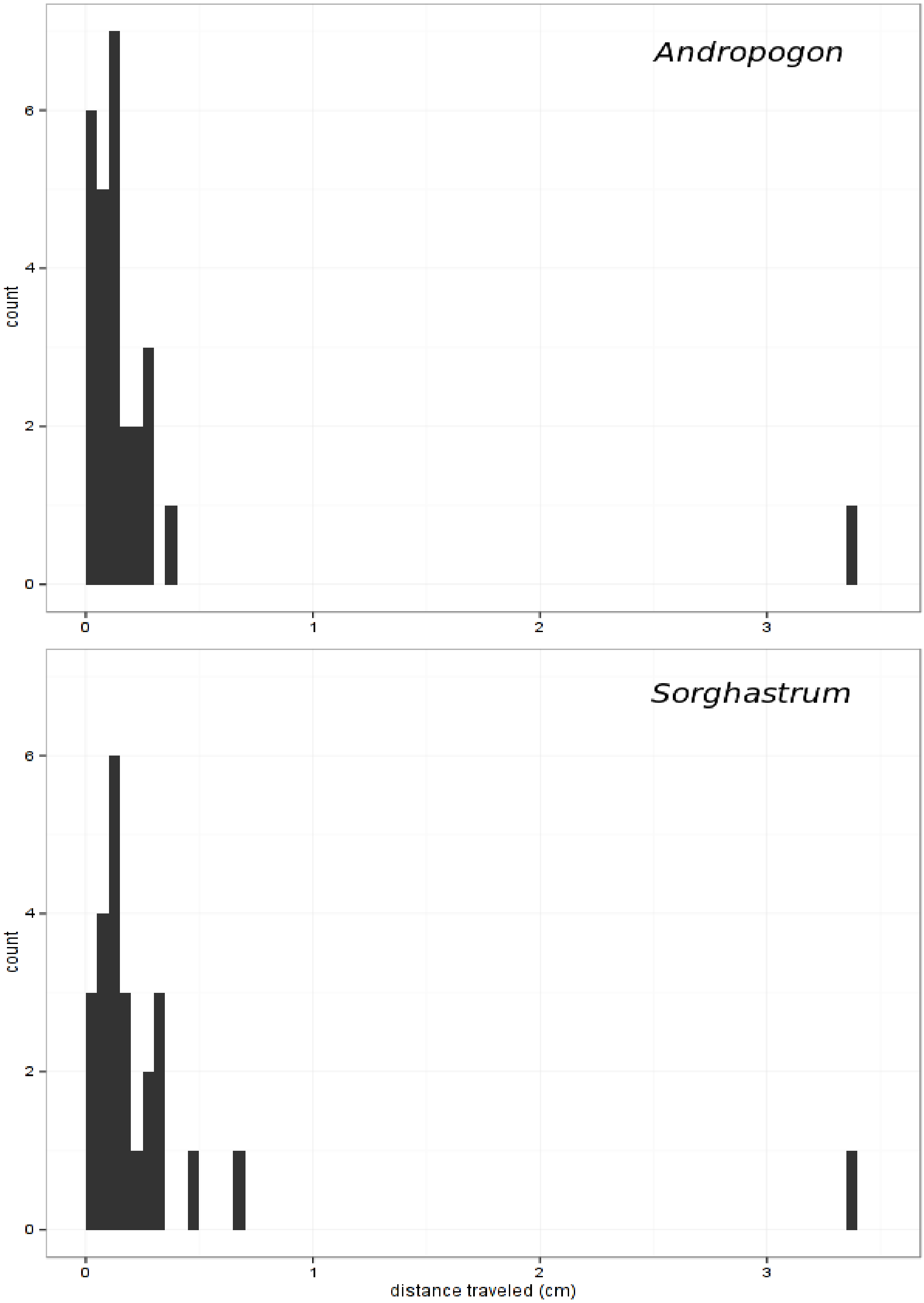

Figure 5. Histogram of distance traveled over the “ground” by diaspores. Seeds did not travel far, instead moving back and forth in a small area. Only one diaspore of either species traveled farther than one centimeter. Counts are grouped by 0.05cm. *Andropogon*: n = 28, *Sorghastrum* n = 25.

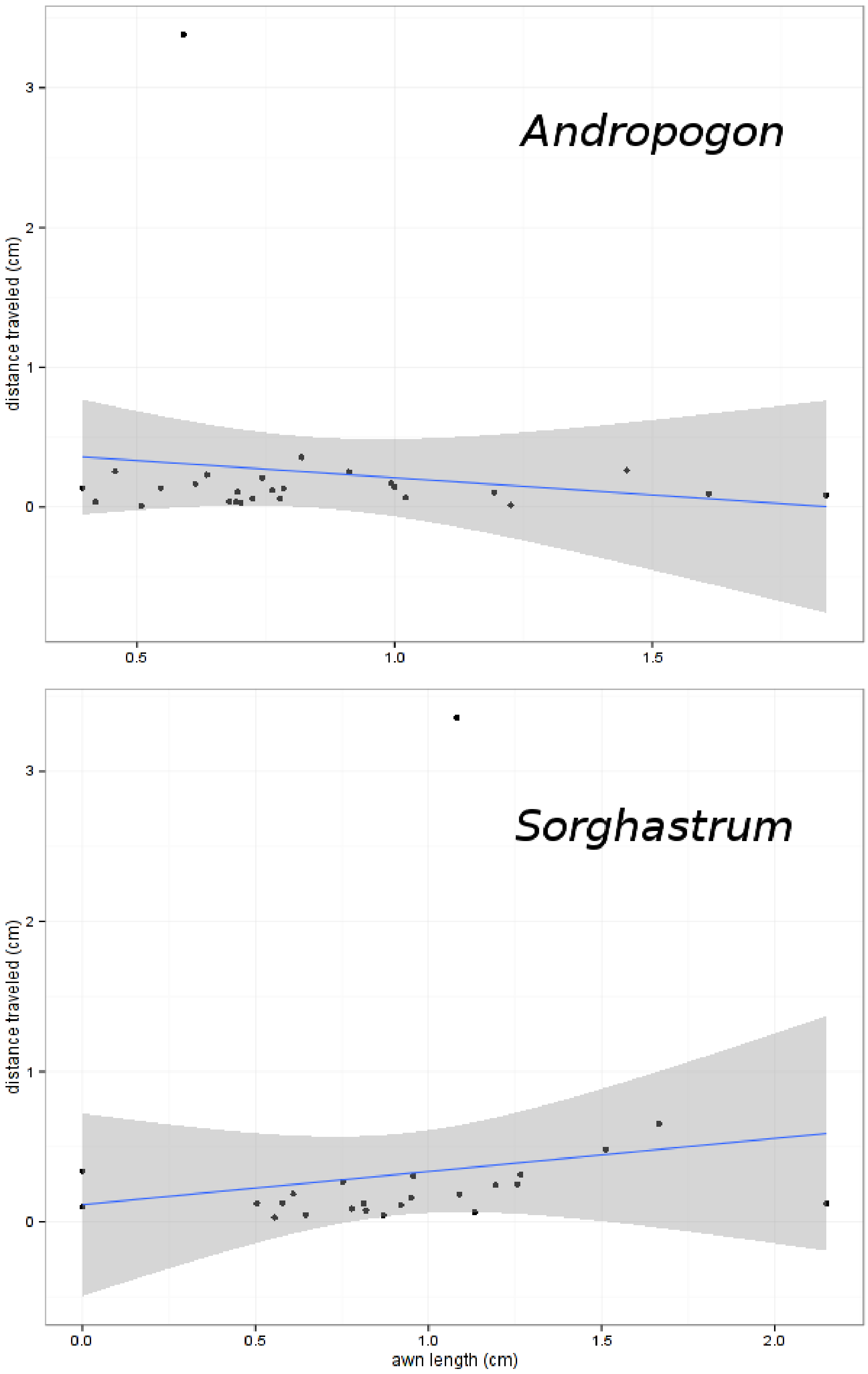

Figure 6. The relationship between awn length and distance traveled along the ground. Seed source was included in the ANCOVA, but was not a significant predictor (*Andropogon* p = 0.55, *Sorghastrum* p = 0.46). Awn length was not a predictor of distance traveled. Grey regions are 95 % CI. *Andropogon*: p = 0.48, n = 28, *Sorghastrum* p = 0.45, n = 25.