Rodriguésia 74: e00292023. 2023
http://rodriguesia.jbrj.gov.br
DOI: http://dx.doi.org/10.1590/2175-7860202374086

Ferns and Lycophytes as new challenges

Annual variation in growth and reproduction of three fern species of *Danaea* (Marattiaceae) in the hurricane-prone Luquillo mountains in Puerto Rico

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Abstract
A long-term fern demography study that included measurements of plant traits of three species in the dimorphic genus *Danaea* (1991-2009) was conducted in a rainforest in Puerto Rico beginning two years after the first major hurricane (Hugo) since the early 1930s. Both vegetative (sterile) leaves and spore-bearing (fertile) leaves on tagged plants were monitored repeatedly to document not only differences between two types of leaves, but also patterns of annual variation during a timespan that included the passage in 1998 of hurricane Georges. While all three species had fertile leaf lifespans of six mo or less, *Danaea geniculata* and *D. polymorpha* had much longer mean sterile leaf spans (54.4 mo, 52.7 mo) than *D. nodosa* (33.5 mo). All three species had significant year-to-year trait differences, often with immediate increases after Hurricane Georges levels returning to or below pre-hurricane levels in subsequent years. Long-term observations of annual variation in traits of herbaceous layer ferns that mainly follows the passage of a major hurricane highlight the importance of this study as the frequency and magnitude of hurricanes due to climate change are predicted to increase, although more experimental studies to identify specific causes of these long-term trends are needed.
Key words: dimorphism, interannual variation, plant traits, pteridophyte, tropical.

Resumen
Un estudio demográfico a largo plazo de helechos que incluyó mediciones de rasgos de plantas de tres especies del género dimórfico *Danaea* (1991-2009) se realizó en un bosque lluvioso en Puerto Rico, comenzando dos año después del primer huracán (Hugo) de gran impacto desde principios de los 1930. Se monitorearon repetidamente tanto las hojas vegetativas (estériles) como las hojas productoras de esporas (fértiles) en plantas determinadas, para documentar no solo las diferencias entre los dos tipos de hojas, sino también los patrones de variación anual durante un período de tiempo que incluyó el paso en 1998 del huracán Georges. Aunque las tres especies tenían una vida útil de hojas fértiles de seis meses o menos, *Danaea geniculata* y *D. polymorpha* tenían hojas estériles con una media de vida mucho más larga (54,4 meses, 52,7 meses) que *D. nodosa* (33,5 meses). Las tres especies mostraron diferencias significativas en sus rasgos característicos de un año a otro, a menudo con aumentos inmediatos después del paso del huracán Georges, volviendo a niveles similares o inferiores a los previos al paso del huracán en años posteriores. Las observaciones a largo plazo de la variación anual en los rasgos de helechos de la capa herbácea, tras el paso de un huracán de mayor impacto, resaltan la importancia de este tipo de estudio, ya que se predice un aumento en la frecuencia y la magnitud de los huracanes debido al cambio climático. Se necesitan más estudios experimentales para identificar causas específicas de estas tendencias a largo plazo.
Palabras clave: dimorfismo, variación interanual, rasgos de la planta, pteridofitos, tropical.

See supplementary material at <https://doi.org/10.6084/m9.figshare.24431293.v1>

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Introduction

Ferns are often very common components of a rainforest understory (Royo *et al*. 2011) but like much of the herbaceous layer are overlooked in studies of whole ecosystems (Murphy *et al*. 2016). Part of the reason may be that so little is known about fern life histories in contrast to woody plants. In an effort to address this problem a fern demographic study of about 20 terrestrial and low trunk ferns monitored morphological and functional traits for almost 20 years (1991–2009) in the rainforest of northeast Puerto Rico at the Luquillo Long-term Ecological Research (LTER) site. Although a major hurricane had not passed over the site since 1934, two such storms severely impacted the forested study area in 1989 (Hugo) and 1998 (Georges) providing an opportunity for LTER researchers to assess their effects on numerous species within the ecosystem (Brokaw *et al*. 2012). For example, the 20-year demographic study of the fern *Steiropteris deltoidea* (Sw.) Pic. Serm. [Thelypteridaceae; formerly *Thelypteris deltoidea* (Sw.) Proctor], the most common fern in the research area, led to its inclusion in a multi-researcher large-scale and long-term experiment to evaluate hurricane impacts on the forest (Sharpe & Shiels 2014; Sharpe 2022; Hogan *et al*. 2022). Long-term trends in growth and reproductive characteristics for several other fern species in the Luquillo LTER have been published (Sharpe 1997, 2010a). In this paper I report on interannual variation in leaf traits (lifespan, length) and whole plant traits (leaf production rate, leaf count, height, and annual percent of plants fertile) for three species in the dimorphic fern genus *Danaea*.

The neotropical fern genus *Danaea* belongs to the ancient lineage of the Marattiales dating back more than 400 mya (Nitta *et al*. 2022) with evidence for extant *Danaea* appearing ~220 mya (Lehtonen *et al*. 2020). This group of fern taxa has weathered many changes in climate over that evolutionary timescale and around 50 species of this genus (Christenhusz 2010) continue to be found on rainforest floors throughout the Neotropics. The distribution of species of *Danaea*, especially in the Amazon, has been well-documented in biogeographical studies (*e.g.*, Tuomisto & Ruokolainen 2005; Zuquim *et al*. 2014). The study of the growth and reproductive habits of this ancient group over an 18-year period that included a major hurricane may shed light on fern life history strategies that could insure their survival throughout future challenges of climate change (Hogan *et al*. 2022; Sharpe 2022). Here we report on long-term observations of individuals of the three species [*Danaea geniculata* Raddi, *D. polymorpha* Leprieur, and *D. nodosa* (L.) Sm.] found in the LTER in Puerto Rico at the northern limit of their range. A recent study of *D. geniculata* near the southern limit of its range in Brazil (Farias *et al*. 2018) and an earlier study of *Danaea wendlandii* Rchb.f. in Costa Rica (Sharpe & Jernstedt 1990) have both described growth and reproduction in the genus but at limited timescales of less than two years. A seven-year study of phenological patterns of *Angiopteris somae* (Hayata) Makino & Nemoto, another understory species in the Marattiaceae, was conducted in Taiwan, an island that, like Puerto Rico, is subject to hurricane (typhoon) impacts (Huang *et al*. 2019).

In Puerto Rico individuals of *Danaea* are generally found along riparian slopes and in ravines. These habitats are less common and less accessible than the uplands and ridges of the rainforest where the focus has been on experiments by researchers associated with the Luquillo LTER [*e.g.*, carbon cycling (Halleck *et al*. 2004); hurricane simulation (Sharpe & Shiels 2014)]. In spite of the limited area of their habitat in the LTER, abundance of *Danaea* was in the top quarter of the twenty terrestrial ferns (Portugal-Loayza 2005) in a 16-ha FORESTGEO plot (Thompson *et al*. 2004; Davies *et al*. 2021) and had the highest cover in long-term surveys of herbaceous layer species in a nearby Luquillo LTER watershed (Royo *et al*. 2011).

The main objective of this study was to document growth and reproduction of herbaceous layer ferns of the rainforest in order to detect the extent of annual variation of three species of *Danaea*. Our study focused on selected morphological and functional traits of reproductively mature plants in order to 1) document the extent of temporal differences between morphologically distinct fertile and sterile leaves of these dimorphic species; 2) describe annual variation in traits for individuals observed for as long as 16 years; 3) evaluate the effects of hurricane disturbance on annual variation in traits.

Material and Methods

Study site

The Luquillo Long-term Ecological Research site (LTER) is within and shares the boundary of the entire United States El Yunque National Forest in north-eastern Puerto Rico (18.3215°N, 65.8141°W) (Shiels & González 2014). The forest has a canopy characterized by the presence of Tabanuco trees [*Dacryodes excelsa* Vahl (Burseraceae)]. The fern study included different areas of the LTER in the vicinity of the El Verde Research Area (EVRA) from ridge top to the edge of the Sonadora river and along streams in the Bisley Experimental Watersheds. Study areas were located at approximately 400 m elevation and understory plants, including ferns, are listed in Areces Berazain *et al.* (2015) and in Royo *et al*. (2011). Understory temperatures at two meters above the ground within the EVRA have been recorded since 1993 (Ramirez 2022) and ranged from 28.9±1.90 °C in 1993 to 26.3±1.75 °C in 2004 (Fig. 1a) with significant differences among years (KWA: F = 512.2, P = 0.0000). The site has an aseasonal everwet climate (Hogan *et al*. 2022). Mean annual rainfall, also recorded in the EVRA (Ramirez 2023) was available for the 18 years of *Danaea* monitoring (Fig. 1b) was 3,584±912 mm with a low of 1,404 mm in 1994 and a high of 5,293 mm in 1998 with significant differences among years (KWA: F = 209.3, P = 0.0000). Although major hurricanes had not occurred since Hurricane Cyprian in 1934, Hurricane Hugo (Category 5, September 18, 1989) passed over three years before our study began and Georges (Category 4, September 23, 1998) during the study had a major impact on the fern research areas (Zimmerman *et al*. 2021).

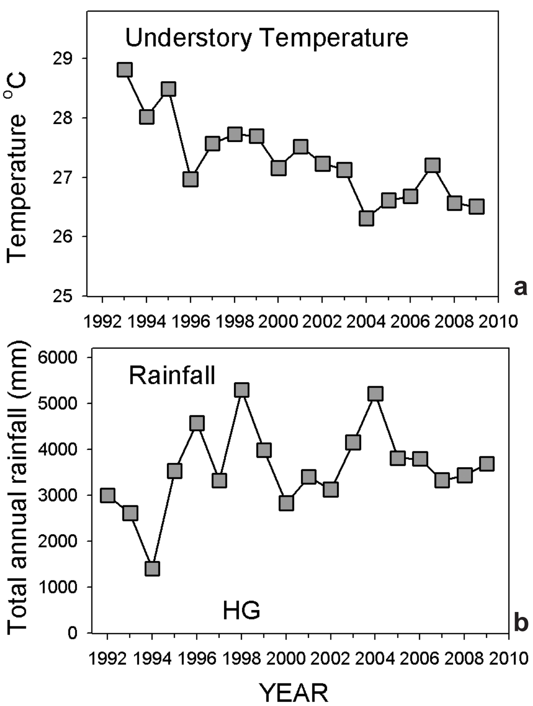

Figure 1 – Annual temperature and rainfall in El Verde Research Area, Luquillo Experimental Forest for the years of the study (1992-2009) – a. mean maximum forest understory temperatures two m above the ground (Ramirez 2022); b. total annual rainfall (Ramirez 2023).

Species

Although there are six species of *Danaea* in Puerto Rico (Proctor 1989), only three are found in the island's northeast rainforests and were included in this study: *Danaea geniculata*, *D. polymorpha* and *D. nodosa* (Fig. 2). The first two species had been called *D. elliptica* variant 1 and 2 by Proctor (1989). In recent taxonomic work Christenhusz & Tuomisto (2006) have retired the name *D. elliptica* Sm. (found to be a synonym for another species of *Danaea*) and assigned variant 1 to the *D. geniculata* and variant 2 to *D. polymorpha*. Our study began before the taxonomic revisions were made, but because of their strikingly different morphology, these two species were monitored separately. Although crowns are similar in height, leaflet pair counts for *D. geniculata* (4–6) and *D. polymorpha* (3–4), and the elongated terminal leaflet of *D. polymorpha* and its vertical rhizome (ca. 30 cm. in the study sample) easily differentiate these two species. Scattered individuals of *D. geniculata* were found on mid- to lower riparian slopes. *Danaea polymorpha*, though locally common elsewhere in Puerto Rico, was found at only one streamside location in the research area. *Danaea nodosa* was much more common (Portugal-Loayza 2005), generally growing in lower riparian slope habitats and occasionally occurring on midstream boulders. Leaves of *D. nodosa* are much longer, have at least two to three times as many leaflet pairs and a creeping rhizome. Individuals of the genus *Danaea* in Puerto Rico are terrestrial and strongly dimorphic with dark green sterile leaves and yellow to yellow/green often quite succulent fertile (spore-bearing) leaves (Fig. 2b; Proctor 1989; Christenhusz 2010). Plants in this genus do not have branching rhizomes. As leaves emerge sequentially and senesce over time they form a rosette that consists of leaves of different ages.

Fern monitoring

Repeated non-destructive observations and measurements of individual ferns began in late 1991 and lasted through early 2010. Plant selection prioritized locations where, if possible, individuals of several fern species could efficiently be measured safely long-term and without damage to either vegetation or substrate. Individuals were added to the study throughout the early years until a representative number of adult-size plants of each species had been included for long-term observation. For *D. geniculata* that occurred in 1994 (n = 19), for *D. polymorpha* in 1992 (n = 6), and for *D. nodosa* in 1995 (n = 63). Plant mortality before 2010 reduced the sample size for long-term study analysis with 10 (53%) lost for *D. geniculata*, one (17%) lost for *D. polymorpha*, and 18 (29%) for *D. nodosa* with overall post-hurricane mortality of 62% mostly caused by tree and branch fall or streamside erosion after Hurricane Georges. Observations of *D. polymorpha* ended in 2000 (9 years) when the site became unavailable to researchers due to the discovery of the presence of endangered Puerto Rican parrots.

Every four months (in early January, May and September) from September 1991 until early January 2001 and then annually through early January 2010 individual plants were monitored during two-week visits to the forest. Only sterile leaves were monitored after January 2001 because leaf lifespans of fertile leaves in these three dimorphic species tended to be shorter than six months, and therefore annual monitoring could not accurately account for their presence or traits measurements. To identify each plant a numbered tag was affixed to the youngest mature leaf with a short length of plastic-coated wire, with wire color used to identify each leaf throughout its lifetime. Tags were transferred (and replaced if necessary) to a younger leaf at each monitoring session. All leaves were identified as sterile (vegetative) or fertile (spore-bearing) and whole unbroken leaves had the petiole and lamina measured and summed to obtain leaf length. Leaf lifespans begin in the monitoring period that the leaf matures (Kikuzawa & Lechowicz 2011) and therefore calculations do not include the expansion phase. Leaf lifespan ended with loss of a leaf. Plant leaf count (number of leaves in crown) and plant height (maximum

Figure 2 – Morphology and leaf types of study species: a. *Danaea geniculata* crown of sterile leaves; b. *D. geniculata* fertile leaf above sterile leaves; c. *D. polymorpha* sterile leaf and trunk; d. *D. nodosa* sterile leaves on several plants.

leaf length) were summarized for each plant from the leaf observations. Individuals were then chosen and included in this long-term analysis if they were reproductively mature as indicated by production of at least one fertile leaf during the study. Plant fertility is the percentage of the reproductively mature sample that produced spores during a given year. For additional details on monitoring protocols see Sharpe (1997, 2010a, 2022).

Data analysis

Measurements of traits of individual plants were averaged for each monitoring period prior to the analysis of annual variation. Repeated-measures one-way ANOVA (plant ID as subject and year as within subject factor) was used to compare interannual differences in plant traits (leaf production, plant height and plant count). When leaf traits (leaf length, lifespans, and often plant heights) had missing cases then a general ANOVA was used with ID and year as variables. All annual mean differences detected by ANOVAs were evaluated with a Least Significant Difference (LSD) pairwise comparison test. Paired t-tests were used to compare annual means for fertile and sterile traits for each species. Means ± standard deviation (SD) are reported throughout. Annual N, mean and standard deviation for points on the graphs in Figures 3 and 4 as well as an LSD year mean comparisons and fertile/sterile ratios (F/S) are listed in Appendix S1 (available on supplementary material <https://doi.org/10.6084/m9.figshare.24431293.v1>). Data were analyzed using Statistix 10 software (Analytical Software 2022). Three publicly available Luquillo LTER datasets were used in this report with URLs listed in Reference section: Fern demography data (Sharpe 2015), El Verde understory mean maximum temperatures (Ramirez 2022), and El Verde precipitation (Ramirez 2023).

Results

Fertile/Sterile leaf dimorphism

Low ratios of mean fertile and sterile traits (F/S) for each species (Tabs. 1-2) highlight different degrees of dimorphism for each trait (Figs. 3-4). There were large differences in leaf lifespans with fertile leaves having only about a tenth the longevity of sterile leaves for all three species (Tab. 1 a1, b1, c1) during the early years of the study when the short-lived fertile leaves were observed (Fig. 3). While mean fertile and sterile leaf lengths (F/S: 1.06–1.14) were about the same (Tab. 1 a2, b2, c2), petiole measurements of fertile

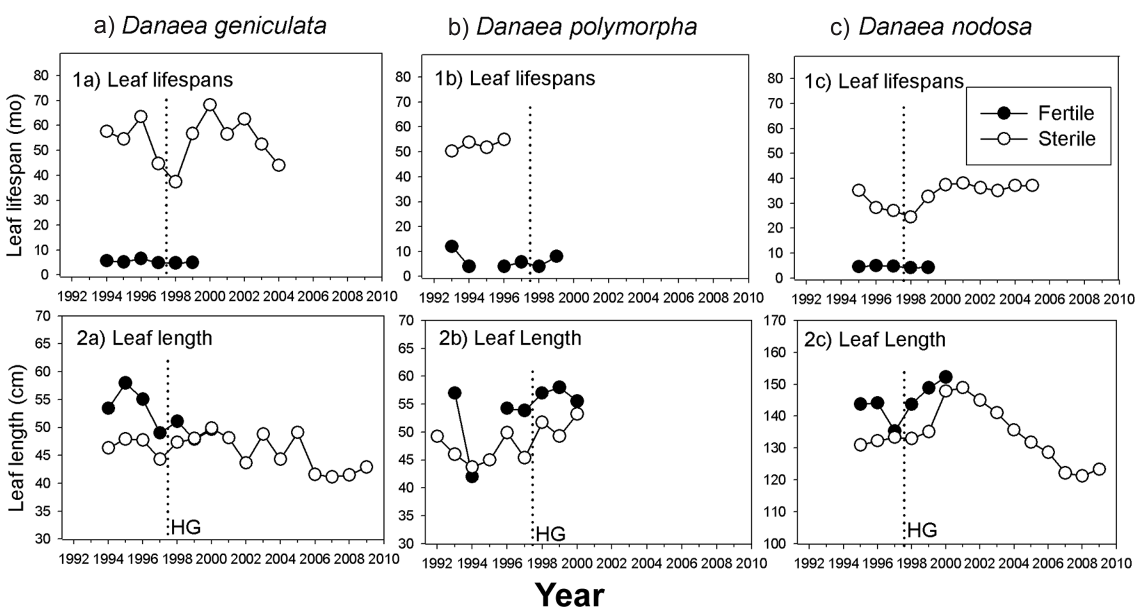

Figure 3 – Annual variation in two leaf traits of three species of *Danaea* in the El Verde Research Area. The vertical dashed line separates the observation timespans before and after Hurricane Georges (HG) in 1998. See Table 1 for summaries and Appendix S1 (available on supplementary material <https://doi.org/10.6084/m9.figshare.24431293.v1>) for yearly means±standard deviations and statistical results.

leaves were 48% greater than the petiole lengths of sterile leaves for *D. geniculata*, 25% greater for *D. polymorpha* and 20% greater for *D. nodosa.* Mean fertile leaf production rates for *D. geniculata* were about half that of the sterile leaf production rate (F/S: 0.52) while with F/S ratios for *D. polymorpha* (F/S: 0.22) and *D. nodosa* (F/S: 0.28), about a quarter of the leaves produced were fertile (Tab. 2 a1, b1, c1). Very low F/S ratios characterized mean plant leaf count with fertile leaves comprising only 7% of the leaves in the crown (Tab. 2 a2, b2, c2).

Annual variation

Three factors complicated the analysis of annual variation that had not been foreseen when observations and measuring of three *Danaea* species began in 1991: 1) reduced study length for *D. polymorpha*, 2) short lifespans of fertile leaves and 3) passage of Hurricane Georges in 1998. 1) Not only could few specimens of *D. polymorpha* be found, but the long-term observation interval was limited to 9 years when the habitat requirements of the endangered species

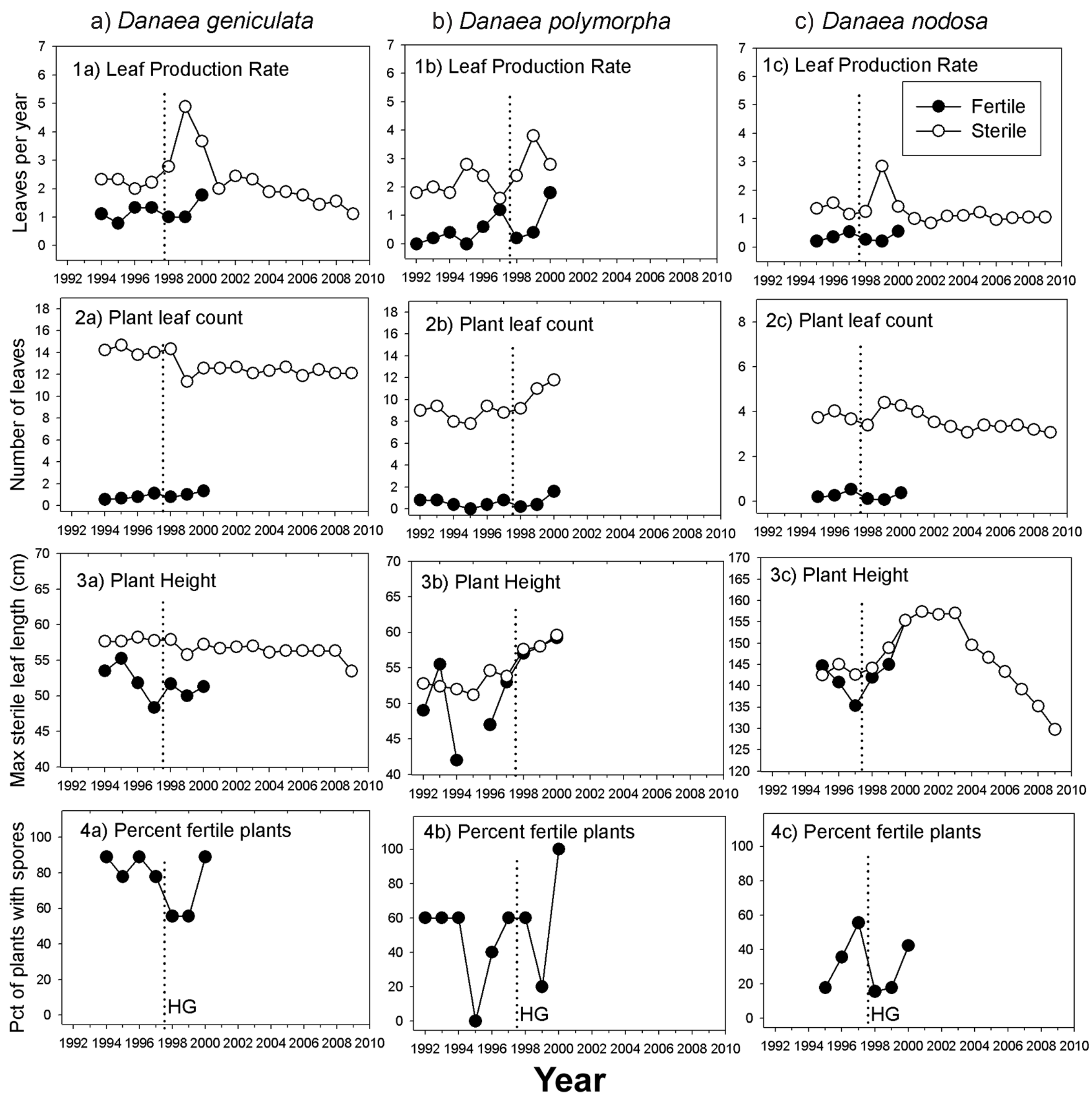

Figure 4 – Annual variation in four plant traits of three species of *Danaea* in the El Verde Research Area. The vertical dashed line separates the observation timespans before and after Hurricane Georges (HG) in 1998. See Table 2 for summaries and Appendix S1 (available on supplementary material <https://doi.org/10.6084/m9.figshare.24431293.v1>) for yearly means±standard deviations and statistical results.

Table 1 – Leaf trait comparisons among three dimorphic understory species of *Danaea* [(N) = number of plants] within the Luquillo Experimental Forest in Puerto Rico. Both leaf traits represent observations of whole unbroken leaves. Means and standard deviation for N years, differences among years [Repeated measures ANOVA (F,P)], differences between leaf types through 2000 [Paired T-test, (T, P)] and Fertile (spore-bearing)/Sterile (vegetative) leaf ratio. Significant differences (p-values < 0.0500) among years and between leaf types (see Fig. 3) are marked with *** in contrast to non-significant differences (NS).

			Interannual		Leaf Type		F/S
	N	**Mean±SD**	**F**	**P**	**T**	**P**	**Ratio**
a. *Danaea geniculata* (9)							
1. Leaf lifespan (mo)							
Fertile	6	5.4±0.68	0.70	0.6242 NS	-12.7	0.0001 ***	0.10
Sterile	11	54.4±9.26	2.23	0.0212 ***			
2. Leaf length (cm)							
Fertile	7	52.0±3.65	0.96	0.4649 NS	-3.16	0.0196 ***	1.14
Sterile	16	45.8±2.99	1.87	0.0340 ***			
b. *Danaea polymorpha* (5)							
1. Leaf lifespan (mo)							
Fertile	6	6.3±3.21	1.44	0.5567 NS	-89.03	0.0072 ***	0.14
Sterile	4	52.7±2.11	0.29	0.8352 NS			
2. Leaf length (cm)							
Fertile	7	53.9±5.48	0.69	0.6821 NS	2.84	0.3630 NS	1.06
Sterile	9	48.2±3.29	1.65	0.1495 NS			
c. *Danaea nodosa* (45)							
1. Leaf lifespan (mo)							
Fertile	5	4.5±0.34	0.38	0.8188 NS	-12.85	0.0002 ***	0.14
Sterile	11	33.5±4.75	8.44	0.0000 ***			
2. Leaf length (cm)							
Fertile	6	144.68±5.73	0.54	0.0320 ***	4.66	0.0055 ***	1.08
Sterile	15	134.01±8.68	8.36	0.0000 ***			

took precedence, and the site was dropped. Very small sample sizes resulted in significant annual variation in only two of the five traits of *D. polymorpha* (Tab. 2 b1, leaf production rate and b3, sterile plant height). 2) As monitoring initially proceeded at 4-month intervals, it became obvious that short mean lifespans of fertile leaves [4.5 – 6.3 (Tab. 1)] would prevent the observation of reproductive function after 2000 when annual monitoring would begin. However, comparisons of fertile and sterile traits of *Danaea* were possible for the first six to nine years of the study (depending on the species), longer than for most fern demographic studies. 3) Hurricane Georges in 1998 (highlighted in Figs. 3-4; Appendix S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.24431293.v1>) resulted in observations in a very different forest before (up to 5 years) and after (three years for fertile traits and 12 years for sterile traits) a major disturbance (Appendix S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.24431293.v1>). Therefore different environmental conditions underlie the patterns of annual variation (Figs. 3; 4). While fertile leaf lifespans were short with means representing only the year of emergence, sterile leaf lifespans were long enough to be affected by different conditions over several years resulting in premature hurricane mortality for those that had emerged before the hurricane in 1997 for *D. geniculata* (Fig. 3 1a) and in 1996 and 1997 for *D. nodosa* (Fig. 3 1c).

Table 2 – Plant trait comparisons among three dimorphic understory species of *Danaea* [(N) = number of plants] within the Luquillo Experimental Forest in Puerto Rico. Means and standard deviation for N years, differences among years [Repeated measures ANOVA (F, P)], except when no usable cases (ANOVA, NS[a]), differences between leaf types through 2000 [Paired T-test, (T, P)] and Fertile (spore-bearing)/Sterile (vegetative) leaf ratio. Significant differences (p-values < 0.0500) among years and between leaf types (see Fig. 4) are marked with *** in contrast to non-significant differences (NS).

			Interannual		Leaf Type		F/S
	N	**Mean±SD**	**F**	**P**	**T**	**P**	**Ratio**
a. *Danaea geniculata* (9)							
1. Leaf production Rate (-yr)							
Fertile	7	1.19±0.325	1.39	0.2375 NS	-4.22	0.0056 ***	0.52
Sterile	16	2.29±0.906	6.69	0.0000 ***			
2. Plant leaf count							
Fertile	7	0.89±0.272	0.95	0.4694 NS	-24.46	0.0000 ***	0.07
Sterile	16	12.86±1.003	1.37	0.1752 NS			
3. Plant height (cm)							
Fertile	7	51.70±2.245	1.38	0.2814 NS[a]	-2.29	0.0620 NS	0.91
Sterile	16	56.73±1.154	0.65	0.8304 NS			
4. Percent plants fertile (-yr)							
	7	76.2%±14.95	N/A		N/A		N/A
b. *Danaea polymorpha* (5)							
1. Leaf production rate (-yr)							
Fertile	9	0.53±0.600	3.19	0.0089 ***	-6.16	0.0003 ***	0.22
Sterile	9	2.38±0.689	3.36	0.0066 ***			
2. Plant leaf count							
Fertile	9	0.60±0.469	1.55	0.1804 NS	-27.30	0.0000 ***	0.06
Sterile	9	9.38±1.294	9.47	0.0000 NS			
3. Plant height (cm)							
Fertile	8	52.59±6.070	0.79	0.6776 NS[a]	-1.74	0.1422 NS	0.93
Sterile	9	54.67±3.012	2.93	0.0142 ***			
4. Percent plants fertile (-yr)							
	9	48.9%±28.48	N/A		N/A		N/A
c. *Danaea nodosa* (45)							
1. Leaf production Rate (-yr)							
Fertile	6	0.35±0.160	4.12	0.0013 ***	-4.25	0.0081 ***	0.28
Sterile	15	1.26±0.477	20.08	0.0000 ***			
2. Plant leaf count							
Fertile	6	0.26±0.174	6.80	0.0000 ***	-20.59	0.0000 ***	0.07
Sterile	15	3.59±0.417	6.64	0.0000 ***			
3. Plant height (cm)							
Fertile	6	143.9±6.62	6.39	0.0006 ***[a]	-1.88	0.1192 NS	0.98
Sterile	16	146.2±8.17	10.72	0.0000 ***			
4. Percent plants fertile (-yr)							
	7	31.0%±26.33	N/A		N/A		N/A

The overall mean for sterile leaf lifespan for *D. geniculata* was 54.4 mo (Tab. 1 a1) but the highest mean pre-hurricane was 63.5 mo (1996) and post-hurricane was 68.3 mo (2000) while at the end it was only 44.0 mo (2005; Fig. 3 1a). For *D. geniculata* there were pre-hurricane decreases in fertile leaf length (Fig. 3 2a) and plant height (Fig. 4 3a) with a post-hurricane increase of 20% in fertile leaf production (Fig. 4 1a). Sterile leaf production for *D. geniculata* (Fig. 4 1a) increased 120% one year after the hurricane but declined to less than 50% of the pre-hurricane rate long-term. Other sterile traits of this species showed little post hurricane variation [plant leaf count (Fig. 4 2a), plant height (Fig. 4 3a)]. Fertile leaf production rates of *D. polymorpha* were rising before the hurricane while sterile leaf production was dropping, a pattern which reversed post-hurricane with a 75% increase in sterile leaf production from 1.8^{-yr} to 2.8^{-yr} (Fig. 4 1b; Appendix S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.24431293.v1>).

Most traits measured for *D. nodosa* had significant annual variation (Tabs. 1c; 2c) with the pattern typically showing a short period of increase after the hurricane (*e.g.*, leaf length, Fig. 3 2c) followed by gradual decline (*e.g.*, sterile leaf length (Fig. 3 2c), sterile leaf production (Fig. 4 1c) and plant height (Fig. 4 3c). By the end of the study (2009) all four of these trait means were 8% to 16% lower than pre-hurricane means. The most complex pattern of annual variation (revealed by pairwise comparisons) was for sterile plant height for *D. nodosa* (Fig. 4 3c) with seven groups having different means (Appendix S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.24431293.v1>) with pre-hurricane means of 142.5–145.0 cm (1995–1997) midway between post-hurricane highs of 155.3–157.1 cm (2000–2003) and a low of 129.8 cm in the last year of the study (2009).

Discussion

Dimorphism

Species of *Danaea* can be classified as dimorphic based on the leaf morphology alone (Fig. 2) but Wagner & Wagner (1977) identify a number of other characteristics that can differ between sterile and fertile leaves that have been included in our study such as leaf lifespan and phenology. Although leaf lengths of the fertile leaves were only slightly longer than sterile leaves, longer petioles raised the fertile leaflets presumably for more optimal spore dispersal (Wagner & Wagner 1977). Mean fertile leaf lifespans were all six mo or less, but the mean sterile leaf lifespans were almost 10 times that with an annual mean maximum of 68.5 mo in 2000. Older sterile leaves also exhibited a dense covering of epiphylls although the timing of the appearance and growth of these obviously diverse communities were not noted. Identification of the lichen component has been a topic of study by Farias *et al*. (2021) in Brazil who found that *D. geniculata* and *D. nodosa* each hosted one species of foliicolous lichen [*Porina epiphylla* (Fée) Fée (Trichotheliaceae) and a *Tricharia* species (Gomphillaceae), respectively]. However, Cerón-Carpio *et al*. (2023) found that *D. nodosa* sterile leaves, with a mean lifespan of 30.7 mo in a rainforest in Mexico (compared to 33.5 mo in this study) hosted 27 species of foliicolous lichens, three or more times as many as the other seven fern species they surveyed. Low ratios of fertile to sterile lifespans in all three *Danaea species* corresponded to other dimorphic species reviewed by Mehltreter & Sharpe (2013) including the congeneric *D. wendlandii* in Costa Rica (Sharpe & Jernstedt 1997). Other dimorphic ferns in the Luquillo LTER [*Meniscium angustifolium* Humb. & Bonpl. *ex* Willd. (Thelypteridaceae) (Sharpe 1997); *Elaphoglossum latifolium* (Sw.) J.Sm. and *E. simplex* (Sw.) Schott (Dryopteridaceae) (Sharpe 2010a] have similar patterns of differences between sterile and fertile lifespans.

In a comparison of ecological traits Watkins Jr. *et al*. (2016) noted that tropical dimorphic species produce fewer fertile leaves than monomorphic species and comprise a lower percentage of plant leaf count, and these growth patterns that were characteristic of all three *Danaea* species in this study. In contrast, at the start of a simultaneous study in the LTER of the monomorphic *S. deltoidea* fertile leaf production rates were 12% higher and percentage of fertile leave in the crown 81% higher than for sterile leaves (Sharpe 2022).

An intra-annual phenological study of *D. geniculata* in Pernambuco, Brazil (Farias *et al*. 2018) lasting 18 mo provides an opportunity to compare the overall results with a population near the southern end of its distribution range (Tab. 3). Length of both fertile and sterile leaves are much longer in Brazil while lifespans of fertile leaves are about the same and sterile leaves much shorter. Fertile leaf production rates were lower in Puerto Rico and sterile leaf production higher.

Table 3 – Comparison of traits of *Danaea geniculata* in the Luquillo Experimental Forest, Puerto Rico (Tabs. 1 and 2, this study) and in Pernambuco Brazil (Farias *et al.* 2018, with monthly leaf production rates converted to yearly). F = Fertile; S = Sterile. Brazil/PR Ratio between Brazil and Puerto Rico studies.

	Puerto Rico			Brazil			Brazil / PR	
	F	S	F/S	F	S	F/S	F	S
Max length (cm)	51.70	56.73	0.91	85.04	80.73	1.05	1.64	1.42
Lifespan (mo)	5.40	54.40	0.10	5.60	24.7	0.23	1.04	0.45
Leaf production	1.19	2.29	0.52	0.72	2.72	0.19	0.61	1.19
Plant leaf count	0.89	12.86	0.07	0.45	7.56	0.06	0.51	0.59

Plant leaf count overall is greater in Puerto Rico but the ratio of fertile to sterile leaves is about the same for the two locations. There are several potential reasons for such differences that need further exploration. For example, the two studies took place in very different environments with the Brazilian study conducted in a forest at higher elevation (lower montane) with a lower and non-overlapping temperature regime (21.7 °C to 25 °C) compared to the lowland rainforest in Puerto Rico (25.4 °C to 28.5 °C). The Brazil site has distinct wet and dry seasons with annual means of 1,103 mm (Farias *et al*. 2018) in contrast to the 3,584 mm annual mean and aseasonal pattern of precipitation for Puerto Rico during this study. Drought stress during the dry season could also explain the shorter sterile lifespans of *D. geniculata* in Brazil, a pattern seen in *M. angustifolium* at the Puerto Rico site after a drought year in 1994 (Sharpe 1997). Other comparisons of results for the same species from different sites have shown similarities and differences in a few studies of other understory ferns [*e.g.*, several species in the different environments of northeast and southeast Taiwan (Lee *et al*. 2009, 2016); *Acrostichum danaeafolium* Langsd. & Fisch. (Pteridaceae) in Mexico (Mehltreter & Palacios-Rios 2003) and in Puerto Rico (Sharpe 2010b)].

Annual variation

When observations of *Danaea* began in September 1991 it was just two years after the first major hurricane (Hugo) since the early 1930s had had devastating impacts on the forest including major loss of the existing canopy (Zimmerman *et al*. 2021) with another major hurricane (Georges) occurring during the study in 1998. Structural and functional responses of the Luquillo LTER research forest following Hurricane Hugo have been described by Zimmerman *et al*. (1996) and after Hurricane Georges by Ostertag *et al*. (2005) and have also been described in detail for various abiotic and biotic elements of the terrestrial ecosystem for both hurricanes by Brokaw *et al*. (2012). To summarize: during each hurricane, forest biomass was reduced by about 50% as high winds snapped branches and trunks resulting in higher light levels at the forest floor where woody and leafy debris were deposited. Comita *et al.* (2009) reported a 400% increase in light levels after Hurricane Georges and Van Beusekom *et al*. (2020) estimated that solar radiation levels took approximately 8–9 years to recover. Tree damage was highest on ridges but also in the valley habitats of *Danaea.* Higher light levels on the forest floor post-hurricane stimulated tree sprouting, recruitment and plant growth and therefore many of the features of the forest returned to near pre-hurricane conditions within about five years (Hugo 1994; Georges 2003) while forest canopy re-establishment and associated lower understory light levels after Hugo was considered nearly complete after around 18 years in 2007 (Brokaw *et al*. 2012).

Interannual differences of several traits of the three *Danaea* species appear to be 1) a generally rapid and positive response to Hurricane Georges (1998) with a fast return to or below pre-hurricane levels and 2) an often negative difference between the first and last years of the study. Sterile leaf production reached a maximum in 1999 just one year after the hurricane for all three *Danaea* species followed by an increase in fertile leaf production a year later. At the same time, a different pattern of response to Hurricane Georges was exhibited by the monomorphic fern *S. deltoidea* (Sharpe 2022). *Steiropteris deltoidea* experienced a rapid increase in fertile leaf production after Hurricane Georges but no increase in sterile leaf production. Perhaps a monomorphic fern like *S. deltoidea* can more rapidly develop a modified photosynthetic structure (leaf) for spore production than a dimorphic fern can produce an entirely different reproductive structure (sporophyll). This is a question that can perhaps be answered with molecular studies (*e.g.*, Vasco & Ambrose 2020) of leaf and sporophyll development in dimorphic ferns. A long-term (2002–2009) multi-researcher experimental simulation of a hurricane in which canopy was removed was conducted in the LTER upland of the *Danaea* study sites (Sharpe & Shiels 2014). In the hurricane simulation experiment rapid and positive growth responses by several organisms (including understory ferns) were shown to be triggered by the sudden post-hurricane increase in their light environment (Zhu *et al*. 2016) and secondarily by soil moisture changes (Van Beusekom *et al*. 2020; Hogan *et al*. 2022).

End-of-study means for sterile traits of *D. geniculata* and *D. nodosa* were significantly lower than in first monitoring year. For example, for sterile plant leaf count for *D. geniculata*, the high mean was 17% lower in 2009 than in 1994. A gradual long-term decline in temperature and greater annual variation in precipitation were both observed within the research forest at 2 m above the ground (Ramirez 2022, 2023). Willig & Presley (2022) conducted herbaceous layer snail monitoring at the same time as the fern study and have suggested that the declining trend in understory temperatures (Fig. 1a) could be interpreted as the result of the gradual increase in shading of the understory in the 8-9 years perhaps signaling the end of Hugo's influence on forest floor communities (Brokaw *et al*. 2021). Therefore, it is possible that the lower means for leaf production, plant leaf count and height near the end of the fern study (2009) may represent a return to growth and reproduction patterns characteristic of a low-light undisturbed forest that may prevailed before Hurricane Hugo.

Not all multi-year studies of understory ferns in hurricane (typhoon) prone forests have detected significant annual variation in leaf production or other traits (*e.g.*, Lee *et al*. 2009, 2016; Huang *et al*. 2019). For example, typhoons of the same magnitude as Hurricanes Hugo and Georges are common in a research forest in subtropical Taiwan. In a seven-year demographic study of the monomorphic *Angiopteris somae* at least one category 4 hurricane (among a total of 11) occurred in each of the last five years of the study (Huang *et al*. 2019). Although leaf production was 27% higher in typhoon years than non-typhoon years, this result was not significant, nor were there significant differences in crown size (plant leaf count). These results were unexpected in light of hurricane responses of *Danaea* and other ferns in the Luquillo LTER (Sharpe 2010a, 2022). Hogan *et al*. (2018) suggest that these two forests are structurally different with an uneven canopy in Puerto Rico resulting from infrequent hurricane damage and a more even canopy at the Taiwan study site resulting from a much higher frequency of typhoon pruning the emergent tree canopies over time. Thus it would be mortality and branch fall from damaged canopy emergents that cause the more significant effects on the environment and stronger responses by the understory community in Puerto Rico. Such geographical comparisons of long-term studies are especially important with changing patterns of hurricane frequency expected worldwide due to climate change (Sharpe 2019; Jones & Driscoll 2022).

Because of the extreme dimorphism in *Danaea* with very different vegetative leaves and spore-bearing reproductive structures, it has been possible to identify very different temporal patterns in reproductive and vegetative function. Fertile leaf lifespans of less than a year, and low production rates combined with very specific seasonality patterns noted in this and several other phenological studies of ferns can contribute to the reproductive function of a fern species being overlooked or ignored, but long-term research plans that take those challenges into account will benefit from a better understanding of temporal variation in fern reproduction and recruitment. Long-term studies of annual variation are going to be more important as changes in hurricane cycles accompany climate change in order to predict reproductive potential in response to drought and hurricanes. This study that actually set out to document limits on variation in an undisturbed environment ended up providing valuable insights into disturbance responses, but not definitively meeting the original goal. We are only just beginning to be able to generalize about variability in timing of fertile and sterile leaf production rates that are basic to predicting recruitment and maintenance of viable populations in the understory. The design of a long-term fern monitoring project, especially one including dimorphic ferns would benefit from an initial year of monitoring to ensure that the timing of annual observations results in optimal data collection for both vegetative and reproductive function.

Therefore, ideal locations would be any of the sites listed in the review of fern phenological studies by Lee *et al*. (2018) where such valuable short-term phenological information is already available. A thorough understanding of the volatility (or lack thereof) in pre-study years would also provide necessary context for planning. Comparing observations from studies in different locations in the tropics could not only add to essential ecological knowledge of tropical fern life histories, but also elicit taxonomic insights from studies of species across their distribution range as these ranges change with climate change. Such research would benefit from being conducted in well-established research locations such as the Luquillo LTER where long-term studies are encouraged, and infrastructure can facilitate an investment in month-to-month monitoring for at least a year followed by annual observations. There are now many such research centers world-wide where the key to success in the future will be to include long-term studies of selected organisms (including ferns) in the standard observations of the center itself (like temperature and rainfall) rather than relying on individual researchers. The key to the success of such studies will be spatial and temporal collaboration among sites (Huang *et al*. 2020).

Acknowledgements

For field assistance on the fern demography study, I thank Tapley Bennett, Thomas Bennett, Leslie Finical, Meredith Nash Fossel, Jessie Hopkins, Jude Jardine, Jane McKinney, Henry Minot, Bella Provan, Julie Rea, Kathryn Stack Schwertfeger, Lars Walker and Megan Weaver. This research would not have been possible without the collaborative attitude of all my Luquillo LTER and fern colleagues from around the world and the El Verde field station staff in Puerto Rico. The Luquillo LTER is supported by the following research grants from NSF to the former Institute for Tropical Ecosystem Studies, within the Department of Environmental Sciences at the University of Puerto Rico: BSR-8811902, DEB-9411973, DEB-9705814, DEB-0080538, DEB-0218039, DEB-0620910, DEB-1239764, DEB-1546686, DEB-1831952. Additional support was provided by the University of Puerto Rico.

Data availability statement

In accordance with Open Science communication practices, the authors inform that all data used in this manuscript is publicly available.

As indicated in Data Analysis section, all original data for Luquillo LTER (temp, rainfall, fern study observations) are stored at Environmental Data Initiative.

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Area Editor: Dra. Lana Sylvestre
Received on March 15, 2023. Accepted on September 21, 2023.