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Source: Natural Areas Journal, 44(2) : 87-97

Published By: Natural Areas Association

URL: https://doi.org/10.3375/2162-4399-44.2.87

Research Article

Plastic Demographic Responses of Wiregrass (*Aristida beyrichiana*) Translocated to Contrasting Habitats[a]

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Associate Editor: Sarah Hamman

ABSTRACT

Wiregrass, *Aristida beyrichiana*, is frequently employed for habitat restoration of southeastern pine forests due to its flammability and dominance. We used data from translocations of wiregrass to assess restoration practices and to evaluate plastic responses of survival, growth, and reproduction to translocation into different microhabitats characterized by the relative occurrence of dominant shrub species. Data were collected between 2013 and 2016 and in 2019 and 2020. Target microhabitats included areas near oaks, palms, pines, and in open gaps, randomly selected at two paired elevations on three parallel ridges in the Lake Wales Ridge State Forest, Polk County, central Florida, USA. Height and number of tillers were relevant in explaining vital rate variation across microhabitats. We found a unimodal nonlinear relationship between plant height and number of tillers that varied after translocation to different habitats. Areas near pines and with enough ground cover allowing burning increased plant survival, growth, and production of caryopsides, while locations farther from the ridge crests and in open areas, and near palms and oaks, were less favorable. Plastic phenotypic adjustments between number of tillers and plant height may explain commensurate reproductive outputs of wiregrasses in open habitats and near oaks and palms.

Index terms: Aristida beyrichiana; Florida sandhill pine-savannas; management; modeling; wiregrass

INTRODUCTION

Wiregrass (*Aristida beyrichiana* Trin. & Rupr, formerly called *Aristida stricta*) is a native grass in the southeastern United States. It is a dominant component of the herbaceous layer in several pine-dominated communities (Gordon and Rice 1998). Often, wiregrass occurs in association with many other native and rare plant taxa, and it is considered an essential element of the groundcover (Hardin and White 1989). Because it contributes a considerable amount of fuel, is highly flammable, and creates favorable fuel beds by keeping pine needles and other litter off of the ground (Clewell 1989; Platt et al. 1991; Fill et al. 2016), this grass plays a major role in the fire dynamics of these ecosystems and is frequently used in restoration efforts in the southeastern coastal plain (Brockway 2005; Walker and Silletti 2007). Fire, particularly during the growing season, is essential for the onset of flowering and fruit production of this grass (Seamon et al. 1989; Streng et al. 1993; Outcalt 1994; Fill et al. 2021). Plants burned early during the wet season produced seeds with the highest probability of establishment as seedlings (Baruzzi et al. 2022). *A. beyrichiana* reached higher densities, larger vegetative growth, and greater recruitment in more frequently burned areas (Shearman et al. 2019). However, burn planning should require consideration of density and size structure of local and translocated populations, as fire may kill seedlings and small individuals in areas with recently transplanted plants (Mulligan et al. 2002).

Human-aided species translocations (IUCN 2013) are increasingly used to preserve biodiversity (Griffith et al. 1989). Translocations consist of (1) movement of individuals to areas outside their historical ranges, (2) reintroduction of individuals to locations where populations were extirpated, and (3) addition of individuals to existing populations. These management actions offer opportunities to learn about ecological determinants of species dynamics and persistence. This information is required to guide restoration decisions and to develop comprehensive management and conservation plans. Wiregrass translocation efforts in degraded areas with soil perturbation have been problematic and frequently unsuccessful (Clewell 1989; Outcalt and Lewis 1990; Outcalt 1992). Information on the demographic variation of wiregrass when planted into common habitats in these degraded areas can improve chances of establishment and propagation (Outcalt and Lewis 1990).

Allometry examines the constrained relationships among body parts, their scaling with size, and their changes during development (Gayon 2000; Shingleton 2010). The description of allometric relationships and the understanding of the processes generating them are essential topics in ecology and evolution (Gould 1966; Niklas 1994; Pélabon et al. 2014). Allometric models describe differences in the growth of focal parts and the relationships between them and to the whole individual (e.g., Houck et al. 1990). These relationships can vary among environments and the

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[a] Editor Eric Menges recused himself from all decisions on this manuscript as one of the authors is a collaborator.

understanding of their functional responses can inform vital rate variation and demographic models aimed at understanding species persistence. As an individual plant grows, it might devote resources to enhance height or length of standing structures, increase their number, or increase both proportionally. These plastic growth patterns might change with the age of an individual or vary according to the habitat characteristics where they grow. Understanding these allometric relationships can identify ecological mechanisms behind species responses to management allowing better restoration.

Our aim was to describe demographic plastic changes revealed by variation in plant height and number of tillers of *A. beyrichiana* in different habitats affecting its survival, growth, and reproduction. Tiller number and plant height are essential features influencing plant architecture and reproductive output in grasses (Wang et al. 2018). We hypothesize that (1) since previous studies of other grass species have shown a negative relationship between plant height and number of tillers (Lush and Rogers 1992; Liao et al. 2019), a similar phenomenon will be observed in wiregrass and that tradeoffs in these variables will better predict variation in vital rates compared to the variables separately; and (2) these morphological and demographic changes are associated with differences among common habitats in the target ecosystem for restoration. We used data collected after the experimental translocation of single source greenhouse germinated seedlings to different habitat field conditions in replicated locations. Data were collected annually between 2013 and 2016 and then in 2019 and 2020. Target microhabitats included areas near palms, near oaks, near pines, and in open gaps, randomly selected within two paired relative elevations in each of three parallel ridges. Our first objective was to evaluate the relationship between stem height and number of tillers over time in translocated wiregrass. Our second objective was to assess the influence of this relationship on wiregrass survival, growth, and reproduction across different habitats.

METHODS

Study Area

The Walk-in-Water tract is part of the Lake Wales Ridge State Forest, Polk County, in central Florida, USA (Figure 1). Before the property was protected, the natural sandhill was degraded using roller choppers to create habitat for nonnative grasses (mostly bahia grass, *Paspalum notatum*). This disturbance reduced the ground cover of native species but did not create favorable conditions for nonnative grasses. The local ridges in the Walk-in-Water tract occupy an area of approximately 364 ha. The current vegetation in the ridges is a mosaic of patches of overgrown pine-oak sandhill interspersed with large open sandy gaps, patches of nonnative grasses, and scattered individuals of widespread native plant species (such as *Polygonella robusta*, *Rynchospora megalocarpa*).

Plant Translocation and Measurements

In March 2013, we collected *A. beyrichiana* caryopses in the Hesperides tract of the Lake Wales Ridge State Forest (LWRSF). This protected forest tract is approximated 10 km north of the translocation sites and has vigorous populations of *A. beyrichiana*. Before fragmentation associated with agricultural and other human disruption, the communities in the Hesperides and Walk-in-Water were part of a relatively continuous ecosystem. We sowed the caryopsides in commercial soil inside plastic pots (10 cm wide × 8 cm high) and kept them in a greenhouse at the University of Central Florida, Orlando. Five caryopsides were initially sowed per pot and then thinned when transferred to keep only the largest plant per pot. In May 2013, established plants were transferred to a shade house in the LWRSF headquarters in Frostproof, Florida. In June 2013, we measured the length of the longest tiller and counted the tillers of grass clumps of each plant scheduled to be transplanted to the field.

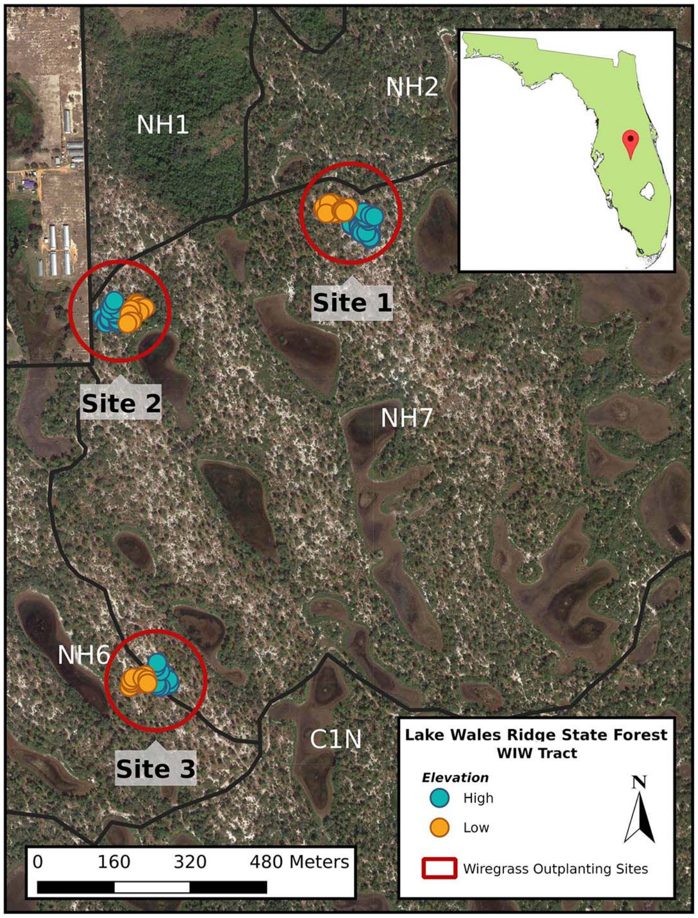

Figure 1.—Location of wiregrass plug out-planting on the WIW Tract of the Lake Wales Ridge State Forest. The three-character acronyms correspond with the management units.

In July 2013, 641 plants were transplanted to four microhabitats in two elevations in three independent parallel ridges at the Walk-in-Water tract of LWRSF. We marked each plant with a steel wire pin with plastic-colored flags and with a unique numbered circular aluminum tag inserted. Microhabitats were (1) near oak: plants were translocated under the canopy and 0.5 m from the main stem of an oak (*Quercus geminata* or *Quercus laevis*) with >2 m height; (2) near palmetto: plants were translocated approximately 0.5 m from the dripline of a >0.5 m tall palmetto (*Sabal etonia* or *Serenoa repens*); (3) near pine: plants were translocated under the canopy approximately 0.5 m from the trunk of a >5 m tall pine (*Pinus palustris*); and (4) in open gaps: plants were translocated in areas with bare sand ground cover and more than 2 m from any woody plant larger than 0.5 m in height. Ridge position was determined by the distance to the highest point of the ridge and the nearest wetland. Approximately half of the plants per ridge were translocated <10 m from the local ridge crest, and the other half >20 m from this point and >20 m from the nearest wetland. We considered the plant communities across the whole elevation gradient in the study area as examples of degraded pine-oak sandhill and potential habitat for *A. beyrichiana* because of its vegetation composition and structure.

We attempted to keep the sample size homogeneous but not all the habitats were equally available (Supplemental Table S1). The minimum number of plants translocated per treatment combination for each site was 25 and the maximum 36. Survival, maximum height, and number of tillers were determined in December 2013, March 2016, and September 2019. In May of 2020, a prescribed fire was initiated from an airplane in the Walk-in-Water tract affecting the study area. In November 2020, we measured the height of the tallest reproductive and vegetative stalks, counted the number of vegetative and reproductive stalks, and counted the number of caryopses in a randomly selected fruiting stalk on each reproductive plant. Even with the aid of GPS points and pin flags, we were able to find only a subsample of the initially translocated plants for the analysis of the response to fire (Supplemental Table S1).

Analysis

We started by exploring functional equations describing the allometry of these data in the different anticipated (just before transplant in June 2013, and soon after it in December 2013) and realized (6 y after transplant in September 2019) habitats and ridges. We evaluated the relationship between stem height and number of tillers over time in translocated wiregrass. We used generalized linear models with Poisson error distribution and logarithm link to assess variation in number of tillers at transplant date and at the initial and concluding sampling dates before the fire (June 2013, December 2013, and September 2019, respectively), and as a function of plant height per microhabitat, ridge, and elevation. Reciprocally, we used linear models with Gaussian error distribution to assess variation in height at transplant date and at the initial and concluding sampling dates before the fire (June 2013, December 2013, and September 2019, respectively), and as a function of number of tillers, microhabitat, ridge, and elevation.

We evaluated vital rate variation as a function of state variables, initial height and number of tillers, habitat, elevation, and ridge. We used generalized linear models with binomial error distribution and logit link to assess plant survival and probability of reproduction as a function of plant height, number of tillers, microhabitat, ridge, and elevation. We used generalized linear models with negative binomial error distribution and logarithm link to assess the number of fruiting spikes per reproductive plant as a function of plant height, number of tillers, microhabitat, ridge, and elevation. We used generalized linear models with Poisson error distribution and logarithm link to assess number of caryopses per fruiting stalk in reproductive plants as a function of plant height, number of tillers, microhabitat, ridge, and elevation. All independent variables were considered as fixed effects. We used model selection based on a Bayesian approximation to the Akaike information criterion (WAIC; Burnham and Anderson 2002; Watanabe 2013) to identify the most parsimonious fit from the proposed set. Our reference set of models included a semi-saturated model with the additive effects of height, number of tillers, microhabitat, the two-way interaction between height and microhabitat, ridge, and elevation. The remaining models in this set were nested models of the semi-saturated model. Statistical literature recommends limiting the number of models evaluated to avoid spurious associations (Burnham and Anderson 2002) and we did not explore all possible models of these variables and concentrated on those allowing us to evaluate our hypotheses. The models were implemented using Bayesian methods with diffuse priors and 10,000 iterations, discarding the first 5000. We present the posteriors of these models. The Bayesian posteriors are probability distributions of the predicted variables as a function of the focal deterministic variables evaluated (Quintana-Ascencio et al. 2022). We checked models for consistency among chains using R-hat as criteria. We conducted statistical analyses using R 3.4.4 (R Core Team 2019) and Stan 2.18.0 (Carpenter et al. 2017; Stan Development Team 2018).

Modeling of Grain Yield Among Habitats

We used the posteriors of models for the vital rates in an integrated model with a 6 y interval simulating population change from establishment after transplant in 2013 to flowering in 2020 to estimate reproductive output (grain yield) as the projected total caryopsides produced by *A. beyrichiana* per habitat. We assumed per simulation that all introduced plants were translocated to the focal condition for each combination of habitat, elevation, and ridge. We used an arbitrarily binned data matrix with combinations of 10 evenly distributed values of the observed initial height and number of tillers to represent the range of initial plant attributes (1–18 for initial number of tillers and 1–60 cm for initial height). We calculated the observed total frequencies per cell of joint height and number of tillers (81 potential cells). This number allowed a reasonable exploration of the data combined with ease of computation. We obtained 1000 posteriors of survival and growth using the midpoint for the cell attributes. We multiplied the frequency of initial individuals in each cell by the survival expected given the mid-point of height. We obtained a projected estimate of the final height of the survivors taken as random normal sample with the predicted posterior heights as a function of the initial mid-point by cell as the mean and the square root of the observed residual variance. We predicted probability of reproduction of each of the survivors using their estimated size and compared it to a random number. If the random number was smaller than the predicted probability the individual was assumed reproductive. We calculated the number of stalks produced by a plant with the height of the focal reproducing plant and multiplied this estimate to the number of estimated caryopsides by stalk produced by an individual with this size.

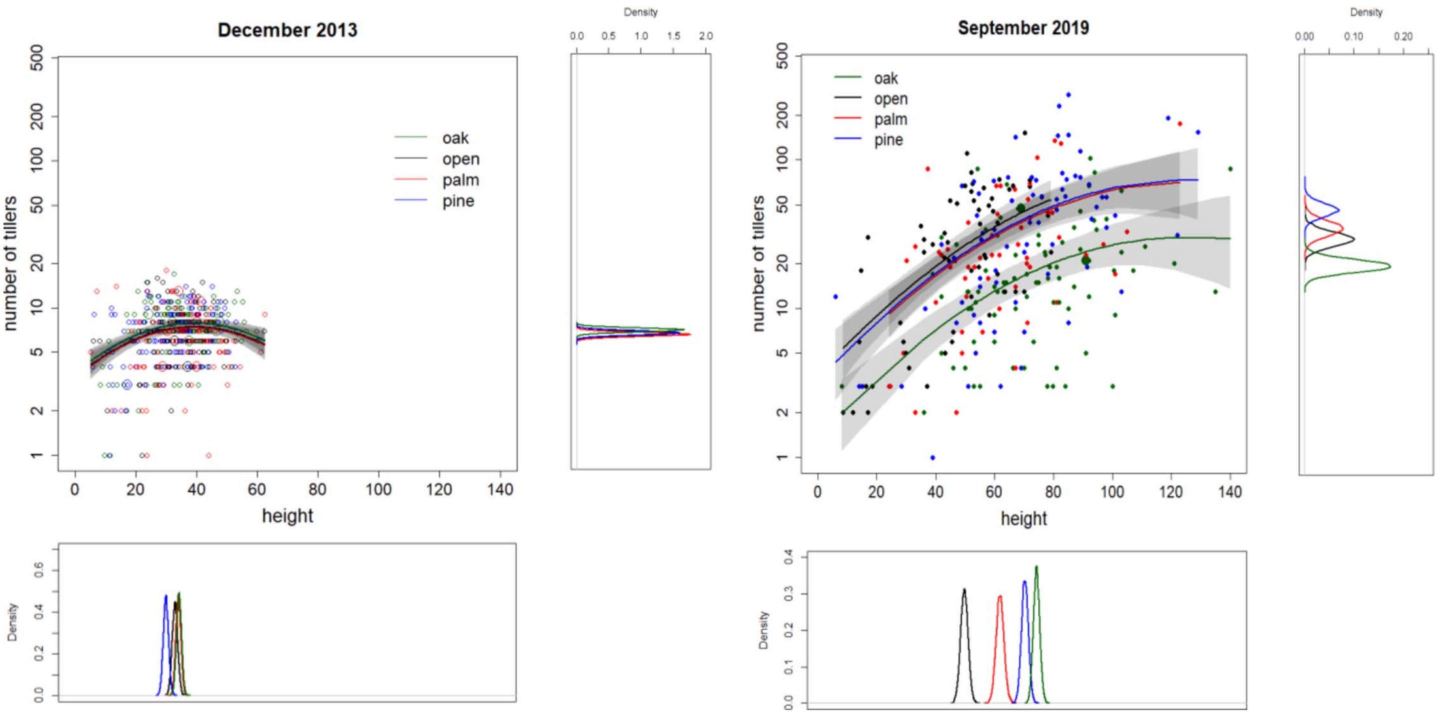

Figure 2.—Number of tillers as a function of plant height and microhabitat. Large subplot in the left just before transplanting in December of 2013 and large subplot in the right after 6 y of the translocation in September 2019. The posterior distribution of average heights and number of tillers by microhabitat are shown on the exterior subplots. Lower subplots depict the distribution of average height and right subplots the distribution of average number of tillers.

Using the same algorithm, we generated yield posteriors of models with height as the only state variable. We compared the differences in yield between the two integrated models.

RESULTS

Initial Effects of the Transplant

We detected several initial transient effects after the transplant. Animals discovered the translocated plants after their transplant in July 2013 and 59 of the initial 641 plants were dug out and dead by the next field evaluation in December 2013. Individuals in open habitats were the most disturbed ($n = 27$) and those near oaks were the least disturbed ($n = 6$; Supplemental Table S2). Plants in the Low elevation were more frequently dug out ($n = 41$) than those in the High elevation ($n = 18$). Plants in ridge 2 had the lowest disturbance ($n = 9$) and those in ridge 1 the highest ($n = 32$). Additional mortality due to other unknown reasons ($n = 46$) in the interval between transplant and the first field evaluation was relatively even among treatment combinations and on average 1.92 ± 1.3 SE plants died between July and December 2013 among treatments (Supplemental Table S2). The average number of tillers in June 2013 was 6.45 while average number of tillers in December 2013 was 7.09. The average height of the plants when measured in their pots in June 2013 before the translocation was 38.8 cm (9.21 SE). In December 2013, after 6 mo in the field, the average size decreased to 33.76 cm (0.37 SE); the reduction in size was higher among larger plants. For both dates, number of tillers increased with height for smaller plants, reached a peak around the mean plant height value, and decreased for taller plants (for December in Figure 2). Similarly, plant height increased as a function of number of tillers for plants with fewer tillers, reached a peak around the overall mean number of tillers, and decreased for plants with more tillers (for June in Supplemental Figure S1). We only included in further analyses individuals that survived the first 6 mo after translocation (alive in December 2013), for models of survival and growth through September 2019, and of fecundity after the 2020 fire.

Initial Attributes of the Assessed Plants

The total number of plants for the analysis of vital rate variation, defined by those available in December 2013, was 534 (maximum 77, minimum 56 per microhabitat; Supplemental Table S1). At this sampling date there was no evidence of clear differences on average number of tillers among plants in different translocation microhabitats (Oak: 7.4 ± 2.67 SD, Open: 7.0 ± 2.95 SD, Palm: 6.9 ± 2.89 SD, Pine: 7.1 ± 2.89 SD; Figure 2), nor among ridges (ridge 1: 7.0 ± 2.97 SD, ridge 2: 6.8 ± 2.61, ridge 3: 7.4 ± 2.93 SD), nor elevations (Low: 7.2 ± 2.80, High: 7.0 ± 2.91). There was also no evidence of clear differences on average plant height among plants in different microhabitats (in cm; Oak: 35.0 ± 11.17 SD, Open: 33.7 ± 9.43 SD, Palm: 34.8 ± 10.86 SD, Pine: 30.7 ± 11.78 SD; Figure 2), nor among ridges (ridge 1: 33.3 ± 9.48 SD, ridge 2: 34.1 ± 10.89, ridge 3: 33.2 ± 12.43 SD), nor elevations (Low: 33.5 ± 10.3, High: 34.1 ± 11.25 SD).

Table 1.—Summary of WAIC statistics for models of vital rate variation as a function of stem height (H), number of tillers (T), and Habitat. For models of survival and growth the state variables were the initial height and number of tillers. For models of reproduction, stalks and caryopsides were the current height and number of tillers at sampling time. We present WAIC differences between each and the most likely model in the set (dAIC) and their relative model weights (W). All models included additive effects of ridge and elevation position. The most likely model(s) is in bold. We considered that models within two dAIC provided undistinguishable evidence.

	Survival #		Growth #		P(rep) ##		Stalks ##		Caryopsides ##	
Model	dAIC	W	dAIC	W	dAIC	W	dAIC	W	dAIC	W
H * Habitat + T	3.6	0.10	2.6	0.21	7.3	0.02	NC	NC	**0.1**	**0.48**
H * Habitat	5.8	0.03	9.9	0.006	5.0	0.05	NC	NC	**0.0**	**0.51**
H + T + Habitat	**2.1**	**0.21**	**0.0**	**0.77**	**1.8**	**0.26**	**0.3**	**0.42**	13.6	<0.001
H + Habitat	**0.0**	**0.61**	8.5	0.01	**0.0**	**0.65**	**0.0**	**0.48**	15.6	<0.001
Height	10.2	0.004	65.0	<0.001	7.6	0.001	3.1	0.10	25.0	<0.001
Tillers	19.0	<0.001	80.3	<0.001	18.2	<0.001	17.5	<0.001	158.8	<0.001
T + Habitat	8.0	<0.001	23.3	<0.001	25.7	<0.001	21.4	<0.001	213.7	<0.001
Habitat	6.0	0.03	31.9	<0.001	27.8	<0.001	32.1	<0.001	213.9	<0.001

Initial state variables; ## Current state variables; NC: model did not converge.

Effects of Size State Variables per Microhabitat, Ridge, and Elevation on Vital Rates

In March 2016, 90.4% (483/534) of the transplant locations were found and of those recovered 94% had live plants (86.6% in open areas, 93.7% near palms, 97.1% under oaks, and 98.2% under pines were alive). Five years and nine months after their translocation, in September 2019, 73.6% (393/534) of the plants were accounted for. The remaining plants (47 near oaks, 3 in open areas, 55 near palms, and 36 under pines) could not be found because their markers were lost, and they were not included in the analysis. Of those plants accounted for, 80.1% remained alive. Stem height, number of tillers, and microhabitat consistently affected vital rates (Table 1). Among the proposed set of models, variation in survival was most likely explained by the model including the effects of plant height, microhabitat, ridge, and elevation. Larger plants had higher probability of survival in all microhabitats (Table 2 and Figure 3). Survival was lowest among plants in open areas, higher under the canopy of pines and near palms, and highest under oaks (92.3% near oaks, 82.0% under the canopy of pines, 80.1% near palms, and 67.0% in open areas; Table 2 and Figure 3). Survival was higher in low elevations and in ridge 2 (Table 2).

Variation in plant height in September 2019 was best explained by a model including the effects of initial plant height, initial number of tillers, microhabitat, ridge, and elevation. Plant height in September 2019 changed in response to both size variables, increased as a function of initial height, and decreased as a function of the initial number of tillers (Table 2, Figure 2, and Supplemental Figure S1). Across all surviving individuals,

Table 2.—Summary of mean coefficients and the standard deviation (SD) of the most informative model of probability of plant survival and plant height change (growth; data were centered) between December 2013 and September 2019; also models for probability of reproduction, number of reproductive stalks, and number of caryopsides by stalk in November 2020. Models included effects of plant height (H), number of tillers (T), habitat, ridges, and elevation. For models of survival and growth the state variables were the initial height and number of tillers. For models of reproduction, stalks and caryopsides ware the current height and number of tillers at sampling time. The intercept was set for oak habitat, ridge 1, and high elevation. All the parameter in every model reached R-hat = 1.

	Survival #		Growth #		P(rep) ##		Stalks ##		Caryopsides ##	
Model	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Intercept	−0.09	0.79	55.57	7.12	−9.01	1.85	−6.86	1.44	2.75	0.26
H	0.05	0.02	0.66	0.13	0.08	0.02	0.08	0.02	0.01	0.002
T	–	–	−1.72	0.53	–	–	–	–	–	–
Palm	−1.02	0.48	−25.40	3.22	0.89	0.86	0.29	0.71	−1.00	0.40
Pine	−1.00	0.53	−13.01	3.24	2.62	0.89	0.61	0.65	0.05	0.28
Open	−1.81	0.56	−4.58	2.07	2.92	1.01	2.53	0.90	−1.00	0.40
H * Palm	–	–	–	–	–	–	–	–	0.01	0.004
H * Pine	–	–	–	–	–	–	–	–	0.003	0.003
H *Open	–	–	–	–	–	–	–	–	0.02	0.006
Ridge 2	0.84	0.38	14.60	2.91	0.76	0.65	0.28	0.57	0.38	0.06
Ridge 3	0.51	0.36	1.64	2.92	−2.87	1.40	−3.19	1.08	0.10	0.15
Elevation (low)	0.83	0.32	−3.24	2.31	−0.07	0.64	−0.88	0.55	0.49	0.06
Sigma	–	–	18.51	0.81	–	–	–	–	–	–
Scale	–	–	–	–	–	–	0.26	0.07	–	–

Initial state variables; ## Current state variables; – It was not necessary to estimate.

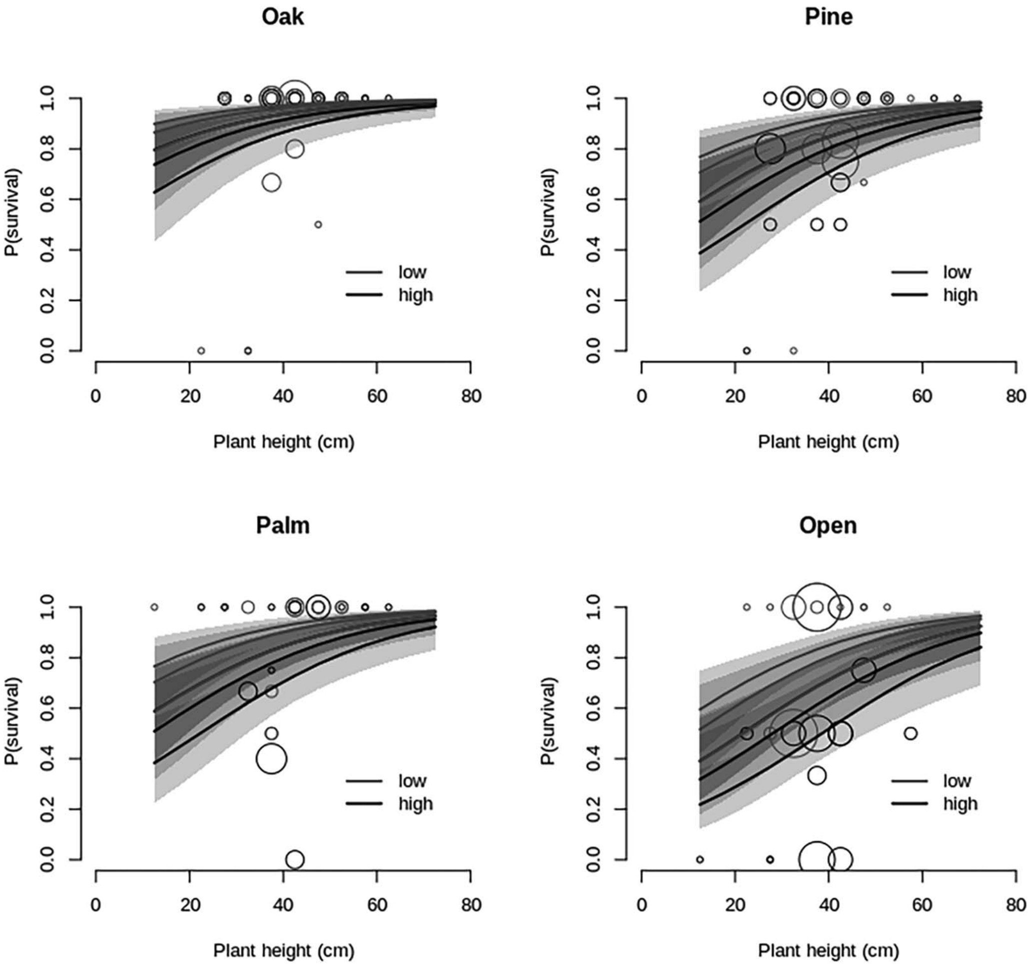

Figure 3.—Survival of translocated plants from December 2013 to September 2019 as a function of plant height, microhabitat, elevation, and ridge. The size of the circles conveys the relative sample size by height class (binned arbitrarily). Polygons indicate 95% credibility intervals of the predicted mean survival posterior by treatment combination.

there were clear differences on average plant height across microhabitats by September 2019 (Figure 2). Individuals in open areas were on average shortest (48.9 cm ± 17.34 SD). Plants near palms were on average taller than those in open areas (61.54 cm ± 20.63 SD). Plants transplanted under pine canopy (70.52 cm ± 23.07) were taller than those near palms and in open areas. Individuals transplanted near oaks were on average the tallest (74.09 cm ± 22.24 SD) among all the microhabitats. Plants were on average taller in ridge 2 than in ridges 1 or 3 (ridge 1: 59.22 cm ± 21.82 SD, ridge 2: 72.74 cm ± 24.00, ridge 3: 62.40 cm ± 21.74 SD). There were no clear differences in plant height between relative elevations.

Overall, the average number of tillers per plant by microhabitat in September 2019 did not follow the same order among microhabitats as overall average plant height (Figure 2). Plants transplanted near oaks had on average the lowest number of tillers (20.10 ± 20.90 SD). Plants in open areas and near palms had an intermediate number of tillers and there was no evidence of clear difference between these two microhabitats (34.43 ± 29.37 SD and 40.31 ± 60.70 SD, respectively). Individuals transplanted under pines had on average the highest number of tillers (59.06 ± 65.05 SD) among all the microhabitats. Plants had more tillers in ridge 2 than in ridges 3 and 1 (ridge 1: 27.67 ± 28.66 SD, ridge 2: 50.46 ± 59.25, ridge 3: 32.33 ± 44.44 SD). Number of tillers had a quadratic function with plant height among these plants (Figure 2) with plants reaching an asymptotic number of tillers (Figure 2). Allometric change was different among habitats. For example, plants translocated near oaks developed the largest average height and the lowest average number of tillers while plants translocated to open habitats developed an intermediate average of number of tillers but the lowest average height (Figure 2).

The prescribed burn in 2020 was patchy and heterogeneous among ridges, causing approximately only a quarter of the located plants to reproduce after the fire (34/133). Variation in probability of reproduction was most likely explained by the model including the effects of plant height, microhabitat, ridge, and relative elevation (Table 2). Taller plants had a higher probability of reproduction in all microhabitats (Table 2 and Figure 4). Probability of reproduction was lowest among plants under the canopy of oaks, intermediate for plants in open habitats

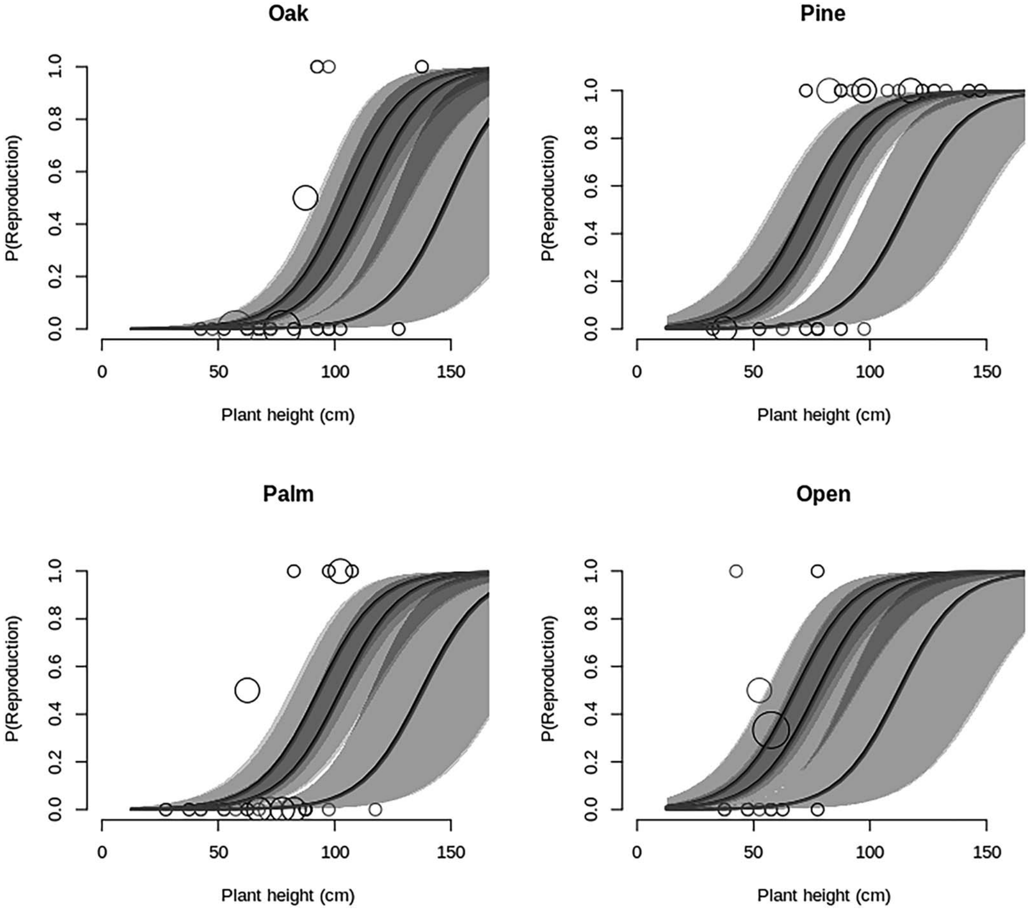

Figure 4.—Probability of reproduction of translocated plants in November 2020 as a function of plant height, microhabitat, and ridge. The size of the circles conveys the relative sample size by height class (binned arbitrarily). Polygons indicate 95% credibility intervals of the predicted mean probability of reproduction posterior by treatment combination.

and near palms, and highest under pines (0.13 under the canopy of oaks, 0.19 near palms, 0.20 in open areas, and 0.49 under the canopy of pines; Figure 4). Fewer plants reproduced in low elevations than high elevations (20% vs. 28%, respectively). There was large variation in probability of reproduction among ridges with ridge 3, the least affected by the fire, having very few reproductive individuals (ridge 1: 25%; ridge 2: 41%; and ridge 3: 3%).

Number of fruiting stalks per plant increased with height and number of tillers and varied among microhabitats, ridges, and relative elevations (Table 2, Figure 5). Fruiting stalks were more numerous in plants under pines. Plants under oaks and near palms had an intermediate number of reproductive stalks, and those in the open habitats had the fewest. Plants in ridge 3 and those in low elevation had the fewest reproductive stalks. Number of caryopsides per stalk increased with height and number of tillers and varied among microhabitats, ridges, and relative elevations (Table 2, Figure 6). Caryopsides were more numerous in plants under pines than in oaks. Plants in these two habitats had higher number of caryopsides than plants in open habitat and near palms, but the number of caryopsides per plant in open habitat and near palms increased faster with plant height than plants under pines or near oaks.

Estimates of Reproductive Output

Total modeled estimated production of caryopsides varied by habitat, ridge, and elevation. Posterior estimates of reproductive output (grain yield) of both sets of models, those with both height and number of tillers or with height as the only state variable, usually ranked consistently among habitats, ridges, and elevations. Predicted grain yield was greater in the higher elevations than in the lower elevations (Figure 7). Plants translocated to ridge 2, the one with denser ground cover and more homogeneously burned, had the highest yield, while those translocated to ridge 3, the most sparsely covered and less affected by the 2020 fire, had the lowest yield. In the ridges better burned (1 and 2), plants under pine canopy and in open gaps had higher predicted yield, while plants near oaks had intermediate yields and plants near palms had the lowest yield. Ranking in yield was more consistent with average number of tillers by habitat than with average stalk height by habitat. The model with height as the only state variable projected yield estimates that were slightly biased to lower values, particularly for plants in open and pine habitats, in lower elevations and in the ridges with highest yield (Figure 7).

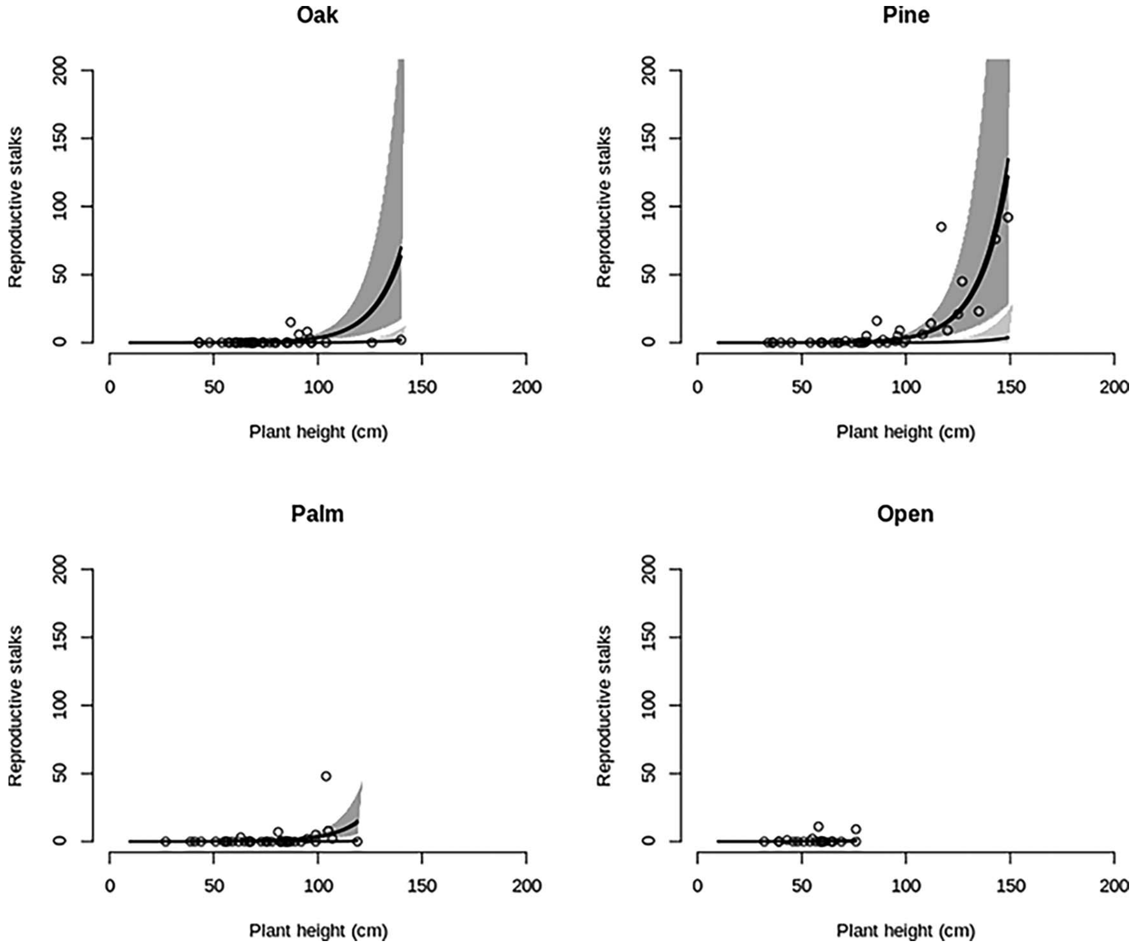

Figure 5.—Number of reproductive stalks by reproductive translocated plants in November 2020 as a function of plant height, microhabitat, and ridge. Polygons indicate 95% credibility intervals of the predicted mean number of stalks posterior by treatment combination. Points indicate observed data.

DISCUSSION

Restoration of pine savanna in the southeastern United States will benefit from better understanding of wiregrass propagation and transplantation techniques (Duever 1989). Direct seeding can be more uncertain, expensive, and time intensive than transplants of plant plugs (Seamon 1998), so effective ways to plant plugs may be essential for wise management of these ecosystems. Our data indicate that characteristics of the target communities are important factors in the success of the restoration attempts involving translocation of plant plugs with *A. beyrichiana*. As has been shown in previous studies, ground cover and relative abundance of different dominant shrubs and trees influenced vital rates of individuals of this species (Mulligan et al. 2002; Baruzzi et al. 2022). Transplanted plants near or under palm and oak canopies had similar survival but grew taller vegetative stalks, probably because of shadow avoidance, than transplanted plants under pines, but had lower reproduction. Presence of pine trees and larger ground cover would likely increase chances of establishment, persistence, and reproduction of *A. beyrichiana.* The positive effects of larger ground cover and pines on the production of grain can at least partially be explained because they increase chances of fire ignition in these habitats. Our results confirm previous studies indicating the critical importance of fire for the post-translocation propagation of *A. beyrichiana* (Seamon et al. 1989; Streng et al. 1993; Outcalt 1994; Shearman et al. 2019; Baruzzi et al. 2022). Previous data indicated that too dense pine stands may not be favorable for wiregrass. Pine densities around 8 m^2 basal area/ha resulted in larger *A. beyrichiana* individuals and greater number of seedling recruits than 16 m^2 or 25 m^2 basal area/ha (Mulligan et al. 2002). Relative position within the ridges affected vital rates of this species, so translocation in relation with these types of variables may affect restoration success. We found that higher elevations in the local ridges were more favorable environments for wiregrass resulting in larger grain production. Previous data suggested relative elevation also influenced vital rate variation in other endemic species in central Florida ridges (Quintana-Ascencio et al. 2018).

Our results indicate that, at least for *A. beyrichiana*, using height as a single state variable in the models produced grain production predictions commensurate with a model that uses

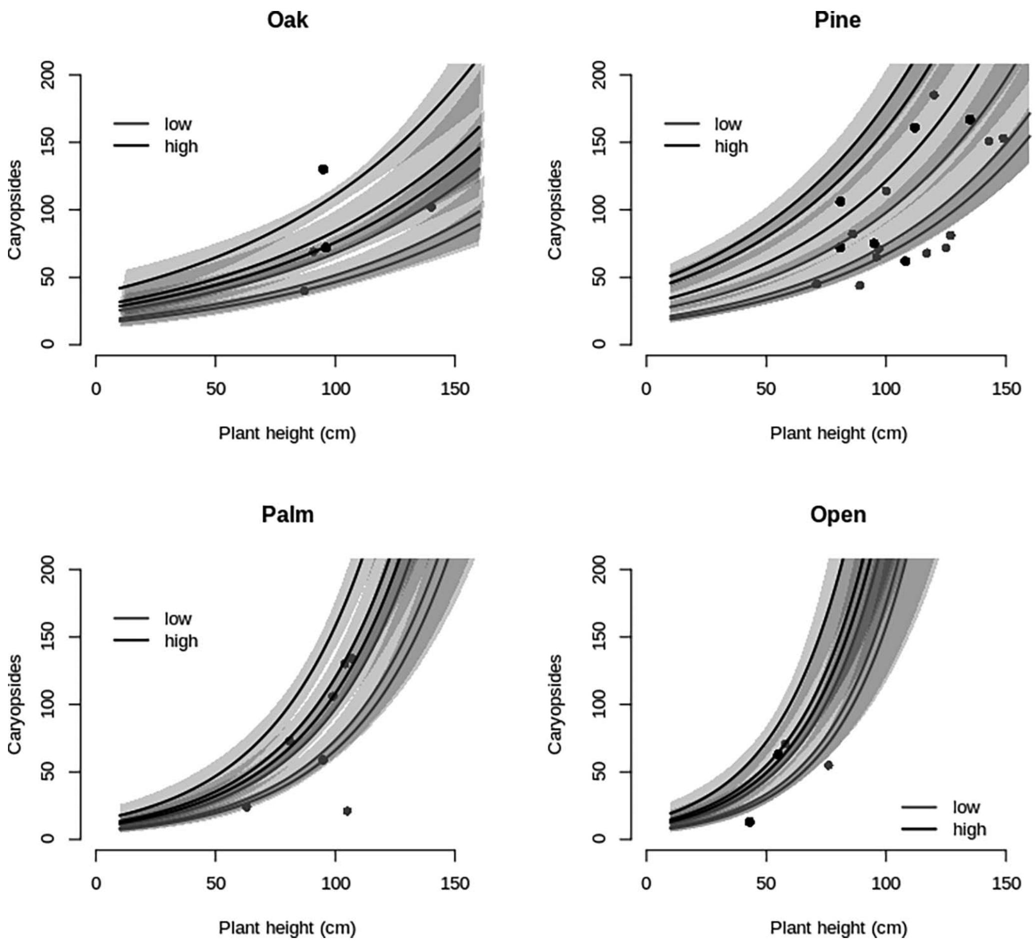

Figure 6.—Number of caryopsides by reproductive stalks in November 2020 as a function of plant height, microhabitat ridge, and elevation. Polygons indicate 95% credibility intervals of the predicted mean number of caryopsides by treatment combination. Points indicate observed data.

height and number of tillers as predictors. Our models also predicted similar grain production projections in plants with different shapes living in contrasting habitats. Plasticity in body shape can at least partially explain the consistent grain production across different habitats. The seminal work of Thompson (1917) superbly describes how the body structure of organisms is shaped by natural selection affecting organism proportions and attributes while influencing species persistence and reproduction. Adaptive plasticity allows organisms to modify their shape to respond to changes in the environment and during development (Sultan 1987). Many organisms respond to environmental variation by simultaneously changing their shape. The shape of organisms is rarely defined in one dimension, thus, measurements in several dimensions are often required to meaningfully characterize plant architecture.

We could not build demographic models because studied plants were a single cohort, and we lacked estimates of recruitment and of the relative frequency of habitats. Our analyses and models convey robust predictions of grain yield allowing control of many confounding variables by standardizing plant origin, age, establishment and planting time, and neighbor herbaceous ground cover. We reduced some pitfalls of translocation studies by using plants surviving transplant shock during the 6 mo post-transplant (Close et al. 2013). We minimized confounding effects due to unintended disturbance by animals attracted to the sampling units immediately after planting. We also accounted for background environmental variation determined by relative elevation and ridge differences. These types of effects due to spatial variation in sampling units are frequently ignored in population models. This standardization allowed us to better concentrate on effects of habitat defined by presence or absence of dominant woody species.

We compared two model specifications predicting grass yield per habitat and location. One used the most likely models of the proposed set, including models for vital rates simultaneously affected by initial height and number of tillers. The second approach was done with models only including plant height as the single state. Height is a commonly used state variable in the literature (summarized in Salguero-Gómez et al. 2015). The integrated model algorithm with height as the sole state variable consistently, but lightly, biased the prediction of grain yield to lower values, particularly for habitats with smaller average plant height, larger average number of tillers, and in locations with largest yields. We argue that, although models with more than one state variable are more difficult to implement than those with simpler specifications, more complex models can be necessary

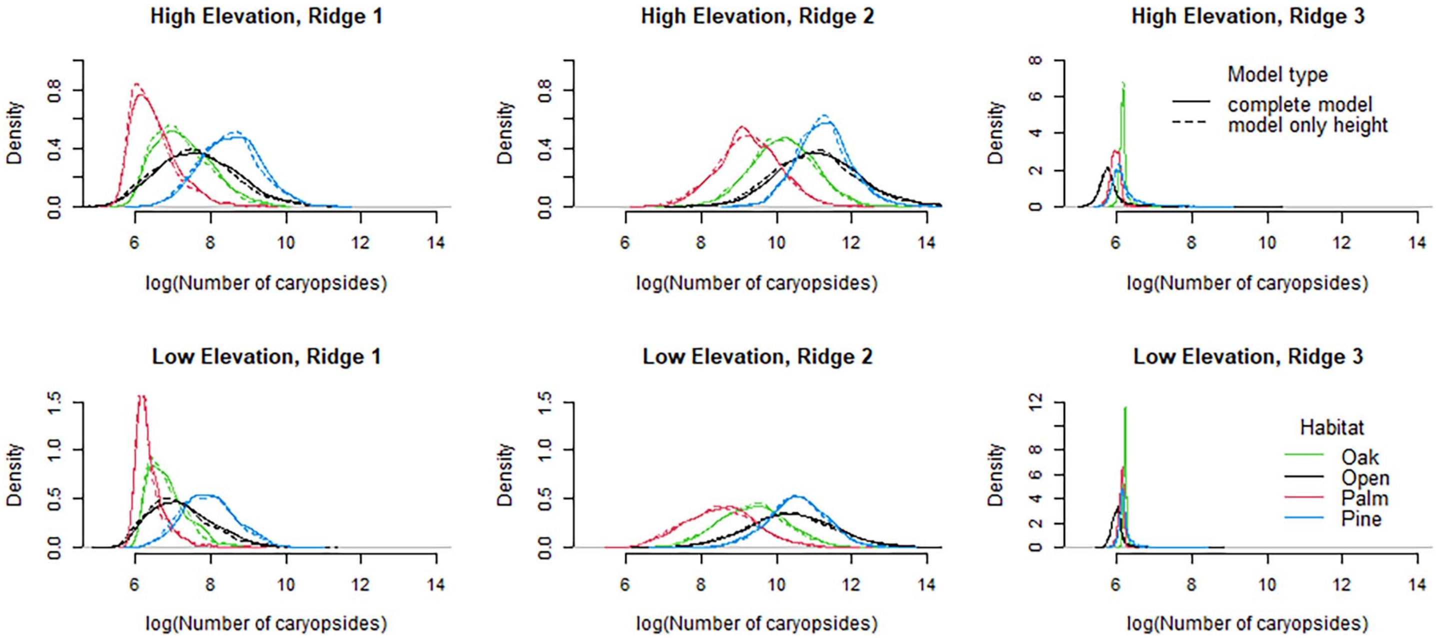

Figure 7.—Density of predicted grain yield posterior distributions (total number caryopsides) of the integrated model with the most likely vital rate model and the model with height as the sole state variable as a function of microhabitat, ridge, and relative elevation position.

to better understand population dynamics when relationships among plant attributes determine plant demographic performance.

ACKNOWLEDGMENTS

We thank the staff at the Lake Wales Ridge State Forest for their continuous support. Their efforts are crucial for the management and conservation of the beautiful ecosystems under their responsibility. Graduate students from the Department of Biology, University of Central Florida, and many kind volunteers helped setting the experiment and collecting the data. This work could not have been completed without the aid of María Cristina Morales Hernández. The Department of Biology at UCF partially funded this research. Comments from Eric S. Menges, Federico López Borghesi, Ian Biazzo, Diego P. Vélez Mora, and two anonymous reviewers improved the manuscript.

Consent for publication: All participants consent to the publication of this information.
Availability of data and material: Data will be deposited for public access once the manuscript is accepted.
Code availability: Code will be deposited for public access upon manuscript acceptance.
Author contributions: PFQA and JN conceived and designed the experiments. All authors conducted field work. PFQA analyzed the data and wrote the manuscript; other authors provided editorial advice.
Conflict of interest: The authors declare that they have no conflict of interest.

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