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Long-term Studies of Annual Variation in Growth and Reproduction of the Understory Fern *Steiropteris deltoidea* in a Hurricane-prone Rainforest in Puerto Rico

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Abstract.—Two long-term studies were conducted in a rainforest in Puerto Rico that included measurements of leaf and plant functional traits of the common fern species *Steiropteris deltoidea*. A Fern Demography study (1993-2009) compared annual variation and effects of a category 3 hurricane (Georges, 1998) on fertile and sterile leaf traits. A second long-term study (2003-2019), the Canopy Trimming Experiment, evaluated annual variation in growth and reproduction of *S. deltoidea* in response to two experimentally simulated and one category 4 hurricane (Maria, 2017). In the Fern Demography study, differences between fertile and sterile leaf production rates and plant leaf count of *S. deltoidea* were significant while leaf lengths and lifespans did not differ between leaf types. Fertile (but not sterile) leaf production increased three-fold after Hurricane Georges but declined 10-fold by the end of the study. Leaf lifespans of cohorts emerging before and in the three years after Hurricane Georges were significantly shortened by tree and debris fall. Elevated production of fertile leaves and increased plant leaf counts followed the two simulated hurricanes of the Canopy Trimming experiment and two natural hurricanes. *Steiropteris deltoidea* exhibits a level of interannual flexibility in some growth and reproductive traits in response to a changed understory environment that suggests it may be a good indicator species for evaluating microhabitat hurricane effects. Although *S. deltoidea* exhibited resilience, predicted increases in frequency and magnitude of hurricanes in response to climate change may test the limits of life history strategies of rainforest understory ferns.

Key Words.—functional traits, demography, leaf lifespan, phenology, plant leaf count, plant height, sporophyll production

Recent field studies of patterns of growth and reproduction in ferns (reviewed in Lee, Huang, and Chiou, 2018) have expanded our knowledge of a range of differences between fertile leaf (sporophyll) and sterile leaf (foliage) for such traits as plant leaf count (leaf numbers), leaf production rates, lengths, and lifespans. Most of these studies have addressed short-term seasonal variation, but there is a need for long-term studies of interannual variation (Mehltreter, 2008; Vasco, Moran, and Ambrose, 2013). In 1991, I began a long-term study of fern demography in the El Verde Research Area in the rainforests of the Luquillo mountains in northeastern Puerto Rico. In this area individual researchers and multidisciplinary teams focus on a variety of long-term studies under the auspices of the NSF-funded Luquillo Long-Term Ecological Research program (LTER) that had been established in 1988. For the Fern Demography study, terrestrial and low-trunk fern species were chosen with the goal of documenting details of their life history at a time when temporal aspects of tropical fern growth and reproduction had only been studied for a few ferns (reviewed in Sharpe and Jernstedt, 1990). By the end of the study in 2009, varying numbers of individuals of 24 species had been tagged, monitored, and measured for between six and 19 years.

Two earlier publications have reported on results from the Fern Demography study. First, in a four-year study of the rheophytic fern *Meniscium angustifolium* Willd. (formerly *Thelypteris angustifolia* (Willd.) Proctor) leaf production rates of fertile leaves and plant leaf count ratio (F/S) were much lower, especially during a drought, but leaf lengths and leaf lifespans were similar (Sharpe, 1997). The second publication documented seasonal and annual variation after ten years of observation of five fern species that were uncommon in the Luquillo forest. Although most sample sizes were too small to detect interannual patterns, *Elaphoglossum simplex* (Swartz) Schott did exhibit an approximately 50% increase in fertile leaf production rates and an almost 20% increase in fertile leaf lengths after Hurricane Georges (Sharpe, 2010). This report will focus on annual variation in selected traits of *Steiropteris deltoidea* (Sw.) Pic. Serm. (formerly *Thelypteris deltoidea* (Sw.) Proctor), found to be the most common terrestrial fern species in earlier studies throughout the research area, (Smith, 1970; Proctor, 1989; Halleck, Sharpe, and Zou*,* 2004; Portugal-Loayza, 2005).

Ferns were also among the many organisms monitored during the nearby Canopy Trimming Experiment (CTE), a long-term, multidisciplinary ecosystem experiment that began in 2003 and simulated selected effects of severe hurricanes in the Luquillo rainforest. The main objective of this experiment was to identify the key environmental factors that triggered the variety of responses of the organisms and biochemical processes that had been documented after Hurricane Hugo (1989, category 4) the first major hurricane since San Cyprián (1934), and Hurricane Georges (1998, category 3; Shiels and González, 2014). In addition, climate change research predictions have been calling for more frequent and catastrophic hurricanes in the tropics (Uriarte, Thompson, and Zimmerman*,* 2019). To improve predictions of the effects of future hurricanes on the Luquillo Experimental Forest ecosystem a plot-based (and ongoing) experiment was established whereby rainforest canopy is removed by arborists at ten year-intervals (2004 (Trim1) and 2014 (Trim2)) to simulate the effect of tree canopy loss in order to identify drivers of subsequent changes to canopy as well as the understory environment (Zimmerman *et al.,* 2021).

A pre-treatment survey (2003) of the ferns in all CTE plots indicated that *S. deltoidea* had the highest density (2,558 ha^{-1}) of the 16 understory ferns present, almost three times the abundance of the next most common fern, the Puerto Rico endemic *Cyathea borinquena* (Maxon) Domin. (Sharpe and Shiels, 2014). Although there were significant annual differences in some growth and reproductive traits of *S. deltoidea* following Trim1, values returned to pre-treatment levels within five years of the disturbance, thus demonstrating resilience to canopy opening (Sharpe and Shiels, 2014). The passage of Hurricane Maria during Phase 2 (2017, Category 4) interrupted the recovery phase of the 2014 simulation but resulted in quantification of the effects on ferns from another natural hurricane (Zhang, Heartsill-Scalley, and Bras, 2022).

Here we evaluate differences between fertile and sterile traits of the common fern *S. deltoidea* over time and in response to a natural hurricane (Georges) observed during the long-term Fern Demographic study. We then compare long-term changes in functional traits in the Fern Demography study to the responses of two simulated hurricanes and a natural hurricane in the CTE. We address the following questions through these two partly overlapping studies spanning almost 30 years: 1) are there differences between sterile and fertile leaf traits (leaf production rates, leaf length, leaf lifespan) and plant leaf count (the number of sterile and fertile leaves in the crown) and does the magnitude of these demographic traits change from year to year (1993-2009)? 2) how did Hurricane Georges (1998) affect plant height, plant leaf count, and reproductive status of plants that were observed during the Fern Demography study? 3) how did Hurricane Maria (2017) and simulated hurricane conditions affect annual levels of plant height, plant leaf count, and reproductive status in the CTE Control and Trim plots (2003-2019)?

Material and Methods

Study site.—All monitoring was done in the Luquillo Experimental Forest (LEF) in the United States El Yunque National Forest in north-eastern Puerto Rico (18.3215°N, 65.8141°W) (Shiels and González, 2014) that has an aseasonal everwet climate (Hogan *et al.*, 2022) with mean annual rainfall of about 3500 mm (Zimmerman *et al.,* 2007). Study sites were located in the El Verde Research Area (EVRA) section of the LEF at about 300-400 m elevation and have a canopy characterized by the presence of Tabanuco trees (*Dacryodes excelsa* Vahl.). Areces Berazain, Vega López, and Ackerman (2015) describe the plant community in more detail in a flora of the EVRA. Fern monitoring locations were near the 16-ha Luquillo Forest Dynamics Plot (LFDP), part of the worldwide group of 71 ForestGEO plots (Davies *et al.*, 2021). Thompson *et al.,* (2004) describe the Luquillo LFDP and Uriarte, Thompson, and Zimmerman (2019) summarize the damage to and mortality of trees in the LFDP resulting from hurricanes Hugo (HH), Georges (HG) and Maria (HM). For a more complete review of the history of disturbance research in the LEF see Zimmerman *et al.* (2021).

Study species.—Steiropteris deltoidea (Fig. 1) is a tropical terrestrial fern with limited distribution in the Greater Antilles, St. Thomas, and Martinique and is referred to as "the most ubiquitous species of fern in the moist mountain forests of Puerto Rico" (Proctor, 1989). Portugal Loayza (2005) identified 24 terrestrial fern species in a comprehensive survey of 254 5 m x 5 m plots in the LFDP and found that in the varied topography of the site the abundance of *S. deltoidea* was much higher than other ferns in valley, slope, bench, and ridge habitats. Plants (sporophytes) of this fern species can reach a height (longest leaf in crown measured from shoot apex to tip of leaf) of about 60 cm and form compact rosettes with no evidence of vegetative reproduction. Fertile and

FIG. 1. *Steiropteris deltoidea* plant (sporophyte) in the El Verde Research Area of the Luquillo Experimental Forest in Puerto Rico (October 2009) showing the reduced leaflets along the lower third of the rachis. Photo credit: Fabiolo Aceres-Berazain.

sterile leaves are similar with a morphology that is characterized by a short (2-6 cm) petiole and with the lower third of the lamina bearing reduced leaflets (Fig. 1) only 7-15 mm long with the upper 2/3 of the lamina deltate and up to 40 cm long and 10-25 cm wide (Proctor, 1989).

Fern Demography Study.—During the period from 1991 through early 2010, repeated non-destructive observations and measurements were made of over 1,000 tagged individuals of 24 species of terrestrial and low-trunk epiphytic ferns. Plant selection focused on different areas from ridge top to the edge of the Sonadora river in places where groups of reproductively mature plants could be measured safely long-term and without damage to either vegetation or substrate. Fern individuals of different species were added to the study at various locations throughout the early years of the study until a representative number of each species had been included for long-term observation. For *S. deltoidea*, that point was reached by the beginning of 1993 when 46 reproductively mature individuals had been tagged in the EVRA in the area between the El Verde field station and the Sonadora River suspension bridge near the LFDP and CTE plots. Monitoring of plants ended in early January

2010, thus spanning a period of 17 years that included the passage of a major hurricane (Georges (HG) in 1998.

Plants were monitored during two-week visits to the forest from September 1991 through January 2001 at four-month intervals (early January, May, and September) and annually thereafter in early January. Each plant was identified with a numbered tag 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. All whole leaves had the length of the petiole (including lower rachis section with reduced leaflets in *S. deltoidea* (Fig. 1)) and lamina measured and summed for leaf length. The leaf lifespan begins in the year the leaf matures and calculations do not include the expansion phase estimated from a subset of observations to be 2.5 ± 0.94 mo (mean ± SD) for fertile leaves and 1.1 ± 0.78 mo (mean ± SD) for sterile leaves. Plant height and plant leaf count (number of leaves in crown) were summarized for each plant from the leaf observations. For additional details on monitoring protocols see Sharpe (1997, 2010).

Canopy Trimming Experiment.—The Canopy Trimming Experiment (CTE) involves evaluation of many abiotic elements (Van Beusekom *et al.,* 2019) and biotic elements (both flora and fauna) of the site with the methodology most fully described by Shiels and González (2014) for Phase 1 (2002-2013) and by Presley and Willig (2021) for Phase 2 (2014-2019). All ferns in the CTE were counted and identified in 2002 and 2003 in six 20 m x 20 m experimental plots prior to application of the treatments. Three plots retained their canopy (Control). To simulate hurricane damage, arborists trimmed the canopy in the other three plots in 2004 (Trim1) and 2014 (Trim2) by removing tree branches (<10 cm) and leaves of the canopy of trees > than 15 cm dbh. Trees between 10 cm and 15 cm dbh were cut back to 3 m above the ground as were palm leaves > 3 m in height. Five 1 m x 3.5 m subquadrats within each plot were roped off and dedicated to the monitoring of understory plants (including seedlings) from 2003 (the year before treatments were applied) through 2019. For this study, trait data (plant leaf count, height, and sporangia-bearing status of the longest leaf) for reproductively mature plants were taken from individually tagged plants greater than 10 cm tall that project researchers, staff, and volunteers monitored and measured annually.

Data Analysis.—Repeated-measures two-way ANOVAs were used to identify significant differences between fertile and sterile traits and among all years in the Fern Demography study and to detect differences between treatments (Control and Trim) and years in the CTE. Repeated-measures one-way ANOVAs were used for both Fertile and Sterile traits to compare differences in four key years in the Fern Demography study. Multiple measurements of individual plants in the Fern Demography study and replicate values in the five plant subplots of each of the six CTE plots were averaged prior to analysis. All mean differences were evaluated with a Tukey HSD pairwise comparison test. Means ± standard deviation (SD) are reported throughout. N, mean and standard deviation for points on the graphs in Figs. 2

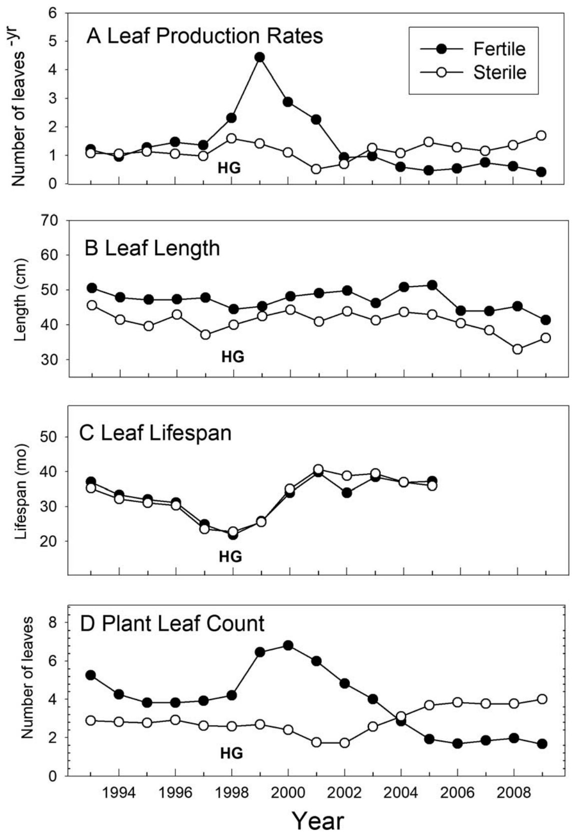

FIG. 2. Fern Demography study comparisons of annual variation in fertile and sterile elements of leaf and plant traits of the understory fern *S. deltoidea*. Observations span a 17-year period that was preceded by Hurricane Hugo (HH 1989) and includes Hurricane Georges (HG 1998). N, means and standard deviation are listed in Appendix 1.

and 3 and fertile/sterile ratios (F/S) are listed in Appendix 1. Data were analyzed using Statistix 10 software (Analytical Software, 2022). Four publicly available datasets were used in this report with URLs listed in the Literature Cited section (Fern Demography data, Sharpe, 2015; CTE solar radiation data, González *et al.*, 2019; CTE fern data, Zimmerman, 2020; El Verde understory mean maximum temperatures, Ramirez, 2022).

RESULTS

Fern Demography Study.—Of the 46 individuals of *S. deltoidea* present in 1993, only 7 (15%) of the plants had died by 2009: two before, one during, and four after Hurricane Georges (HG), leaving 39 reproductively mature plants that were monitored annually for the entire study and were the basis for this evaluation of sterile-fertile dimorphy and interannual variation in three leaf

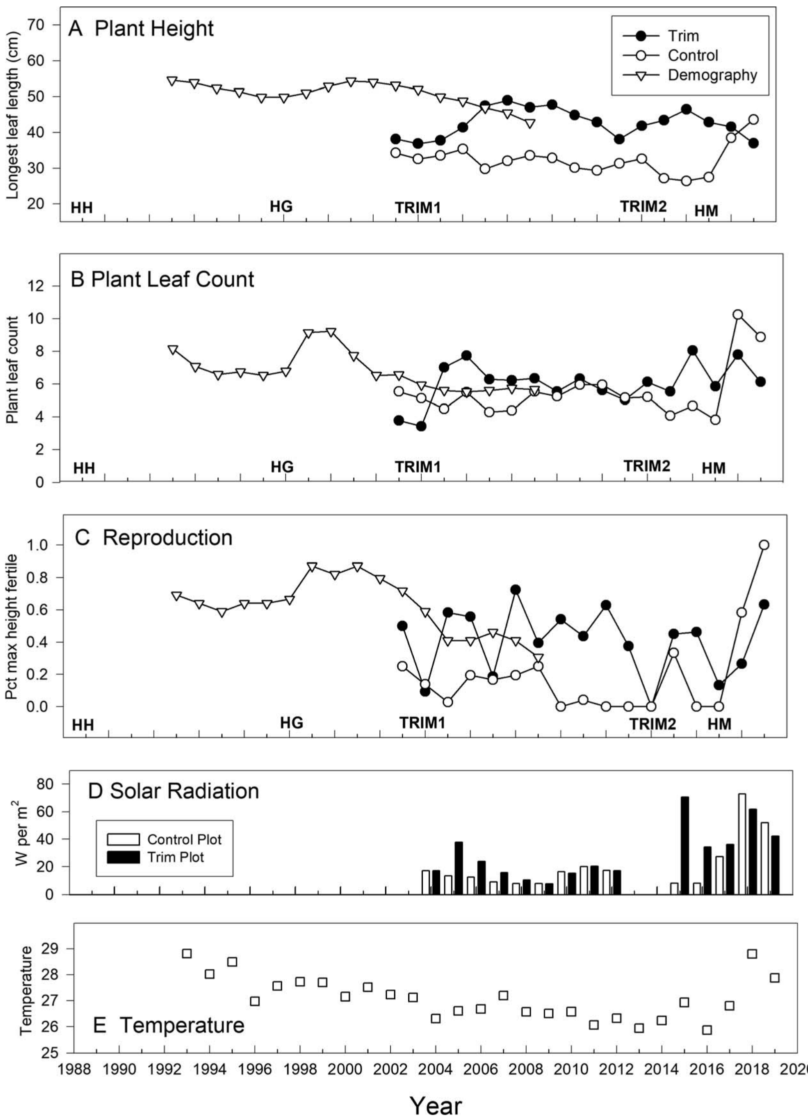

FIG. 3. Annual variation in fern plant traits span a 27-year period (2003-2019) preceded by Hurricane Hugo (HH 1989) and that includes Hurricane Georges (HG 1998) and Hurricane Maria (HM 1917) as well as CTE) simulated hurricanes (Trim1 and Trim2). N, means and standard deviation are listed in Appendix 1 for A, B and C. Annual understory solar radiation (D) (Van Beusekom *et al.*, 2019; González) *et al.,* 2019) and (E) maximum annual temperatures 2 m above the ground (Willig and Presley, 2022; Ramirez, 2022) reflect changes in two key abiotic factors.

traits and one plant trait over a period of 17 years (1993-2009). Leaf production rates (Fig. 2A) exhibited a significant difference in leaf production rates among years ($F = 21.13$, $p = 0.0000$) and a significant interaction (leaf type × year) due to increases in fertile leaf production ($F = 22.18$, $p = 0.0000$). Both fertile and

TABLE 1. Comparison of fertile and sterile leaf and plant traits for four key years in the 17-year Fern Demography study of *Steiropteris deltoidea*: Start, Hurricane Georges (HG), Peak Response after HG and End of study. For each trait type (fertile and sterile), repeated measures ANOVA was used to assess differences among the plant responses during four key years for each trait. Fertile/Sterile (F/S) ratios indicated the magnitude of differences. **Bold** indicates significant differences (p-values < 0.0500), and different letters indicate significant mean differences among years (Tukey test).

	FERTILE			STERILE			F/S
	Year	**N**	**Mean ± SD**	**Year**	**N**	**Mean ± SD**	**Ratio**
A. Leaf Production Rate							
Start	1993	39	1.21 ± 1.06 **c**	1993	39	1.08 ± 1.06	1.12
HG	1998	39	2.31 ± 1.40 **b**	1998	39	1.59 ± 1.04	1.45
Response	1999	39	4.44 ± 2.27 **a**	1999	39	1.41 ± 1.79	3.15
End	2009	39	0.41 ± 0.82 **c**	2009	39	1.69 ± 1.10	0.24
	F = 39.33, **p** = **0.0000**			F = 2.25, p = 0.0865			
B. Leaf Length (cm)							
Start	1993	26	50.6 ± 6.23	1993	22	45.5 ± 8.32 **a**	1.11
HG	1998	34	44.4 ± 6.13	1998	32	40.0 ± 8.55 **b**	1.11
Response	2002	35	49.8 ± 8.60	2002	17	43.8 ± 9.70 **a**	1.12
End	2009	8	41.3 ± 8.30	2009	32	36.2 ± 9.18 **b**	1.14
	F = 4.45, p = 0.1258			F = 5.98, **p** = **0.0029**			
C. Leaf Lifespan (mo)							
Start	1993	36	37.0 ± 9.77 a	1993	22	35.3 ± 11.3	1.05
HG	1998	39	21.9 ± 9.53 **b**	1998	32	22.8 ± 9.38	0.96
Response	2001	38	39.8 ± 9.15 **a**	2001	9	40.7 ± 17.9	0.98
End	2005	35	37.3 ± 10.2 **a**	2005	29	36.0 ± 10.7	1.04
	F = 23.69, **p** = **0.0000**			F = 3.18, p = 0.0633			
D. Plant Leaf Count							
Start	1993	39	5.26 ± 3.18 **b**	1993	39	2.90 ± 1.96 **b**	1.81
HG	1998	39	4.21 ± 2.65 **b**	1998	39	2.59 ± 1.93 **b**	1.62
Response	2000	39	6.82 ± 3.04 **a**	2000	39	2.41 ± 1.90 **b**	2.83
End	2009	39	1.67 ± 1.96 **c**	2009	39	4.00 ± 1.81 **a**	0.42
	F = 29.53, **p** = **0.0000**			F = 6.76, **p** = **0.0003**			

sterile leaf production rates were similar at the start of the study but with the passage of HG in 1998 fertile rates nearly doubled and within a year were three times the rate of sterile leaf production, although rates declined to only 25% of sterile leaf production rates by the end of the study (Table 1A). Fertile leaves were consistently about 5 cm longer than sterile leaves throughout the study (Fig. 2B) with a fertile/sterile ratio of about 1.1 and differed significantly among the four key years of the study ($F = 9.59$, $p = 0.0113$) with a decline in fertile leaves after HG and higher sterile leaf lengths by the end of the study (Table 1B). Fertile and sterile leaf lifespans (Fig. 2C) had no significant differences in four key years of the study ($F = 0.04$, $p = 0.8403$) but lifespans were significantly shorter in 1998 (Table 1C) with shorter lifespans in the two years before and three years after HG as well (Fig. 2C). Because leaf lifespans were approximately 36 mo or more (Table 1C), data for this trait are only available through 2005 as mortality for several plants in the final four annual cohorts (2006-2009) had not yet occurred by the end of the study. There were significant differences in plant leaf count between numbers of sterile and fertile leaves in the crown ($F = 9.12$, $p = 0.0033$) and among years ($F = 8.32$, $p = 0.0000$) with the highest counts after HG in 1999 and 2000 and the lowest in the last five years of the study (Fig. 2D). There was also a significant interaction (leaf type × year) reflecting an increase of sterile leaves and decrease of fertile leaves by the end of the study ($F = 31.57$, $p = 0.0000$). These differences (Fig. 2D) reflect the patterns of change seen in leaf production rates for each leaf type (Fig. 2A) with a positive fertile/sterile ratio of 1.81 at the start of the study reduced to 0.42 by the end of the study in 2009 (Table 1D).

Three additional plant traits of *S. deltoidea* from the Fern Demography study data set (plant height (length of longest leaf), plant leaf count (total) and plant reproductive status (presence or absence of sporangia on the longest leaf)) were also monitored for comparison to patterns of annual variation observed in the CTE Control and Trim plots (Fig. 3). Plant height exhibited a downward trend (Fig. 3A) interrupted by a significant four-year increase after HG ($F = 27.93$, $p = 0.0000$). Plant leaf count also showed a significant pattern of decline of 30% by 2009 (Fig. 3B), that was also interrupted by two years of significantly higher means immediately after HG ($F =18.22$, $p = 0.0000$). There was also a downward trend in the fertility status of the longest leaf from 60% in 1993 to 31% by 2009 despite evidence of greater spore production in the three years after HG (Fig. 3C).

Canopy Trimming Experiment.—There were significant differences between the CTE Control treatment and the Trim treatment ($F = 32.98$, $p = 0.0105$) and significant interaction (treatment x year, $F_{, 15} = 2.21$, $p = 0.0208$) for plant height. The Control plots showed an interannual decline in plant height of 20% in the years preceding HM (2017), although mean heights almost doubled by 2019 (Fig. 3A). In contrast, the trend for plant height in the Trim plots showed an increase after Trim1, followed by decline then an increase after Trim2 and decline thereafter (Fig. 3A) despite HM. For plant leaf count, there was a significant difference over time with pre-treatment years (2003 and 2004) the lowest and post-HM (2018) the highest ($F_{,} = 1.95$, $p = 0.0426$) but no significant treatment differences ($F = 0.5$, $p = 0.5312$). Plant leaf counts in the Control plots generally declined through 2017 followed by plant leaf counts that more than doubled in 2018 the year after HM (Fig. 3B). Plant leaf counts in the Trim plots showed increases in 2005 and 2006, the two years following Trim1 and for one year following Trim2 and then in the year after HM, but the magnitude of those increases was less than in the Control plots after HM (Fig. 3B). Although in the Control plots the percent of plants that were fertile was near 0% for most of the years after 2009, there was a dramatic shift from 0% to 100% within 2 years after HM (Fig. 3C). In the Trim plots, evidence of reproduction was highly variable from year to year but there were increases after Trim 1 (9% to 58%), Trim2 (0 to 46%), and HM (13% to 63%) (Fig. 3C).

Discussion

Since this research on tropical fern demography began over 30 years ago, there has been an increase in the number of studies on seasonal aspects of fern growth and reproduction. Differences in traits of fertile and sterile leaves have been the subject of numerous intra-annual phenological studies of about 2% of fern species (Lee, Huang, and Chiou, 2018). Recent studies of tropical and subtropical ferns coming from various parts of Taiwan (*e.g.,* Lee *et al.,* 2016) and Brazil (*e.g.,* Farias *et al.,* 2018; Schmitt and Windisch, 2012) have reported on fertile/sterile ratios for several traits such as leaf lifespans and plant leaf count but most of these studies are short-term and may have only partial multi-year overlaps that often hint at annual differences (*e.g.*, Sharpe and Jernstedt, 1990; Silva *et al.,* 2019). *Steiropteris deltoidea* would be classified as a monomorphic fern species because fertile and sterile leaf shapes are similar with relatively small differences in leaf length (Wagner and Wagner, 1977), however there can be fertile/sterile differences in other traits of monomorphic ferns. In a four-year study of 13 monomorphic ferns Lee *et al*. (2016) found significant differences between fertile and sterile phenologies and Watkins, Churchill, and Holbrook (2016) have shown that several physiological traits can differ for fertile and sterile leaves in the monomorphic tropical fern *Adiantum latifolium* Lamarck. Leaves of tropical fern plants emerge sequentially (Sharpe and Shiels, 2014), and in *S. deltoidea* there was a three-fold increase in fertile (but not sterile) leaf production rates immediately after Hurricane Georges. To switch not only from prioritizing vegetative function to reproductive function but also to release three additional leaves so immediately after disturbance suggests either a strong environmental trigger or sensitive physiological fern response (or both) that determines fertile leaf emergence. White (1971) reviewed several studies on the control of fertile leaf development in ferns and concluded that it does occur relatively late in leaf development. Vasco and Ambrose (2020) have made advances in identifying the molecular basis for the development processes leading to the ultimate shape of a fern leaf, but research into the evolution of gene lineages in ferns that are related to activation of sporophyll meristems (comparable to well-studied floral meristems) has yet to identify the specific pathways of reproductive organ development in ferns (Rodriguez-Pelayo *et al.,* 2022).

Lee, Huang, and Chiou (2018) list 32 studies of fertile-sterile leaf dimorphy in leaf lifespans and leaf counts in 26 monomorphic species based on 1 (21), 2 (3) or 3 (2) studies. As for *S. deltoidea,* lifespans of fertile and sterile leaves are within 10% of being equal in 18 of these 26 monomorphic species. Fern leaf lifespans are often estimated from leaf production rates and plant leaf count (*e.g.*, Tanner, 1983) but that approach assumes an environment with little annual variation (Kikuzawa and Lechowicz, 2011). Leaf lifespan determinations for *S. deltoidea* were based on observations of leaf maturity and subsequent mortality for individual leaves making it possible to document leaf lifespans that were considerably shorter in the years both immediately before and after Hurricane Georges. In comparing leaf lifespans in old growth forests and disturbed forests Zhu *et al.* (2016) noted that shorter lifespans were associated with higher light levels in disturbed forests. This suggests that while leaf cohorts of *S. deltoidea* emerging before the hurricane would have experienced premature mortality due to tree and branch fall damage, the shorter lifespans in the cohorts immediately after may also have been due to the suddenly much higher light conditions in the understory (Sharpe and Shiels, 2014).

In *S. deltoidea* the fertile/sterile ratio for plant leaf counts ranged from a high of 2.53 two years after Hurricane Georges to a low of 0.42, a five-fold decrease, by the end of study in 2009. A 5-year study of an understory tree fern (*Cyathea atrovirens* (Langsd. & Fisch.) Domin) in southern Brazil (Schmitt and Windisch, 2012) also found that annual fertile leaf counts were significantly different with a 30% difference between the lowest year and the highest year. Variation on a spatial scale also resulted in very different sterile/fertile ratios in plant leaf counts for *Cyathea podophylla* Copel. (1.17, 3.73, and 4.91) as well as for *Diplazium dilatatum* (Retz.) Sw. (7.15, 0.91 and 1.08) at three different sites in Taiwan (Lee, Huang, and Chiou, 2018). These multi-year and multi-location study results for other monomorphic ferns show that sterile/fertile leaf ratios in plant leaf counts based on a single location or a single year may not be typical. On the other hand, even a single study in one location could provide baseline on traits for evaluating change should the site be affected by predicted increasing frequency and severity of hurricanes in a future defined by climate change (Sharpe, 2019).

Unlike fertile leaf production and plant leaf count, plant heights in *S. deltoidea* did not respond directly to passage of natural hurricanes (Georges) or simulated hurricanes Trim1 or Trim2. However, plant heights did steadily decline within the forest (1993-2019) from highs at the start of the Fern Demography study four years after Hurricane Hugo to plants about half as tall in CTE Control plots the year before Hurricane Maria, followed by an increase to almost original heights in the following two years. Willig and Presley (2022) summarize studies that show that the understory temperature trend (Fig. 3E) in our study period (1993-2009) reflects the higher temperatures resulting from loss of canopy cover from earlier Hurricane Hugo (1989) for first three years, followed by gradual canopy closure resulting from secondary succession until Hurricane Maria when temperatures rose to post-Hugo heights. They also noted that Hurricane Georges resulted in leaf loss but not the magnitude of canopy openness and debris fall effects that the two category 4 hurricanes exhibited. This suggests that differences in storm intensity (category 3 *vs.* 4) may be an important factor in triggering responses from some fern traits such as leaf length.

CTE results supported findings in the Fern Demography study that interannual differences in plant leaf count and spore production in *S. deltoidea* were mostly likely the consequence of environmental changes following hurricane disturbance. Significant changes in these two traits were observed in the CTE Control plots after Hurricane Maria and after Trim1, Trim2, and Hurricane Maria in the Trim plots. The trends in timing and magnitude of these responses reflected the annual solar radiation differences (Fig. 3D) resulting from both simulated and natural hurricanes (Van Beusekom *et al.,* 2019). *Steiropteris deltoidea* appears to be a species that conserves energy in low light environments by not producing spores or even very long leaves but can immediately take advantage of higher solar radiation levels presented by hurricanes to increase growth rates and spore production.

Lee *et al.* (2016) surveyed traits of 13 monomorphic fern species in a tropical monsoon forest in southern Taiwan for four years with no mention of the kind of significant annual variation seen in *S. deltoidea*, perhaps because the Taiwan study was done during a period between catastrophic typhoons. If the observations of *S. deltoidea* in Puerto Rico had been limited to a four-year period (*e.g.*, 2005 through 2009), little annual variation in plant leaf count would have been observed (Fig. 3B). Another explanation suggested by Hogan *et al.* (2018) is that tropical forests that are prone to very low levels of disturbance (*e.g.*, Barro Colorado Island, Panama) or very high frequency of cyclonic windstorms (*e.g.,* Fushan, Taiwan) will have low levels of life history variability while a forest with intermediate frequency (*e.g.*, Luquillo Experimental Forest, Puerto Rico) will have higher levels of response. In Puerto Rico the canopy is uneven with taller trees subject to mortality that opens the canopy and causes damage from falling branches to the understory during less frequent (3 in a 33-year period) storm events compared to Taiwan forests with their low even canopy that seems resistant to understory damage from their very frequent cyclonic windstorms (13 in the same 33-year period; Hogan *et al.,* 2018).

The results of a long-term study of a fern species that is common in two locations within the same forest and under two different investigative regimes (observation, experimental) has led to new insights into the functional flexibility of *S. deltoidea* both morphologically and temporally. The Fern Demography study has illuminated several hitherto undocumented elements of life histories of a fern that is a major component of the understory in a forest where, in contrast, canopy tree traits had been the subject of long-term study since the 1930s (Brokaw *et al.*, 2012). Fern plants suffered little mortality after Hurricane Georges but exhibited immediate responses to sudden changes in the understory environment that affect growth and reproduction. Future analysis of other ferns (both monomorphic and dimorphic) in the Fern Demography data set should enhance this understanding. Continuing observations of *S. deltoidea* and other ferns in a large-scale experiment (CTE) will lead to greater insights into the role of abiotic and biotic environmental factors that result in changes in fern growth and reproduction.

Walker *et al.* (1996) used differences in fern cover to document fern responses to Hurricane Hugo, but in this project we could assess changes in individual plant growth and reproduction as well. We have identified three easily observed and measured plant traits that, at least for *S. deltoidea,* can rapidly signify the effects of hurricane disturbance on the herbaceous layer when ferns are among the organisms included in a large-scale experiment. The results from two different studies lead to similar conclusions about the effects of hurricanes on ferns, and the collaborative scope of the CTE has resulted in more insights into potential drivers of differing responses (Sharpe and Shiels, 2014; Hogan *et al.,* 2022). Fern traits have been shown in this study and others that they can be sensitive indicators of disturbance. To successfully utilize fern traits as effective indicators of change requires establishing standard protocols for identifying both vegetative and reproductive response. Long-term monitoring has become common in 71 ForestGEO plots (Davies *et al.,* 2021) and over 800 International Long-term Ecological Research (ILTER) sites (Mirtl *et al.,* 2018) throughout the world, yet understory fern species are rarely noticed despite their richness and ubiquity in some rainforest understories (Poulsen and Balslev, 1991). Focusing future efforts on establishing long-term demography studies of fern life histories in collaboration with these research sites to allow monitoring of rapidly responding fern species would be of great benefit to models that predict effects of future climate change.

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Literature Cited

Analytical Software Inc. 2020. Statistix Version 10. Tallahassee, Florida USA.

Areces Berazain, F., V. J. Vega López, and J. D. Ackerman. 2015. Annotated List of the Vascular Plants at El Verde Field Station, El Yunque National Forest, Puerto Rico. Caribbean Naturalist 16:1 – 51.

Brokaw, N., T. A. Crowl, A. E. Lugo, W. H. McDowell, F. N. Scatena, R. B. Waide, and M. R. Willig. 2012. Response to Disturbance. Pp. 201 – 271, *in* Brokaw, N., J, Zimmerman, K. M. Willig, R. G. Camilo, R. Covich, A. P. Crowell, T. A. *et al.* (eds). *A Caribbean Forest tapestry: the Multidimensional Nature of Disturbance and Response*. Oxford University Press, Oxford, United Kingdom.

Davies, S. J., I. Abiem, K. A. Salim, S. Aliguar, D. Allen, A. Alonso, K. Anderson-Teixeira, A. Andrade, G. Arellano, P. S. Ashton, P. J. Baker, M. E. Baker*, et. al.* 2021. ForestGEO: Understanding forest diversity and dynamics through a global observatory network. Biological Conservation 253:108907.

Farias, R. d. P., L. E. N. d. Costa, I. C. L. Barros, and K. Mehltreter. 2018. Leaf phenology of *Danaea geniculata* (Marattiaceae) in a submontane tropical forest, Brazil. American Fern Journal 108:35 – 46.

González, G., A. E. Van Beusekom, S. Stankavich, J. K. Zimmerman, and A. Ramírez, Alonso. 2019. Luquillo Experimental Forest canopy trimming experiment data. Fort Collins, CO: Forest Service Research Data Archive. https://doi.org/10.2737/RDS-2019-0051

HALLECK, L. F., J. M. SHARPE, AND X. ZOU. 2004. Understorey fern responses to post-hurricane fertilization and debris removal in a Puerto Rican rain forest. Journal of Tropical Ecology 20:173–181.

HOGAN, J. A., J. K. ZIMMERMAN, J. THOMPSON, M. URIARTE, N. G. SWENSON, R. CONDIT, S. P. HUBBELL, D. J. JOHNSON, I.-F. SUN, C.-H. CHANG-YANG, S.-H. SU, P. ONG, L. RODRIGUEZ, C. C. MONOY, S. YAP, AND S. J. DAVIES. 2018. The frequency of cyclonic windstorms shapes tropical forest dynamism and functional trait dispersion. Forests 9:404 doi:410.3390/f9070404.

HOGAN, A., J. M. SHARPE, A. VAN BEUSEKOM, S. STANKAVICH, S. MATTA, J. BITHORN, J. TORRES-DIAZ, G. GONZALES, J. K. ZIMMERMAN, AND A. B. SHIELS. 2022. Solar radiation and soil moisture drive tropical forest understory responses to experimental and natural hurricanes. Ecosphere 13: e4150.

KIKUZAWA, K., AND M. J. LECHOWICZ. 2011. *Ecology of Leaf Longevity*. Springer, New York.

LEE, P. H., S. W. CHEN, W. L. CHIOU, Y. M. HUANG, AND H. Y. LIU. 2016. Phenology of 13 fern species in a tropical monsoon forest of southern Taiwan. International Journal of Plant Reproductive Biology 8:87 – 97.

LEE, P. H., Y. M. HUANG, AND W. L. CHIOU. 2018. Fern phenology. Pp. 381 – 400, *in* H. Fernández [ed.], *Current Advances in Fern Research*. Springer International Publishing, Cham, Switzerland.

MEHLTRETER, K. 2008. Phenology and habitat specificity of tropical ferns. Pp. 203-223, *in* T. A. Ranker AND C. H. Haufler [eds.], *Biology and Evolution of Ferns and Lycophytes*. Cambridge University Press, Cambridge.

MIRTL, M., E. T. BORER, I. DJUKIK, M. FORSIUS, H. HAUBOLD, W. HUGO, J. JOURDAN, D. LINDENMAYER, W. H. MCDOWELL, H. MURAOKA, D. E. ORENSTEIN, J. C. PAUW, *et al*. 2018. Genesis, goals and achievements of long-term ecological research at the global scale: a critical review of ILTER and future directions. Science of the Total Environment 626:1439–1462.

PORTUGAL LOAYZA, A. B. D. R. 2005. Effects of environmental factors and past land use on pteridophyte distributions in tropical forests. Masters Thesis. University of Puerto Rico, Rio Piedras.

POULSEN, A. D., AND H. BALSLEV. 1991. Abundance and cover of ground herbs in an Amazonian rain forest. Journal of Vegetation Sciences 2:315–322.

PRESLEY, S. J., AND M. R. WILLIG. 2022. Long-term responses of gastropods to simulated hurricanes in a tropical montane rainforest. Ecosphere 13:e3928

PROCTOR, G. R. 1989. *Ferns of Puerto Rico and the Virgin Islands*. Memoirs of the New York Botanical Garden 53:1 – 389.

RAMIREZ, A. 2022. Maximum temperature at El Verde Field Station, Rio Grande, Puerto Rico since October 1992 ver 538558. Environmental Data Initiative. https://doi.org/10.6073/pasta/e469f34cc86619f8eff5c4f1b1b3526e.

RODRÍGUEZ-PELAYO, C., B. A. AMBROSE, A. VASCO, J. F. ALZATE, AND N. PABÓN-MORA. 2022. Evolution and expression of LEAFY genes in ferns and lycophytes. EvoDevo 13:2.

SCHMITT, J. L., AND P. G. WINDISCH. 2012. Caudex growth and phenology of *Cyathea atrovirens* (Langsd. & Fisch.) Domin (Cyatheaceaea) in secondary forest, southern Brazil. Brazilian Journal of Biology 72:397 – 405.

SHARPE, J. M., AND J. A. JERNSTEDT. 1990. Leaf growth and phenology of the dimorphic herbaceous layer fern *Danaea wendlandii* (Marattiaceae) in a Costa Rican rain forest. American Journal of Botany 77:1040 – 1049.

SHARPE, J. M. 1997. Leaf growth and demography of the rheophytic fern *Thelypteris angustifolia* (Willdenow) Proctor in a Puerto Rican rainforest. Plant Ecology 130:203 – 212.

SHARPE, J. M. 2010. Long term monitoring of five uncommon tropical forest understory ferns in Puerto Rico. Indian Fern Journal 27:242 – 253.

SHARPE, J. M., AND A. B. SHIELS. 2014. Understory fern community structure, growth and spore production responses to a large-scale hurricane experiment in a Puerto Rico rainforest. Forest Ecology and Management 332:75 – 86.

SHARPE, J. 2015. Fern sporophyte growth observation at the Luquillo Experimental Forest (LEF) ver 11034160. Environmental Data Initiative https://doi.org/10.6073/pasta/418b7be566 4176b72d3b047260ed212d.

Sharpe, J. M. 2019. Fern ecology and climate change. Indian Fern Journal 36:179–199.

Shiels, A. B., and G. González. 2014. Understanding the key mechanisms of tropical forest responses to canopy loss and biomass deposition from experimental hurricane effects. Forest Ecology and Management 332:1 – 10.

Silva, M. M., R. d. P. Farias, L. E. N. d. Costa, and I. C. L. Barros. 2019. Leaf phenological traits of the tree fern *Cyathea praecincta* (Cyatheaceae) in a Brazilian lowland tropical forest. Australian Journal of Botany 66:618 – 627.

Smith, R. F. 1970. Vegetation structure of the Puerto Rican rain forest. Pp. D103 – D140, *in* H. T. Odum and R. F. Pigeon (eds.), *A Tropical Rain Forest: A study of Irradiation and Ecology at El Verde, Puerto Rico*, Division of Technical Information, US Atomic Energy Commission, Washington, DC.

Tanner, E. V. J. 1983. Leaf demography and growth of the tree-fern *Cyathea pubescens* Mett. ex Kuhn in Jamaica. Botanical Journal of the Linnean Society 87:213 – 227.

Thompson, J., N. Brokaw, J. K. Zimmerman, R. B. Waide, E. M. Everham III, and D. A. Schafer. 2004. Luquillo forest dynamics plot, Puerto Rico. Pp. 540-550, *in* E. C. Losos and E. G. Leigh Jr. (eds.), *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network*. The University of Chicago Press, Chicago.

Uriarte, M., J. Thompson, and J. K. Zimmerman. 2019. Hurricane Maria tripled stem breaks and doubled tree mortality relative to other major storms. Nature Communications 10:1362.

Van Beusekom, A. E., G. Gonzáles, S. Stankavich, J. K. Zimmerman, and A. Ramírez. 2020. Understanding tropical forest abiotic response to hurricanes using experimental manipulations, field observations, and satellite data. Biogeosciences 17:3149 – 3163.

Vasco, A., R. Moran, and B. A. Ambrose. 2013. The evolution, morphology and development of fern leaves. Frontiers in Plant Science 4, Article 345:1–16

Vasco, A., and B. A. Ambrose. 2020. Simple and divided leaves in ferns: exploring the genetic basis for leaf morphology differences in the genus *Elaphoglossum* (Dryopteridaceae). International Journal of Molecular Sciences 21:5180.

Wagner, W. H., and F. S. Wagner. 1977. Fertile-sterile leaf dimorphy in ferns. Garden Bulletin of Singapore 30:251 – 267.

Walker, L. R., J. K. Zimmerman, D. J. Lodge, and S. Guzmán-Grajales. 1996. An altitudinal comparison of growth and species composition in hurricane-damaged forests in Puerto Rico. Journal of Ecology 84:87 – 889.

Watkins Jr., J. E., A. C. Churchill, and N. M. Holbrook. 2016. A site for sori: Ecophysiology of fertile-sterile leaf dimorphy in ferns. American Journal of Botany 103:845 – 855.

White, R. A. 1971. Experimental and developmental studies of the fern sporophyte. Botanical Review 37:509–540.

Willig, M. R., and S. J. Presley. 2022. Long-term trends in gastropod abundance and biodiversity: distentangling effects of press and pulse disturbances. Global Ecology and Biogeography 31:247–265.

Zhang, J., T. Heartsill Scalley, and R. L. Bras. 2022. Forest structure and composition are critical to hurricane mortality. Forests 13:1 – 12.

Zhu, S. D., R. H. Li, J. Song, P. C. He, H. Liu, F. Berninger, and Q. Ye. 2016. Different leaf cost-benefit strategies of ferns distributed in contrasting light habitats of sub-tropical forests. Annals of Botany 117:497 – 506.

Zimmerman, J. K., S. J. Wright, Calderón, O., M. Aponte Pagan, and S. Paton. 2007. Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: the role of annual changes in irradiance. Journal of Tropical Ecology 23:231 – 251.

Zimmerman, J. K. 2020. Canopy Trimming Experiment (CTE) plant seedling measurements ver 1058120. Environmental Data Initiative. https://doi.org/10.6073/pasta/e4eb7f6d0e8287a36c2ec12be3f781ea (Accessed 2022-03-11)

Zimmerman, J. K., T. E. Wood, G. Gonzales, A. Ramirez, W. L. Silver, M. Uriarte, M. R. Willig, R. B. Waide, and A. E. Lugo. 2021. Disturbance and resilience in the Luquillo Experimental Forest. Biological Conservation 253:108891.

APPENDIX 1. N, mean and standard deviation for Figures 2 and 3 and fertile/sterile Ratio (F/S) Figure 2.

Figure 2: Fern Demography study

	2A. Leaf Production Rate (no. leaves per plant)							2B. Leaf Length (cm)						
	FERTILE			STERILE				FERTILE			STERILE			
Year	**N**	**Mean**	**SD**	**N**	**Mean**	**SD**	**F/S**	**N**	**Mean**	**SD**	**N**	**Mean**	**SD**	**F/S**
1993	39	1.21	1.06	39	1.08	1.06	1.12	26	50.6	6.32	22	45.52	8.32	1.11
1994	39	0.95	0.79	39	1.05	1.05	0.90	22	47.8	7.17	20	41.37	10.18	1.16
1995	39	1.28	1.23	39	1.13	1.20	1.14	26	47.2	7.47	20	39.58	7.98	1.19
1996	39	1.46	1.14	39	1.05	0.86	1.39	28	47.3	8.58	24	42.85	9.67	1.10
1997	39	1.36	1.14	39	0.97	1.16	1.39	28	47.8	5.20	17	37.05	6.54	1.29
1998	39	2.31	1.40	39	1.59	1.04	1.45	34	44.4	6.13	32	39.96	8.55	1.11
1999	39	4.44	2.27	39	1.41	1.79	3.15	37	45.3	5.33	21	42.39	10.55	1.07
2000	39	2.87	1.52	39	1.10	1.43	2.60	34	48.1	7.11	17	44.27	11.68	1.09
2001	39	2.26	1.31	39	0.51	1.00	4.40	35	49.1	8.17	9	40.89	11.86	1.20
2002	39	0.92	0.98	39	0.69	0.77	1.33	20	49.8	8.60	17	43.82	9.70	1.14
2003	39	0.97	1.04	39	1.26	1.02	0.78	21	46.2	7.37	25	41.20	6.48	1.12
2004	39	0.59	0.99	39	1.08	0.90	0.55	9	50.8	7.12	24	43.64	7.01	1.16
2005	39	0.46	0.85	39	1.46	1.02	0.32	9	51.4	5.59	30	42.88	6.85	1.20
2006	39	0.54	0.72	39	1.28	1.02	0.42	15	44.0	8.64	26	40.37	7.64	1.09
2007	39	0.74	0.79	39	1.15	0.93	0.64	15	43.9	7.76	28	38.32	8.60	1.15
2008	39	0.62	0.85	39	1.36	1.11	0.45	14	45.3	6.61	23	32.98	6.90	1.37
2009	39	0.41	0.82	39	1.69	1.10	0.24	8	41.3	8.30	32	36.18	9.18	1.14

	2C. Leaf lifespans (mo)							2D. Plant Leaf Count						
	FERTILE			STERILE				FERTILE			STERILE			
Year	**N**	**Mean**	**SD**	**N**	**Mean**	**SD**	**F/S**	**N**	**Mean**	**SD**	**N**	**Mean**	**SD**	**F/S**
1993	36	37.0	9.77	22	35.3	11.30	1.05	39	5.26	3.18	39	2.90	1.96	1.81
1994	33	33.4	11.05	20	32.2	10.26	1.04	39	4.26	2.62	39	2.82	1.57	1.51
1995	37	32.1	9.49	20	31.1	11.47	1.03	39	3.82	2.49	39	2.77	1.84	1.38
1996	38	31.2	7.76	24	30.4	8.31	1.03	39	3.82	2.63	39	2.92	1.91	1.31
1997	38	24.9	8.36	17	23.5	9.72	1.06	39	3.92	2.60	39	2.62	1.90	1.50
1998	39	21.9	9.53	32	22.8	9.38	0.96	39	4.21	2.65	39	2.59	1.93	1.62
1999	38	25.8	5.97	21	25.5	8.72	1.01	39	6.46	3.33	39	2.69	1.88	2.40
2000	37	33.9	12.87	17	35.1	15.22	0.97	39	6.82	3.04	39	2.41	1.90	2.83
2001	38	39.8	9.15	9	40.7	17.94	0.98	39	6.00	2.55	39	1.74	1.65	3.44
2002	31	34.0	12.67	17	38.8	10.63	0.87	39	4.82	2.34	39	1.72	1.39	2.81
2003	38	38.5	13.12	25	39.5	10.67	0.97	39	4.00	2.46	39	2.56	1.54	1.56
2004	33	36.9	11.14	24	37.0	10.57	1.00	39	2.85	2.24	39	3.10	1.90	0.92
2005	29	37.3	10.22	29	36.0	10.70	1.04	39	1.92	1.87	39	3.69	2.07	0.52
2006								39	1.69	1.89	39	3.85	1.89	0.44
2007								39	1.85	1.91	39	3.77	1.91	0.49
2008								39	1.97	2.03	39	3.77	1.77	0.52
2009								39	1.67	1.96	39	4.00	1.81	0.42

Appendix 1. Continued.

Fig 3. Demography/CTE comparison

3A. Plant Height (cm)

	Demography Study				CTE Control Plots			CTE Trim Plots		
Year	N	Mean	SD	Year	N	Height	SD	N	Height	SD
1993	39	54.6	7.37	2003	3	34.3	4.61	2	38.2	8.53
1994	39	53.9	8.03	2004	3	32.6	2.28	2	36.9	7.82
1995	39	52.4	8.65	2005	3	33.6	4.90	2	37.8	3.46
1996	39	51.4	8.90	2006	3	35.4	6.86	2	41.4	0.57
1997	39	49.8	8.96	2007	3	29.8	9.58	2	47.5	0.24
1998	39	49.8	7.82	2008	3	32.0	6.04	2	49.0	1.62
1999	37	51.0	8.04	2009	3	33.6	6.95	2	47.0	3.67
2000	38	52.9	8.73	2010	3	32.9	7.14	2	47.8	1.03
2001	39	54.3	7.87	2011	3	30.1	6.36	2	44.9	2.32
2002	39	54.0	7.75	2012	3	29.4	5.44	2	42.9	0.69
2003	39	53.2	8.10	2013	3	31.3	3.21	2	38.1	4.48
2004	39	52.0	7.47	2014	3	32.6	2.38	2	41.9	4.08
2005	39	50.0	7.66	2015	3	27.2	8.81	2	43.4	2.26
2006	39	48.8	7.34	2016	3	26.4	4.85	2	46.5	11.36
2007	39	46.9	8.15	2017	3	27.5	6.61	1	42.9	M
2008	39	45.5	8.49	2018	3	38.5	4.92	2	41.6	2.26
2009	39	42.8	9.32	2019	3	43.6	1.27	2	37.0	2.83

3B. Plant leaf count

	Demography Study				CTE Control Plots			CTE Trim Plots		
Year	N	Mean	SD	Year	N	Mean	SD	N	Mean	SD
1993	39	8.15	2.15	2003	3	5.54	1.50	2	3.79	0.24
1994	39	7.08	2.09	2004	3	5.14	2.01	2	3.44	0.09
1995	39	6.59	2.10	2005	3	4.50	1.32	2	7.01	0.02
1996	39	6.74	1.62	2006	3	5.50	0.87	2	7.74	3.73
1997	39	6.54	1.83	2007	3	4.31	0.27	2	6.29	2.77
1998	39	6.79	2.50	2008	3	4.39	0.98	2	6.23	0.38
1999	39	9.15	2.94	2009	3	5.54	1.73	2	6.36	0.51
2000	39	9.23	2.55	2010	3	5.25	0.66	2	5.56	0.98
2001	39	7.74	2.15	2011	3	5.96	0.07	2	6.34	2.00
2002	39	6.54	1.98	2012	3	5.96	1.77	2	5.63	1.24
2003	39	6.56	1.76	2013	3	5.17	1.61	2	5.04	0.65
2004	39	5.95	1.85	2014	3	5.21	0.71	2	6.13	1.23
2005	39	5.62	1.89	2015	3	4.08	1.01	2	5.55	0.78
2006	39	5.54	2.04	2016	3	4.67	0.58	2	8.06	0.62
2007	39	5.62	2.29	2017	3	3.83	1.61	1	5.87	M
2008	39	5.74	2.21	2018	3	10.25	5.45	2	7.80	0.28
2009	39	5.67	1.84	2019	3	8.89	4.17	2	6.13	1.23

Appendix 1. Continued.

3C. Reproduction (pct of longest leaf with sporangia)

	Demography Study		CTE Control Plots	CTE Trim Plots
Year	Pct	Year	Pct	Pct
1993	69%	2003	25%	50%
1994	64%	2004	14%	9%
1995	59%	2005	3%	58%
1996	64%	2006	19%	56%
1997	64%	2007	17%	19%
1998	67%	2008	19%	73%
1999	87%	2009	25%	40%
2000	82%	2010	0%	54%
2001	87%	2011	4%	44%
2002	79%	2012	0%	63%
2003	72%	2013	0%	38%
2004	59%	2014	0%	0%
2005	41%	2015	33%	45%
2006	41%	2016	0%	46%
2007	46%	2017	0%	13%
2008	41%	2018	58%	27%
2009	31%	2019	100%	63%