OBSERVATIONS OF *TRIPSACUM DACTYLOIDES* AND *T. FLORIDANUM* (POACEAE): MEASURING CLIMATE AND SOIL GRADIENT EFFECTS ON *TRIPSACUM* IN TEXAS, U.S.A.

Gary McBryde

3620 Brighton Rd.
Fort Worth, Texas 76109, U.S.A.
azu421@verizon.net

ABSTRACT

Reports of *Tripsacum floridanum* Porter ex Vasey in Texas have been countered with two arguments. First is that narrow-leafed Texas plants, when grown under favorable conditions, are more typical of wider-leafed *T. dactyloides* (L.) L. Second is that the offspring from crosses of *T. dactyloides* with *T. floridanum* are sterile or partially so. The support for these two claims is examined. The conclusion is narrow-leafed Texas plants typical of *T. floridanum* are in Texas, and crosses between the two produce fully fertile offspring. This raises the question of what factors are at play to segregate the wider-leafed from the narrower-leafed Texas populations. To investigate, two statistical models were constructed using separate data. First, a simultaneous system of seven equations was used to predict phenological and morphological plant characteristics given environmental factors. Second, a single logit equation predicted the probability of narrow-leafed diploid versus wider-leafed diploid and tetraploid plants given environmental factors. Predictions allow for the measurement of plant characteristics from climate and soil gradients. Results suggest that narrow-leafed diploid plants occupy distinct habitats with the larger tetraploid plants coping by adapting mechanisms to overcome interspecies competition while the smaller diploid plants adapt with mechanisms to overcome stress. In conclusion, findings support consideration of *T. floridanum* as a variety of *T. dactyloides* and conservation implications are reviewed.

RESUMEN

Informes de *Tripsacum floridanum* Porter ex Vasey, en Texas han resistido con dos argumentos. Primero, que las plantas de hojas estrechas de Texas cuando se cultivan en condiciones favorables son las más típicas de *Tripsacum dactyloides* (L.) L. de hojas más anchas. La segunda afirmación es que la descendencia de cruces de *T. dactyloides* con *T. floridanum* son total o parcialmente estériles. Se examina el apoyo para estas dos afirmaciones y la conclusión es que las plantas de Texas de hojas estrechas típicas de *T. floridanum* están en Texas y los cruces entre las dos producen descendencia completamente fértil. Esto plantea la pregunta de qué factores están en juego para separar las poblaciones de Texas de hojas más anchas de las plantas de hojas más estrechas. Para investigar esta pregunta se construyen dos modelos estadísticos utilizando datos separados. Primero, se usa un sistema simultáneo de siete ecuaciones para predecir las características fenológicas y morfológicas de la planta dados los factores ambientales. En segundo lugar, una única ecuación logit predice la probabilidad de diploides de hojas estrechas frente a plantas diploides y tetraploides de hojas más anchas debido a factores ambientales. Las predicciones permiten la medición de las características de las plantas a partir del clima y los gradientes del suelo. Los resultados sugieren que las plantas diploides de hojas estrechas ocupan hábitats distintos con las plantas tetraploides más grandes que se adaptan mediante mecanismos de adaptación para superar la competencia entre especies, mientras que las plantas diploides más pequeñas se adaptan con mecanismos para superar el estrés. En conclusión, los hallazgos respaldan el reconocimiento de que *T. floridanum* es una variedad de *T. dactyloides*, y se revisan las implicaciones de conservación.

INTRODUCTION

Tripsacum dactyloides (L.) L. ranges from Massachusetts to Iowa and Nebraska southward into Florida and Texas through Mexico into South America (deWet et al. 1982). Its habitat varies widely with populations found on soils ranging from drier deep sandy soils and rocky outcrops to poorly drained heavier clay soils (Cutler & Anderson 1941). Three naturally occurring sympatric cytotypes of *T. dactyloides* exist (Newell & deWet 1974): 1) diploids ($2n = 36$) that reproduce sexually; 2) apomictic (Burson et al. 1990) tetraploids ($2n = 72$); and 3) the less common triploids ($2n = 58$) that act as a bridge for genetic exchange between diploids and tetraploid races (Kindiger & Dewald 1997).

The diploid (Newell & deWet 1974) *T. floridanum* Porter ex Vasey is endemic to Florida and Cuba (deWet et al. 1976). In Florida, *T. dactyloides* is sympatric with *T. floridanum*. Galinat and Craighead (1964) described *T. floridanum* as growing on the higher more xeric Pine Rocklands soils located above the wetter hammock soils occupied by *T. dactyloides*.

J. Bot. Res. Inst. Texas 13(1): 355 – 365. 2019

Morphologically, *T. dactyloides* has short rhizomes; with culms 1–2 (rarely 4) m tall in clumps with shortened internodes so that the leaves are mostly basal; sheaths are usually glabrous but occasionally slightly pilose; leaf blades are 30–75 (rarely 120) cm long and 9–35 (rarely 45) mm wide, and flat. Leaves may be glaucous or green and involute on moisture stress. In Texas, leaf involution in response to desiccation and glaucous coloration is primarily restricted to diploid cytotypes (Dunfield 1984). The terminal inflorescences are erect with 2–3 (rarely 1 or 6) branches, or rames, 12–25 cm long (Barkworth 2003, 2007). *Tripsacum dactyloides* tetraploid cytotypes can usually be distinguished from diploid plants as larger in all respects (Newell & deWet 1974), but they note exceptions exist. *T. floridanum* is typically 1 m tall with a solitary inflorescence rame with leaf blades up to 60 cm long, (1–)4–7 (rarely 15) mm wide, and can be involute or folded (Cutler & Anderson 1941; deWet et al. 1976; Barkworth 2003, 2007).

Hitchcock (1912) indirectly posed the question I seek to investigate by noting taxonomic nomenclature sometimes was subject to revision by being based on species appearing as distinct in the flora of one region but later being found to have transitional forms in another region. With respect to *T. dactyloides* and *T. floridanum* we can ask: 1) are *T. floridanum* and *T. dactyloides* in Florida distinct because they are in unique habitats and, if so, what segregates the smaller-sized plants from the larger plants; and 2) how credible are the reports of *T. floridanum* in Texas and, if credible, do they form a transition, or are Texas populations similar to *T. floridanum* and distinct from *T. dactyloides*.

Tripsacum floridanum in Texas.—Hitchcock (1906) was unable to locate the Texas specimen collected by G.C. Nealley cited in Vasey (1892) and concluded its location uncertain and probably incorrect. However, Tantravahi (1968) and Gray (1974) each reviewed a Nealley specimen labeled as *T. floridanum* from Texas. Gray (1974) noted it as housed with the NY Herbarium. Contact with NY and other herbaria did not locate this specimen for my study.

The question of *T. floridanum* in Texas was given new life when Mangelsdorf and Reeves (1931) published findings of a successful cross between maize and a *Tripsacum* growing near Angleton, Texas. Stating "This form [of *Tripsacum*] has stiff, erect, narrow leaves and resembles *T. floridanum* in some respects, though it has been identified as *T. dactyloides* by Dr. A. S. Hitchcock" (p. 332). Cutler and Anderson (1941) referenced only a single 1903 collection "U.S.A. Texas. Jefferson Co.: Beaumont, damp sandy grounds, 26 Apr 1903, *Reverchon 4188* (MO)." They suggested it was likely introduced from Florida as no collections had been made between its observed habitat in south Florida and the Texas location. As discussed more below, a lack of similar plants between Texas and Florida is unsurprising given the differences in land types between the two locations (NRCS 2006). Tantravahi and Wilkes (1967), while studying crossability relations of *Tripsacum* species, collected 35 specimens they considered possible *T. floridanum* plants in Texas (Table 1). Wilkes (1972), reports the species as native to Florida and Gulf Coast Texas and that crosses of *T. dactyloides* with *T. floridanum* and *T. maizar* Hern.-Xol. & Randolph with *T. zopilotense* Hern.-Xol. & Randolph are fertile and readily accomplished.

Taking a different stance, Newell and deWet (1974) raised issue with the ability of crosses of *T. dactyloides* and *T. floridanum* to produce fertile offspring, stating "However, artificial hybrids between diploid *T. floridanum* and diploid *T. dactyloides* resemble the maternal parent (Farquaharson 1954), and it seems more feasible that the Texas diploids represent just one of the many recognizable entities encompassed by *T. dactyloides*" (p. 662). Two years later, deWet et al. (1976) made explicit the issue of leaf blade width indicating the Texas plants have broader 0.9–1.3 cm and more erect leaf-blades, while maintaining the hybrids between the smaller Texas plants and *T. floridanum* are sterile. Reiterating these earlier positions excluding *T. floridanum* from Texas, deWet et al. (1982) state: "These species [*T. dactyloides* and *T. floridanum*] cross readily. But their hybrids are partially sterile (Tantravahi 1968), *Tripsacum floridanum* differs consistently from *T. dactyloides* by its narrower leaf-blades (0.5–1.5 cm wide). The leaf-blades of *T. dactyloides* are rarely less than 2.0 cm wide (mean 2.3 cm)" (p. 1252).

A careful reading of the statements made by deWet et al. reveals a shift in positions with the position on offspring moving from resembling the maternal parent (suggesting perhaps apomixis and not a sexual cross),

TABLE 1. Texas Specimens collected by Tantravahi and Wilkes as possible *T. floridanum*. Label locality detail, date, ID number, and herbarium with sheet numbers for each ID number is organized by Country, State, and County.

U.S.A. Texas. Brazoria Co.:

1. Alvin, outside of Angleton US 35, 21 May 1967, *4904* (ECON [2 sheets]).
2. Alvin, outside of Angleton on US 35, Red clay, 21 May 1967, *4904 A* (ECON [2 sheets]).
3. Alvin, outside of Angleton on US 35, 21 May 1967, *4904 B* (ECON).
4. Alvin, near Angleton US 35, loam soil, 21 May 1967, *4904 C* (ECON [2 sheets]).
5. Angleton, railroad track near water tank, earth filled dam on the other side of tracks, red soil, May 1967, *4864* (ECON [3 sheets]).
6. Angleton, fence row collection, 20 May 1967, *4867* (ECON [2 sheets]).
7. Angleton, St. Louis, Brownsville and Mexico Railroad, along the railroad, May 1967, *4867 A* (ECON).
8. Near Angleton, Velasco Brazos & Northern Railroad, along the railroad tracks, black loam, May 1967, *4867 B* (ECON).
9. Angleton Experiment Station Loamy soil along the tank margin, 20 May 1967, *4875* (ECON [5 sheets]).
10. 10 mi N of W, Columbia Damon Texas 36, 20 May 1967, *4832* (ECON [2 sheets]).
11. Damon, 10 mi N [of] West Columbia Texas 36, road side field margin, red clay, May 1967, *4832 A* (ECON).
12. Damon, 10 mi N of West Columbia Texas 36, road side field margin, red clay, May 1967, *4832 B* (ECON [2 sheets]).
13. Damon, 10 mi N of West Columbia Texas 36, fields margin, soil medium clay, 20 May 1967, *4832 C* (ECON).

U.S.A. Texas. Harris Co.:

14. Hoffman [sic, Huffman], Liberty and Harris Co. line, 20 May 1967, *4670.1* (ECON [2 sheets]).

U.S.A. Texas. Liberty Co.:

15. Moss Hill, halfway between Bateson [sic Batson] and Moss Hill on Texas 162, road side fence row collection, soil loam, forest vegetation, rhizomes different, 19 May 1967, *4673* (ECON [3 sheets]).

U.S.A. Texas. Orange Co.:

16. Nome (Orange Co. US 90), railroad track, segregating populations (for leaf blade width and tassel branches), 19 May 1967, *4638* (ECON [2 sheets]).
17. Orange, US 87, sandy soils, large clump, 21 May 1967, *5066* (ECON).

U.S.A. Texas. Galveston Co.:

18. Texas City, US 146, fence row, 21 May 1967, *4942* (ECON [2 sheets]).

to sterile, and last settling with partially sterile, while the position of Texas diploids having wider blades takes on a greater quantitative comparison. Turning to Tantravahi and Galinat (1967) to learn what partially sterile entails we find "The hybrids of [diploid] *T. dactyloides* and *T. floridanum* showed an intimate synapsis at pachytene. … The hybrids are vigorous and highly fertile" (p. 49). A year later Tantravahi (1968) states "The F_1 hybrids between [diploid] *T. dactyloides* and *T. floridanum* are vigorous and morphologically intermediate. … The erect leaf habit of *T. floridanum* seems to be partially dominant to the more pendant leaf habit of *T. dactyloides*" (p. 51). He concludes "The hybrids of *T. floridanum* and *T. dactyloides* should be placed in the class of fertile hybrids under any system of classification" (p. 56). Concerning the leaf-blade width, Barkworth (2003, 2007) suggests the Texas narrow-leafed *T. dactyloides* on transplanting to favorable conditions develop wider blades characteristic of *T. dactyloides*. Dunfield (1984), however, collected and grew in controlled conditions 86 specimens of *T. dactyloides* from northeast Texas. Thirteen of those plant leaf widths were between 6–10 mm, measures typical of *T. floridanum*.

Exploring the genetic similarities between the two species Larson and Doebley (1994) used restriction site variation in *Tripsacum* chloroplast DNA to construct a parsimony phylogenetic tree. The ancestry tree indicates that the *T. dactyloides* accession from the U.S., *T. floridanum*, from Florida, and Mexican *T. zopilotense* share an ancestor. They used nuclear ribosomal DNA to investigate the lack of congruence between *Tripsacum* taxonomy and evolutionary lineages. They conclude taxonomic distinctions are confounded by frequent introgression of cytoplasm from interspecific hybridization. Another cytogenetic study of *Tripsacum* by Li et al. (1999) analyzed randomly amplified polymorphic DNA. Using cluster analysis of the similarities in shared DNA, a dendrogram was obtained with four clusters. One cluster has a main trunk that forks with a branch to *T. floridanum*, the other branch in turn forks into two stems first to a diploid *T. dactyloides* from the southcentral United States, and the other stem leading to a tetraploid from central Mexico (a cold hardy accession in Woodward, OK). The shared DNA between *T. dactyloides* and *T. floridanum* led Li et al. to suggest treating *T. floridanum* as a variety of *T. dactyloides*. Along similar lines, Kindiger and Dewald (1997) made a review of the breeding lessons learned while experimenting with *Tripsacum* and maize. They note crosses of *T. dactyloides* with all other *Tripsacum* species are readily accomplished, regardless of ploidy or the taxonomic section a species has been assigned, and that the crosses generate fertile interspecific hybrids with identical reproductive attributes. The outcome from these breeding experiments led them to conclude some of the taxonomic relationships within the genus *Tripsacum* are likely artificial and natural crossing barriers such as topography, precipitation, taxonomic distribution, date of flowering, and elevation are more likely factors placing limitations on the success of hybridizations.

To be certain, Brink and deWet (1983) recognized describing limits of specific taxa in the *Tripsacum* genus was difficult citing local and endemic species as well as races with high interpopulation variation within both apomictic and sexual species causing taxa to intergrade. Recognizing this and the more recent results of genetic analyses and plant breeding research these data suggests for key morphological features small Texas diploid narrow-leafed *T. dactyloides* are very similar to *T. floridanum*. Additionally the more classical distinction between species, a lack of crossability and fertile offspring, also does not appear to hold for *T. floridanum* and *T. dactyloides*. If the evidence for a clear distinction in the morphological and genetic senses are lacking between *T. dactyloides* and *T. floridanum*, then what are the segregating ecological 'natural crossing barriers' mentioned by Kindiger and Dewald (1997) and how do they influence *Tripsacum* morphology and potentially its genetics?

MATERIALS AND METHODS

Two independent methods of statistical analysis are utilized to measure environmental gradient effects on *Tripsacum* in Texas. The first, three-stage least squares (Greene 1997) contains seven equations: three for phenological plant characteristics and four for morphological characteristics. The seven equations are estimated as a system generalizing from independent-dependent relations to simultaneous relations between plant characteristics and environmental factors. The second statistical method, logit analysis (Greene 1997) allows probability predictions for leaf width ranges given a set of environmental factors.

Data Requirements.—Data utilized in the three-stage least squares (3SLS) model included both a data set for model estimation and another for prediction. Model prediction variables included three phenological and four morphological plant variables (Table 2) measured on 44 plants collected throughout Texas and Oklahoma. An additional explanatory plant variable indicated presence (1) or absence (0) the glaucous leaf coloration of 23 plants. The morphological parameters selected were based on the factor differences identified as key to separating *T. floridanum* from *T. dactyloides* by Newell and deWet (1974). Two collections, one from near Stampede, Texas (31.283N -97.447W) and the other from Mesquite, Texas (32.822N -96.625W) exhibit *T. floridanum* characteristics, for example the respective leaf widths are 10.0 and 10.7 mm. Additionally, two collections mentioned below resemble *T. floridanum*, but were not included in the model estimation due to not having been grown a full growing season in the nursery plot. The sample location is centered near Cleburne, Texas with 68 percent within a 211 km radius. Morphological measurements were taken at the end of June on mature plants grown in Fort Worth, Texas in a uniform plot with 1 m centers on a Bolar clay loam Soil Series (NRCS 2016). Phenological data were recorded the day-of-year of occurrence. Besides the Texas and Oklahoma plants, two *T. floridanum* plants were grown. Measurements from the smaller of these plants served to determine if the *T. floridanum* characteristics would register as a statistical outlier, and how it would influence prediction of plant characteristics based on Texas soil and climate conditions when included and excluded from the data set. Given, the objective was to determine if Texas soil and climate conditions could forecast a *T. floridanum* type plant, it is noted inclusion of additional data from Florida populations would confound this objective. Measurements used in the analysis are from the plant obtained from a Florida Association of Native Nurseries member. The second plant—U.S.A North Carolina, Wake Co.: collection in greenhouse, Nov 1970, *Timothy 74599* (NCSU), from the U.S. Dept. of Agriculture Germplasm Repository Information Network—had 10 mm mean leaf width compared to 8 mm for the commercial plant.

At least one complete growing season beyond first inflorescence was provided for plant maturation prior to final data collection. Phenological variables collected included leaf emergence (as 5 leaves > 8 cm), spike

Table 2. Descriptive Statistics for Significant Climate Variables and Plant Characteristics Variables for the 3-Stage Least Squares Model.

(N=44)	Elev	Evap	Rain	JanT	mxSlr	GSn	LfE	StgE	Ht	LfL	LfW	SdD
Mean	290	145.8	88.6	0.3	6.70	242	69	122	130.1	112.2	17.4	5.0
Std Dev	198	11.9	18.5	2.8	0.38	26	6	11	32.4	16.7	5.0	0.6
Min	2	119.4	53.1	-5.1	5.65	200	59	93	78.7	66.9	8.0	3.5
Max	818	177.0	147.8	13.3	7.66	360	82	142	208.3	156.6	28.7	6.2

Abbreviations: Climate variables: Elev, elevation (m); Evap, average evaporation (cm/yr); Rain, average precipitation (cm/yr); JanT, average low January temperature (˚C); mxSlr, highest monthly average all sky insolation incident on a horizontal surface (MJ/m^2/day); GSn, growing season (days). Plant characteristic data: LfE, leaf emergence (day of year); StgE, stigma emergence (day of year); Ht, height - ground to leaf tops (cm); LfL, 3-leaf mean length (cm); LfW, 3-leaf mean width (mm); SdD, cupule diameter (mm).

emergence (as visible staminate spikelet), stigma emergence (as visible stigma color). Morphological variables included 3-leaf mean blade width, 3-leaf mean length, plant height (as soil to leaf tops), and 3-cupule mean width (Table 2).

Associated with each of the plant material collection coordinates are climate and soil data used to determine respective environmental gradients. The ten climate variables collected included: elevation (Google Earth 2018), annual mean evaporation (Texas Water Dev. Board 2018), annual mean precipitation, mean monthly low temperature for January, mean monthly high temperature for July, mean first freeze day, mean last freeze day, mean length of growing season (Texas Almanac 2004), mean maximum monthly solar radiation, and mean annual solar radiation (NASA 2018) (Table 2). Eighteen soil variables were collected for soil gradient determination corresponding to each of the collected plant location coordinates. The 10 significant variables (Table 3) are median slope, median solum depth, calculated solum depth (available water storage/water capacity), calculated water storage (median solum depth*water capacity), saturated hydraulic conductivity, soil pH, percent organic matter in surface layer, and the erosion factor K in the soil loss equation (NRCS 2016).

Prediction climate and soil data for the 3SLS model were obtained from coordinates of 256 additional locations that *T. dactyloides* has been reported or observed growing. The sample is centered near Waco, Texas with 68 percent within a radius of 209 km. Location data sources include BRIT, TAMU, and TEX herbaria, NRCS accession sheets (Shadow 2017), and personal observations. For prediction of plant characteristics using the 3SLS model equations it was convenient to aggregate the plant results obtained into NRCS defined Ecological Sites (Brown 2010; NRCS undated) and by NRCS Major Land Resource Areas (NRCS 2006).

The Florida Natural Area Inventory (2010) provides a general ecological habitat location for *T. floridanum* as the Pine Rocklands, a rocky slightly higher remnant of a limestone reef paralleling the coastline near Miami, Florida. In its natural state, the habitat was a fire maintained community with an open over story of Florida Slash pine, *Pinus elliottii* var. *densa*. Coordinates for climatic and soil data for the Krome and Cardsound Soil Series were based on general location descriptions near Homestead Florida from *T. floridanum* herbarium labels.

The estimation data used in the logit analysis consisted of climate and soil data obtained from the sources described in the 3SLS model estimation data with additional data from Dunfield (1984). The data included 82 observations with a sample location center at Sulphur Springs, Texas with 68 percent of the sample within a 63 km radius. Plants were cultivated in Commerce, Texas in the field and in a greenhouse. Data used here included plant cytotype, soil calcium and magnesium at collections sites, and whether the plant leaves were 6–10 mm or 11–28 mm width. All narrow-leafed plants were diploids.

RESULTS

Estimated coefficients in the equations of the three-stage least squares model indicate the rate of change in the left-hand side variable given a unit change in the right hand side variable (Appendix 1). For example in Equation 6, leaf width would decrease by 0.37 mm with each unit increase in the median slope of the

Table 3. Descriptive Statistics for Significant Soil Variables in the 3-Stage Least Squares Model.

(N=44)	mdSlp	mdSlm	cSlm	aWtStg	cWtStg	WtCap	KSat	pH	OM	KFac
Mean	2.2	143.8	134.6	20.8	22.4	0.15	10.3	7.8	2.3	0.23
StdDev	2.7	37.3	34.5	6.4	7.1	0.03	20.6	0.5	1.0	0.07
Min	0.5	22.9	17.8	1.8	2.3	0.06	0.2	6.4	0.3	0.10
Max	11.5	190.5	175.0	27.4	34.0	0.19	92.0	8.3	6.5	0.37

Abbreviations: mdSlp, median slope (%); mdSlm, median solum depth (cm); cSlm, calculated solum depth (cm); aWtStg, available water storage (cm); cWtStg, calculated water storage (cm); WtCap, available water capacity (cm/cm); KSat, saturated hydraulic conductivity (um/sec); pH, surface layer pH; OM, surface layer organic matter (%); KFac, erosion factor K of universal soil loss equation.

landscape. Coefficients are a complete description of the effect of the modeled gradients on plant characteristics but interpretation is difficult due to simultaneity in plant characteristics. A complementary approach is to conduct simulations using the model to predict plant characteristics at a growth location given the environmental factors at that location. For example, comparing the western part of the Central Rolling Red Plains MLRA to the Gulf Coast Prairies MLRA, the mean length of the growing season decreases 27%, solar radiation increases 35%, and the ratio of precipitation to evaporation decreases 71%. The effect of the harsher conditions in the Rolling Red Plains predicts a more decumbent stature, measured by a 34% reduction in plant height to leaf length, and a 29% reduction in leaf widths relative to the Gulf Coast.

Comparing leaf width predictions farther, the mean leaf width over the 85 NRCS Ecological Sites (ES) in the prediction data is 21 mm with a standard deviation of 7 mm. Sixteen mm is predicted for the Gulf Coast Prairie Tight Sandy Loam ES, while 7 and 13 mm are predicted for the Florida Krome and Cardsound NRCS Soil Series using Florida climate. The narrowest leaf width prediction in Texas is 11 mm on the Shallow ES in the Grand Prairie MLRA. This is expected as the actual, not predicted, narrowest leaf widths are on plants grown from collections at these locations.

Two plants collected, but not mature enough for final data collection, have mean leaf widths of 7 mm (33.1540°, -96.2946°; near Floyd, Texas, northern Texas Blackland Prairie MLRA) and 8 mm (29.7910°, -94.4978°; near Anahuac, Texas, Gulf Coast Prairie, MLRA). The Floyd population is the narrowest leafed of ten collected narrow-leafed plants. Those ten plants are from upland residuum soils in the Texas Blackland Prairie MLRA from Floyd, Texas southward to near Waco, Texas. Hill (1910) describes the area as the Taylor Prairie, an area east and below ridges of the Austin Chalk, or White Rock, Escarpment. The edges of the higher Chalky Ridge ES with the deeper upland soils are likely the habitat with the largest populations of the narrowest-leafed Texas plants. The Anahuac population occupies relic sandy barrier islands formed as the Gulf shoreline receded geologically and clayey Trinity River alluvium filled the areas between the remnants (NRCS 1976). The clayey lower areas are occupied by the larger Texas plants. Inclusion of these narrower leafed plants in the estimation data would reduce the prediction differences between Texas plants for these areas and *T. floridanum*.

Collectively, these simulation results suggest environmental forces are shaping both *T. floridanum* and smaller sized Texas plants. Remaining is a question of how larger sized *T. dactyloides* and the smaller *T. floridanum*, and Texas plants as well, can exist together in similar climatic environments yet remain distinct. That is, what environmental factor segregates the two and led early plant taxonomists to consider the two plants separate species?

To explore these questions, a simulation experiment is conducted to measure separately climate and soil effects on predicted plant characteristics. Placing the effects on a per mile basis provides a measure of how strong one general effect is relative to the other. The experiment includes three scenarios. Scenario 1 is a model prediction of plant characteristics using soil data from the Tinn NRCS Soil Series and climate data for Era, Cooke County, Texas. Scenario 2 uses the same Tinn soil data but changes climate data to that from Martindale, Guadalupe County, Texas. Era is approximately 245 miles north of Martindale. Scenario 3 uses the Era climate data and soil data from the Purvis NRCS Soil Series. The Purvis soil is an upland residuum soil 0.5 miles from the Tinn bottomland alluvium soil. *Tripsacum dactyloides* has been observed on these soils and at the respective locations. Examining the outcome from the predicted heights, the difference between plants at Martindale versus Era with both on a Tinn soil, the predicted climate effect is the Era plants are 14.8 cm shorter, or a difference of 0.06 cm per mile. In contrast, the difference between plant heights holding climate constant and changing soils, the soil effect, is a difference of 38.4 cm in plant height moving from the more xeric soil to the alluvial soil or a difference of 76.9 cm per mile. To compare the relative strength of the soil gradient to the climate gradient divide the soil effect plant height difference of 76.9 per mile by the climate effect difference of 0.06 cm per mile. The value of 1,281 indicates movement along this soil gradient is 1,281 times stronger than movement along the climate gradient as measured by plant height on a per mile basis. The soil effect relative to climate effect on leaf width is likewise dominant at 1,835 times as strong. These large differences in relative effects underscore how strong the difference in the two types of gradient is on plant adaptions.

Results from the 3SLS modeling indicate that plants do adapt to soil and climatic condition along a continuum of smaller size with increasingly xeric conditions and reduced growing seasons. Moreover, these forces explain plant similarities in plants from Florida and Texas. Additionally, the effect from the soil changes can be extremely sharp and pronounced much more so than climatic gradients which tend to change more slowly over greater distances. This seems to be a key factor in segregating large and small plants. Logit modeling can shed additional light on this by addressing two questions. First, do diploid and tetraploid cytotypes segregate along environmental gradients? And second, within the diploid plants do the narrow-leafed plants segregate into a specialized habitat?

The estimated logit equation (Appendix 1) can be evaluated by substituting the applicable numeric environmental values into the explanatory soil and climate variables in the equation to yield a probability of either a narrow 6–10 mm leafed plant or wider 11–28 mm leafed plant, which also separates diploid from tetraploid plants. Substituting the mean environmental numeric values from the sample area into the equation yields no probability of a narrow-leafed plant.

How the applicable environmental variables affect the chances for a narrow-leafed plant can be found by varying one variable while the others are held constant and observing the value that causes the probability to reach 0.5 probability. Conducting this simulation shows the odds favor narrow leaves when soil calcium is relatively more abundant to magnesium and the mean monthly maximum solar radiation is relatively larger. The evaporation to precipitation ratio is particularly interesting because of the squared term in the equation. For example, moving from the mean values towards increasing xeric conditions, the chance of narrow leafed plants increases, but once a ratio of 1.3 is reached the chances of a narrow-leafed plant falls. After the 1.3 ratio is reached, continuing to simulate increasing xeric conditions, stress lowers plant survival on the upland soils and increases the population likelihood in the more mesic alluvial bottomland soils. Because the additional runoff and water capacity of the alluvial soils more than compensates for the precipitation decline the larger tetraploid plants become dominant. The ratio of 1.3 evaporation to precipitation coincides with the three counties Collin, Hunt, and Fannin counties on the eastern edge of the White Rock Escarpment. All these environmental variable changes indicate that diploid plants are more likely to be observed as environmental conditions become more stressful relative to *T. dactyloides* plants generally.

Supporting these results are combined cytotype and location data from Dunfield (1984), Kindiger and Dewald (1997), Schliesing (1974), and Springer and Dewald (2004) on 94 plants showing cytotypes segregate into upland and lowland habitats. Seventy-nine percent of the tetraploids were on alluvium or fluviomarine, bottomland type, soils and the remainder on residuum, upland type soils. With diploids the ratio reversed with 64 percent of the diploids on residuum soils. Moreover, the data used for prediction in the 3SLS model on 290 Texas *T. dactyloides* show that *T. dactyloides* in Texas is restricted to alluvium soils roughly west of the Texas Blackland Prairie.

DISCUSSION

At the outset of my paper I mentioned Hitchcock (1912) noting taxonomic nomenclature sometimes was subject to revision for being initially based on a species appearing as distinct in a given regional flora but later found to have transitional forms in another region. This prompted a set of questions relative to *Tripsacum dactyloides* and *Tripsacum floridanum*. I asked: 1) how credible are the reports of *T. floridanum* in Texas and, if credible, do they form a transition, or are Texas populations similar to *T. floridanum* and distinct from *T. dactyloides*; and 2) are *T. floridanum* and *T. dactyloides* in Florida distinct because they are in unique habitats and, if so, what segregates the smaller-sized plants from the larger plants.

In addressing these questions I examined the arguments advanced for suggesting narrow-leafed Texas plants were not classed as *T. floridanum*. Initially, it appears the infrequency of reports of *T. floridanum* in Texas may have played a role in that assessment. As Hitchcock (1906) conducted his researches he simply was unable to locate any herbarium specimens to authenticate earlier reports of the species in Texas. Cutler and Anderson (1941) mention only one Texas specimen identified as *T. floridanum* and the limited collection appears to have led to their speculation it was an introduction to Texas from Florida. Subsequently, Tantravahi and Wilkes (1967) made extensive collections along the Gulf Coast as they researched the report of a successful cross between maize and a narrow-leafed *T. dactyloides* by Mangelsdorf and Reeves (1931). Questions as to the viability of offspring from crossing *T. floridanum* and *T. dactyloides* and whether narrow-leafed Texas plants were actually narrow-leafed when grown under favorable conditions supported the continuation of the classification of narrow-leafed Texas plants as *T. dactyloides*. Recent work by cytogeneticists and plant breeders, however, indicate genetic similarities and offspring viability between the two species. In this study and work by Dunfield (1984) narrow-leafed Texas plants were found when grown under favorable conditions retain narrow leafs. Moreover, the statistical analyses of adaptation of plant characteristics to soil and climate gradients indicate that not only are narrow-leafed plants likely in Texas, their occurrence is statistically predicted for sites with certain soil and climate conditions.

Interpreting my statistical investigations from the perspective of adaptive strategies employed by Grime (1977), *T. floridanum and* the diploid *T. dactyloides* are adapting with smaller size, glaucous leaves that involute, and decumbent stature to moisture and growing season stress. In contrast, the tetraploid cytotype seeks interspecies advantages by adapting with larger size and increased vigor. Limited genetic exchange between sexual diploids and apomictic tetraploids seem pivotal in this habitat specialization. In Texas this plays out as a complex adaptive response to equally complex environmental gradients. Tetraploids are more successful in the low evaporation-high precipitation southeast Texas area. The narrow-leafed diploids become more successful as stress increases in the relatively more climatically xeric Texas Blackland Prairie uplands partially compensated by mesic deep soils. Whereas in the Gulf Coast Prairie, the narrow-leafed diploid plants adapt to a more xeric soil with a constant climate. West of the Blackland Prairie, *Tripsacum* retreats to the alluvium bottomlands and a trade-off between stress and interspecies competition results in diploids with wider leaves. In the Edwards Plateau area with warmer climate and perennial streams, tetraploids have a comparative advantage in interspecies competition relative to the diploids. Comparative advantage reverses in the Texas Panhandle with its shorter growing seasons and ephemeral water courses and goes to the stress adapting diploids. Although there are transitional plants in Texas, the narrow-leafed diploids have adopted extremes in morphology and phenology from the diploid range of adaptive mechanisms to exist in an upland habitat by balancing climatic and soil adaptive forces. The combined adaptive mechanisms of the narrow-leafed plant along with its unique habitat are what distinguish it from the other Texas *Tripsacum* plants and as in Florida this is accented by sharp soil gradients. What emerges is a uniform ecological reason for observing narrow-leafed *Tripsacum* whether in Texas or Florida.

Collectively, these findings indicate the need for additional study of the taxonomic status of the narrow-leafed Texas *Tripsacum*. The suggestions of the breeders and cytogeneticists of a nomenclature change for *T. floridanum* to a variety of *T. dactyloides* particularly warrant additional consideration. Recognition of the narrow-leafed Texas plants either as a distinct Texas variety or combined with the Florida plants would also likely bring conservation benefits. As an example, Navarro County, Texas admirably posts signs along a *T. dactyloides* roadside population designating it a 'Historical Native Prairie Site: Eastern Gamagrass' and exclude it from mowing and herbicide spraying. Other counties once aware they had a rare remnant population of our natural heritage may be encouraged similarly.

APPENDIX 1

Three-stage Least Squares Model

Equation 1. $LfE = 87.49+0.86*mdSlp+0.17*mdSlm-1.73*cWtStg-0.09*KSat-0.25*Rain-0.33*JanT+0.04*Ht$

Equation 2. $SpkE = 93.8-106.62*WtCap+0.01*Elev+0.26*Ht$

Equation 3. $StgE = 113.1-0.77*cSlm+6.03*aWtStg+19.64*Kfac-340.28*WtCap+0.11*KSat+0.01*Elev-0.47*Evap+0.56*LfE+0.24*Ht$

Equation 4. $Ht = 230.9+20.31*cLF-0.79*cSlm+4.55*aWtStg-18.83*pH-20.10*mxSlr+1.43StgE$

Equation 5. $LfL = -14.4+15.61*pH-0.14*GSn+0.29*Ht$

Equation 6. $LfW = 2.4-0.37*mdSlp+0.25*cWtStg-9.66*Kfac-0.92*OM+0.14*Ht$

Equation 7. $SdD = 4.0-0.0002*Elev+0.01*cSlm-0.03*Rain+0.02*Ht$

Variables (alphabetically): aWtStg, available water storage; cLF, leaf color; cSLM, calculated solum depth; cWtStg, calculated water storage; Elev, elevation; Evap, mean evaporation; GSn, growing season; Ht, height - ground to leaf tops; JanT, mean low January temperature; Kfac, universal soil loss equation K factor; KSat, saturated hydraulic conductivity; LfE, leaf emergence; LfL, 3-leaf mean length; LfW, 3-leaf mean width; mdSlm, median solum depth; mdSlp, median slope; mxSlr, highest monthly mean all sky insolation incident on a horizontal surface; OM, surface layer organic matter; pH, surface layer pH; Rain, mean precipitation SdD, 3-cupule mean diameter; SpkE,spike emergence; StgE,stigma emergence; WtCap, available water capacity.

Four hypotheses tests exist for the three-stage least squares model: (1) Whether there exists correlation between the error terms of each equation, i.e., a null hypothesis that a matrix of the correlated error terms is diagonal, distributed as a chi-square test statistic of 93.0 at 21 df, with a 95% confidence level exceeds the critical value of 32.7, rejecting the null hypothesis. (2) The null hypothesis that slope coefficients are jointly zero, distributed as a chi-squared statistic of 203.4 at 37 degrees freedom, with a 95% confidence level exceeds the critical value of 52.2, rejecting the null hypothesis. (3) Heckman's two-step procedure for testing simultaneity between variables in an equation: the null hypothesis of no simultaneity was rejected for all but Equation 1 between leaf emergent date and plant height. (4) The null hypothesis that a slope coefficient in an equation is zero with a 95% confidence level: all but five of the 37 t-ratios exceed the critical value of 2.0.

Logit Model

Equation 8. $NrwLf = -542.49+0.39*rCM+660.89*ER-255.05*ER^2 +17.36*mxSlr$

Variables: NrwLf, a binary variable with a one indicating leaves with 9–10 mm widths (13 obs) and a zero indicating leaves of 11–28 mm widths (69 obs); rCM, ratio soil calcium to magnesium; ER, ratio evaporation to precipitation (ER^2, ER*ER); mxSlr, highest monthly mean all sky insolation incident on a horizontal surface. The t-value for the four estimated coefficient variables in the equation exceed the critical value of 2.0 at the 95% confidence level, rejecting the null hypothesis the slope coefficient is zero. The null hypothesis that slope coefficients are jointly zero is chi-square distributed at 52.3 with 4 degrees freedom with 95% confidence; the critical value of 9.5 is exceeded, rejecting the null hypothesis. The prediction success rate is 94%.

ACKNOWLEDGMENTS

Grateful acknowledgement is made for collection permission, seeds or other plant material, and site identification to: Terry Blankenship, Welder Wildlife Refuge, Sinton, TX; Stanley Bradbury, NRCS, Lubbock, TX; Melinda Brakie and Alan Shadow, NRCS, Nacogdoches, TX; David Embry and Steve Nelle (ret.), NRCS, San Angelo, TX; Daniel McDonald, U.S. Fish and Wildlife Svc., Wichita Mountain Wildlife Refuge, Indiahoma, OK; John Reilley, NRCS, Kingsville, TX; David Riskind, Texas Parks and Wildlife Dept., Austin, TX; Alex Sanchez USDA Agric. Research. Svc, Coral Gables, FL; and Michelle Villafranca, Fort Worth Parks and Recreation Department, Fort Worth, Texas. Thanks to Anthony Brach, Harvard University Herbaria for finding and providing digital images of the specimens collected by Tantravahi and Wilkes, and Barney Lipscomb and the editorial staff at BRIT for their expert assistance. I appreciate the helpful comments of Charles M. Allen and two anonymous reviewers.

REFERENCES

Barkworth, M.E. 2003. *Tripsacum*. In: Flora of North America Editorial Committee, eds. Flora of North America north of Mexico. Oxford University Press, New York, U.S.A., and Oxford, U.K. 25:693–696.

Barkworth, M.E. 2007. *Tripsacum*. In: Barkworth, M.E., L.K. Anderton, K.M. Capels, S. Long, & M.B. Piep, eds. Manual of grasses for North America. Utah State University Press, Utah, U.S.A. Pp. 343–344.

Brink, D.E. & J.M.J. deWet. 1983. Supraspecific groups in *Tripsacum* (Gramineae). Syst. Bot. 8(3):243–249.

Brown, J.R. 2010. Ecological sites: Their history, status, and future. Rangelands 32(6):5–8. doi: 10.2111/RANGELANDS-D-10-00089.1.

Burson, B.L., P.S. Voigt, R.A. Sherman, & C.L. Dewald. 1990. Apomixis and sexuality in Eastern gamagrass. Crop Sci. 30:86–89.

Cutler, H.C. & E. Anderson. 1941. A preliminary survey of *Tripsacum*. Ann. Mo. Bot. Gard. 28:249–269.

deWet, J.M.J., J.R. Gray, & J.R. Harlan. 1976. Systematics of *Tripsacum* (Gramineae). Phytologia 33:203–227.

deWet, J.M.J., J.R. Harlan, & D.E. Brink. 1982. Systematics of *Tripsacum dactyloides* (Gramineae). Amer. J. Bot. 69:1251–1257.

Dunfield, P.C. 1984. A preliminary evaluation of eastern gamagrass from northeast Texas. Unpublished M.S. thesis, East Texas State University, Commerce, Texas, U.S.A.

Farquharson, L.I. 1954. Apomixis, polyembryony, and related problems in *Tripsacum*. Unpublished Ph.D. thesis, Indiana University, Bloomington, Indiana, U.S.A.

Florida Natural Area Inventory. 2010. Guide to the natural communities of Florida. Tallahassee, Florida, U.S.A. www.fnai.org. Accessed Nov 2018.

Galinat, W.C. & F.C. Craighead. 1964. Some observations on the dissemination of *Tripsacum*. Rhodora 66(768):371–374.

Google Earth. 2018. Google Earth pro. Build 7.3.2.5491(64-bit), Google LLC.

Gray, J.R. 1974. The genus *Tripsacum* L. (Gramineae): Taxonomy and chemosystematics. Ph.D. thesis, University of Illinois at Urbana-Champaign, Illinois, U.S.A.

Greene, W.H. 1997. Econometric analysis. Prentice-Hall Inc., New Jersey, U.S.A.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Amer. Naturalist 111(982):1169–1194.

Hill, R.T. 1910. Geography and geology of the Black and Grand Prairies, Texas. Part VII, Texas. 21st Ann. Rep. U.S. Geological Survey, Washington D.C., U.S.A.

Hitchcock, A.S. 1906. Notes on North American grasses VI. Synopsis of *Tripsacum*. Bot. Gaz. 41:294–298.

Hitchcock, A.S. 1912. Recent work in systematic agrostology. Science 36(916):86–90.

Larson, S.R. & J.R. Doebley. 1994. Restriction site variation in the chloroplast genome of *Tripsacum* (Poaceae): Phylogeny and rates of sequence evolution. Syst. Bot. 19:21–34.

Li, Y.G., C.L. Dewald, & P.L. Sims. 1999. Genetic relationships within *Tripsacum* as detected by RAPD variation. Ann. Bot. 84:695–702.

Kindiger, B. & C.L. Dewald. 1997. The reproductive versatility of eastern gamagrass. Crop Sci. 37:1351–1360.

Mangelsdorf, P.C. & R.G. Reeves. 1931. Hybridization of Maize, *Tripsacum*, and *Euchalaena*. J. Heredity 22(11):328–343.

NASA (National Aeronautics and Space Admin.). 2018. All sky insolation incident on a horizontal surface. NASA Langley Research Center. power.larc.nasa.gov/docs/v1/. Accessed Nov 2018.

Newell, C.A. & J.M.J. deWet. 1974. Morphological and cytological variability in *Tripsacum dactyloides* (Gramineae). Amer. J. Bot. 61:652–664.

NRCS (U.S. Dept. of Agri. Natural Resource and Conservation Svc). 1976. Soil survey of Chambers County, Texas. www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/texas/ TX071/chambers.pdf. Accessed Nov 2018.

NRCS (U.S. Dept. of Agri. Natural Resource and Conservation Svc). 2006. Land resource regions and major land resource areas of the United States, the Caribbean, and the Pacific Basin. Agri. Hdbk. 296.

NRCS (U.S. Dept. of Agri. Natural Resource and Conservation Svc). 2016. Web Soil Survey. websoilsurvey.nrcs.usda.gov. Accessed Nov 2018.

NRCS (U.S. Dept. of Agri. Natural Resource and Conservation Svc). Undated. Ecological site descriptions. www.nrcs.usda.gov/wps/portal/nrcs/main/national/technical/ecoscience/desc/. Accessed Nov 2018.

Schliesing, T.G. 1974. Ecotypic variation in *Tripsacum dactyloides* in Texas. Unpublished M.S. thesis, Texas Tech University, Lubbock, Texas, U.S.A. ttu-ir.tdl.org/handle/2346/14002. Accessed Nov 2018.

Shadow, A. 2017. Personal communication: *T. dactyloides* accession sheets. USDA NRCS, East Texas Plant Materials Center, Nacogdoches, Texas, U.S.A.

Springer, T.L. & C.L. Dewald. 2004. Eastern gamagrass and other *Tripsacum* species. In: L.E. Moser, L.E. Sollenberger, & B.L. Burson, eds. Warm-season (C4) grasses. Amer. Soc. Agron Spec. Publ. 45:955–973.

Tantravahi, R.V. & W.C. Galinat. 1967. Meiosis in diploid interspecific hybrids of *Tripsacum*. Maize Genet. Coop. Newslett. 41:49–51.

Tantravahi, R.V. 1968. Cytology and crossability relationships of *Tripsacum*. Ph.D. thesis, Busey Institute, Harvard University, Cambridge, Massachusetts, U.S.A.

Texas Almanac. 2004. Texas temperature, freeze, growing season and precipitation. texasalmanac.com/sites/default/files/images/almanac-feature/countyweatherA.pdf. Accessed Nov 2018.

Texas Water Development Board. 2018. Precipitation and lake evaporation. www.twdb.texas.gov/surfacewater/conditions/evaporation/. Accessed Nov 2018.

Vasey, G. 1892. Monograph of the grasses of the United States and British America. Contr. U.S. Natl. Herb. 3:6.

Wilkes, H.G. 1972. Maize and its wild relatives. Science 177:1071–1077.