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Description of Life History and Reproductive Size Thresholds in Three High Elevation *Puya* (Bromeliaceae)

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ABSTRACT. The Andes are a hotspot for biodiversity and high species endemism for both plants and animals. The genus *Puya* (Bromeliaceae) lives throughout the Andes, including puna and the páramo ecosystems above 3500m. Here, we studied the life history in three species of *Puya*: *P. raimondii* in the Bolivian puna, and *P. cryptantha* and *P. goudotiana* in the Colombian páramo. We collected data on threshold size at flowering and clonal reproduction. All three species were found to have a consistent minimum size at flowering, while neither of the clonally reproducing species, *P. cryptantha* & *P. goudotiana*, demonstrated a minimum size for clonal reproduction. We also found a positive correlation between leaf length and fruit number for *P. cryptantha*. Our data supported that *P. raimondii* is fully semelparous and indicated that *P. goudotiana* and *P. cryptantha* may be semi-semelparous.

Keywords: Andes, puna, páramo, semelparity, semisemelparous

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INTRODUCTION

The genus *Puya* Molina (Bromeliaceae: Puyoideae) contains 228 species of rosette-forming terrestrial bromeliads endemic to Central and South America, from Costa Rica to Chile and Argentina (Gouda et al. 2018). *Puya* species are endemic to narrow regions at mid to high elevations from 1500 to 4000 m throughout the Andes and are particularly species rich in high elevation páramos and inter-Andean valleys (Jabaily & Sytsma 2013). A phylogenetically distinct group of endemic species lives at low elevations down to sea level in central Chile (Jabaily & Sytsma 2010). *Puya* share a rosette body plan with the rest of the Bromeliaceae, and all produce terminal inflorescences with numerous, showy flowers (Mora et al. 2007, Smith & Young 1987). Species vary greatly in rosette size and leaf number at flowering time and overall size of floral display, which is particularly variable between sympatric *Puya* species in northern Andean páramos (Julian Aguirre-Santorro, personal communication). Species also differ in their ability - or inability - to produce clonal rosettes, a potential mode of asexual reproduction and the mechanism for continuation of the vegetative body after the inflorescence.

Life history is often classified as semelparous (reproducing once during a lifetime) or iteroparous (reproducing multiple times), but this binary character may be more accurately described as a continuum of patterns of reproduction (Hughes 2017, Jabaily et al. 2021, Stearns 1992). *Puya* species span this continuum, and thus the genus may be a model for exploring life history evolution and adaptive life history features within the high Andean hotspots of biodiversity. In all species, the apical meristem produces the vegetative rosette, which switches from producing leaves and growing the vegetative body to making an inflorescence for sexual reproduction (Benzing et al. 2000). Each rosette produces one inflorescence; after the seeds are dispersed, the reproductive rosette begins to senesce. The only mechanism for continuation of that genetic individual is for axillary meristems, located above the base of each leaf, to produce a new clonal ramet. Each ramet has its own apical meristem and potential to produce an inflorescence and additional ramets. The majority of *Puya* species are multi-ramet iteroparous and produce many clonal ramets; individuals appear as a cluster of rosettes, potentially with many inflorescences (Jabaily et al. 2021).

Most *Puya* species are fully multi-ramet iteroparous, readily producing clonal ramets for many attempts at sexual reproduction. *Puya raimondii* is one of the few truly semelparous bromeliads, with individuals senescing without ever producing clonal ramets (Hornung-Leoni & Sosa 2005, Manzanares 2005). Some high-elevation *Puya* species also appear to have a decreased tendency to produce clonal ramets. Jabaily and Sytsma (2013) coined the term "semi-semelparous" to describe *Puya* species in which some individuals never produce clonal ramets prior to or after flowering and the individuals that do, only do so once they have transitioned to producing an inflorescence. Jabaily and Sytsma (2013) hypothesize that these species are in the process of evolving towards semelparity.

Both iteroparous and semelparous plants proceed through life cycle phases when they acquire and store enough energy to move forward, particularly for costly processes like sexual and asexual reproduction (Lacey 1986). Size is observed to be a strong predictor of the initiation of reproduction in a variety of species (Kuss et al. 2008, Lacey 1986, Miller et al. 2012, Mora et al. 2005, Werner 1975, Young 1984). For example, semelparous *Lobelia telekii* Schweinf. ex Engl., and iteroparous *Lobelia keniensis* Hemsl., two high elevation rosette plants on Mount Kenya, have a minimum size at sexual reproduction (Young 1990). Similarly, semi-semelparous *Puya hamata* L.B. Sm. has a uniform rosette diameter at the time of flowering (Garcia Meneses & Ramsay 2014).

In resource-limited habitats, the minimum size at reproduction will take longer to reach, and result in a longer life span, like that of long-lived semelparous plants (Young 1984, 1985). For many plants, both the likelihood of survival and flowering increase alongside plant size (Bonser & Aarssen 2009, Metcalf et al. 2003). This trend holds true in *Puya dasylirioides* Standl., with the number of mature fruits growing exponentially as rosette radius increases (Augspurger 1985). There is significantly less evidence for a size threshold in clonal or asexual reproduction, and evidence that does exist varies widely among genera and species (Ashmun & Pitelka 1985, Jabaily et al. 2021, Jabaily & Sytsma 2013, Mora et al. 2005, Schmid et al. 1995, Young 1984).

Our goal in this study was to determine a threshold in leaf and rosette size metrics for sexual and clonal reproduction. Physiological cues from body scaling for clonal and sexual reproduction in these species are unknown. For species that can reproduce clonally at some level like *P. cryptantha,* threshold size at reproduction is determined by a tradeoff between the benefits of beginning to sexually reproduce and the cost for future clonal rosette production and survival. Semelparous species such as *P. raimondii* do not face this same tradeoff (Wesselingh et al. 1997). For clonal reproduction, there is only evidence of a minimum size in some species, and evidence of tradeoffs is unclear (Ashmun & Pitelka 1985, Jabaily et al. 2021, Mora et al. 2005, Schmid et al. 1995, Young 1984). Here, we test for thresholds in leaf size (length and width) and rosette size (height and width) for sexual and clonal reproduction (pre- and post-flowering and with or without clonal ramets) in three different *Puya* species: *P. raimondii* Harms*, P. goudotiana* Mez and *P. cryptantha* Cuatrec. We predict that all three species will have a minimum size at flowering, but *P. goudotiana* and *P. cryptantha* will not have a minimum size for clonal reproduction.

METHODS

Study system & sites

This research examines three *Puya* species: *P. raimondii, P. goudotiana* and *P. cryptantha*. *Puya raimondii* is the largest bromeliad in the world and is known as the ‘Queen of the Andes’, by far the largest plant found in the central Andean puna region, near 10 m when in flower (Dorst 1957). *Puya raimondii* is a dramatic example of semelparity; individuals flower once at 80-150 years old before senescing, and likely cannot produce clonal rosettes to continue the vegetative body (Lambe 2008). A *P. raimondii* inflorescence can be 4-6 m tall with potentially hundreds of thousands of yellow-ish flowers (Garcia Lino 2005, Hornung-Leoni & Sosa 2005, Sgorbati et al. 2003). It is endemic to the puna of central and southern Peru and northern and central Bolivia, generally above the elevation where other species of *Puya* in the region grow. Populations of *P. raimondii* often live separately from each other in “rodales” on rocky hillsides in nutrient-poor soils (Augspurger 1985, Castillo et al. 2010, Garcia Lino 2005, Hornung-Leoni & Sosa 2005). The isolation of *Puya raimondii* populations has led to low genetic diversity, making it especially vulnerable to human and environmental threats (Lambe 2008, Sgorbati et al. 2003).

The other two focal species are *P. cryptantha* and *P. goudotiana*, both of which grow in boggy, water-logged areas and grasslands of the northern Andean páramo, sometimes at high regional population density. *Puya goudotiana* is one of the largest species of *Puya* after *P. raimondii*, reaching 5 m tall in flower with leaf lengths of over one meter (Smith & Downs 1974). Based on limited field observations, Jabaily and Sytsma (2013) categorized *P. goudotiana* as semi-semelparous. To our knowledge, no ecological studies have focused on *P. goudotiana*. A study by Mora et al. (2005) in the Piedras Gordas section of Chingaza National Park found that *P. cryptantha* generally produces one to three clonal ramets at a leaf length between 8.8 and 20.8 cm, and usually flowers at a leaf length between 12.0 and 35.7 cm, making the species iteroparous. These two species grow in sympatry within the Cordillera Oriental of Colombia in multiple páramos, often with other *Puya* species (e.g., *P. nitida* Mez., and *P. santosii* Cuatrec., etc.).

This research took place in Bolivian puna and Colombian páramo habitats (**Table 1, Figure 1**). The puna includes grass and shrubland above major forest belts between 3600 and 5000 m above sea level (Brush 1982, Morrone 2001). The páramo is similarly high in elevation (up to 4500 m), also above the forest belts, but has higher humidity and annual moisture levels with less seasonality (Balslev & Luteyn 1992, Luteyn 1999). The páramo is thought to be home to some of the fastest evolving lineages, and has high species endemism (Madriñán et al. 2013).

We collected data for *P. raimondii* (n=124, n=11 post-flowering, n=113 pre-flowering) in La Paz and Cochabamba, Bolivia in February 2018, and data on *P. cryptantha* (n=14 post-flowering, n=0 pre-flowering) and *P. goudotiana* (n=12 mother rosettes, n=101 including all clonal ramets) in Chingaza National Park, near Bogotá, Colombia in October 2018. For *P. raimondii*, we constructed four plots of ten plants in each of four sites using a randomly placed plot center, and chose general plot locations to cover the most space possible across the inhabited area. We thoroughly searched plots for small plants. For each plot within a population, we also recorded elevation (see **Table 1**).

For *P. goudotiana*, we constructed two 5 by 5 m plots at only one site, as *P. goudotiana* individuals were difficult to find and access. We selected a random cardinal direction and a random number of steps to walk to determine the location of each plot. Within these plots, we measured all *P. goudotiana* individuals.

Because *P. cryptantha* was very rare in the area we surveyed and only lived in one location we visited, we collected data on all plants without constructing plots.

Site	*Puya* species present	Coordinates	Elevation (m)
Comanche, La Paz, Bolivia	*P. raimondii*	16°96’09”S, 68°42’29”W	4069
Totora Kasa, Cochabamba, Bolivia	*P. raimondii*	17°39'56.8”S, 65°35'09.4”W	3822
Rodeo, Cochabamba, Bolivia	*P. raimondii*	17°23'44.5”S, 65°21'15.1”W	3795
Toro Huarko, Cochabamba, Bolivia	*P. raimondii*	17°36'43.2”S, 65°32'18.9”W	3307
Field Station, Cundinamarca, Colombia	*P. goudotiana*	4°31’32”N, 73°46’16”W	3234
Chingaza Gate, Cundinamarca, Colombia	*P. goudotiana, P. cryptantha*	4°31’32”N, 73°42’24”W	3383

Table 1. Field measurement locations with GPS coordinates, elevation and species present.

Figure 1. Photos **A-C** show *P. raimondii* in the puna of Bolivia. **D.** Many clonal ramets in *P. goudotiana* in the páramo. **E.** Post-flowering P. *goudotiana*. **F.** Post-flowering *P. cryptantha.* A-C, E by Leah Veldhuisen, D, F by Rachel Jabaily.

Size metrics

We measured longest leaf length (LLL), longest leaf width (LLW), rosette width (RW) and rosette height (RH) for all three *Puya* species, although we did not collect all four traits for each different category within each species due to logistical and time constraints. Both leaf measurements were taken from the longest leaf, which we selected visually. We made all measurements using a 100-m transect tape. To measure the longest leaf length, we placed the tape on the leaf tip, and fed it into the center of the rosette. We measured the width one third of the way into the rosette on the same leaf. We measured rosette width with two people holding the transect tape alongside the plant for *P. raimondii*, and with only one person holding the tape for smaller *P. goudotiana* and *P. cryptantha*. We measured *P. raimondii and P. goudotiana* with a clinometer for the plants taller than 150 cm, and *P. cryptantha* by holding the transect tape next to the plant for individuals below 150 cm. We only found *P. cryptantha* individuals submerged in a bog, therefore we could not measure rosette height for any of them. We were only able to find post-flowering *P. goudotiana* individuals on our last day of field work, and therefore only had time to collect LLL.

Reproductive metrics

For sexually reproducing *P. raimondii*, we determined reproductive category solely based on the presence or absence of an inflorescence and categorized individuals as pre- and post-flowering. We were not able to count fruits or seeds for *P. raimondii*, as the inflorescences are many meters off the ground and impossible to reach without a ladder.

For *Puya goudotiana*, we recorded pre and post flowering status in the same way as *P. raimondii*, and counted clonal ramets. We determined clonal ramets by proximity to larger rosettes, and counted individuals within 30 cm of a larger rosette as a ramet. We did not dig up ramets, so we cannot definitively say they were clonal reproduction and not seedlings in close proximity. We did, however, excavate one individual with multiple attached rosettes to confirm that clonal reproduction was possible in this species. We also did not count fruits or seeds for *P. goudotiana*, as all the individuals had decaying inflorescences and many seeds had already dispersed.

For *P. cryptantha*, we categorized individuals as pre and post flowering, counted ramets using the same criteria as *P. goudotiana*, and counted by hand the number of fruits per inflorescence.

Data Analysis

We plotted all size metrics, and performed two-sample t-tests after checking assumptions to test for significant differences between pre- and post-flowering individuals of *P. raimondii* and *P. goudotiana*, and those with and without asexual ramets for *P. cryptantha* and *P. goudotiana*. We tested for a relationship between fruit number and leaf length in *P. cryptantha* using a linear regression and calculated the Pearson correlation coefficient. All analysis was performed in R v 4.1.1 (R Core Team 2021).

RESULTS

Size metrics at sexual reproduction

All three species showed a threshold size for flowering (**Figure 2**). In *P. raimondii*, LLL, LLW, RW and RH were all significantly different for pre- and post-flowering individuals (LLL: *t*=4.56*, P*=.0004; LLW*: t*=5.47, *P*=.0002; RW*: t*=4.63, *P*=.0005; RH: *t*=7.60, *P*=2.64x10^{-5}). Longest leaf length and rosette height showed the greatest difference between pre and post flowering (**Figures 2A, 2D**). All but one post-flowering individual had leaves longer than 120 cm; there were also many individuals above this size that had not yet flowered (**Figure 2A**). Similarly, all but one post-flowering individual had rosette heights above 650 cm (**Figure 2D**).

In *P. goudotiana*, longest leaf length (LLL) was the only trait measured in both pre and post flowering individuals (see Methods), and the difference was significant (*t*=-18.46, *P*=2.26x10^{-10}; **Figure 2A**). Only plants with leaves longer than 77 cm had flowered, and pre-flowering individuals did not have leaves longer than 53 cm.

Finally, we could not find any pre-flowering *P. cryptantha* individuals. None of the flowering individuals had leaves less than 18 cm long, although all measured individuals had flowered (**Figure 2A**).

Size metrics at clonal reproduction

The two clonally reproducing species, *Puya cryptantha* and P. *goudotiana*, exhibited no distinct minimum size for clonal reproduction than for flowering (**Figure 3**). For *P. cryptantha*, individuals with and without clonal ramets had leaves ranging from 18 to 36 cm, and there was no significant difference in leaf length between the groups (t=-0.75, P = .47; **Figure 3A**). For the other two traits we measured in *P. cryptantha*, LLW and RW, there was also no difference in individuals with and without ramets (LLW: t=-1.12, P=.28; RW: t=0.37, P=.72; **Figures 3B, 3C**). In *P. goudotiana*, we found a difference between individuals with and without ramets for longest leaf width and rosette width, but not longest leaf length or rosette height (LLL: t=1.15, P=.25, LLW: t=2.06, P=.04, RW: t=3.35, P=.001, RH: t=0.91, P=.36; **Figure 3A-D**).

Finally, we found a significant positive correlation between longest leaf length and number of fruits per inflorescence for *P. cryptantha* (**Figure 4**; R^2=0.40*, P*=.01).

DISCUSSION

Overall, our results indicate a consistent narrow threshold vegetative size for sexual reproduction within all three species of *Puya*, but no threshold size for clonal

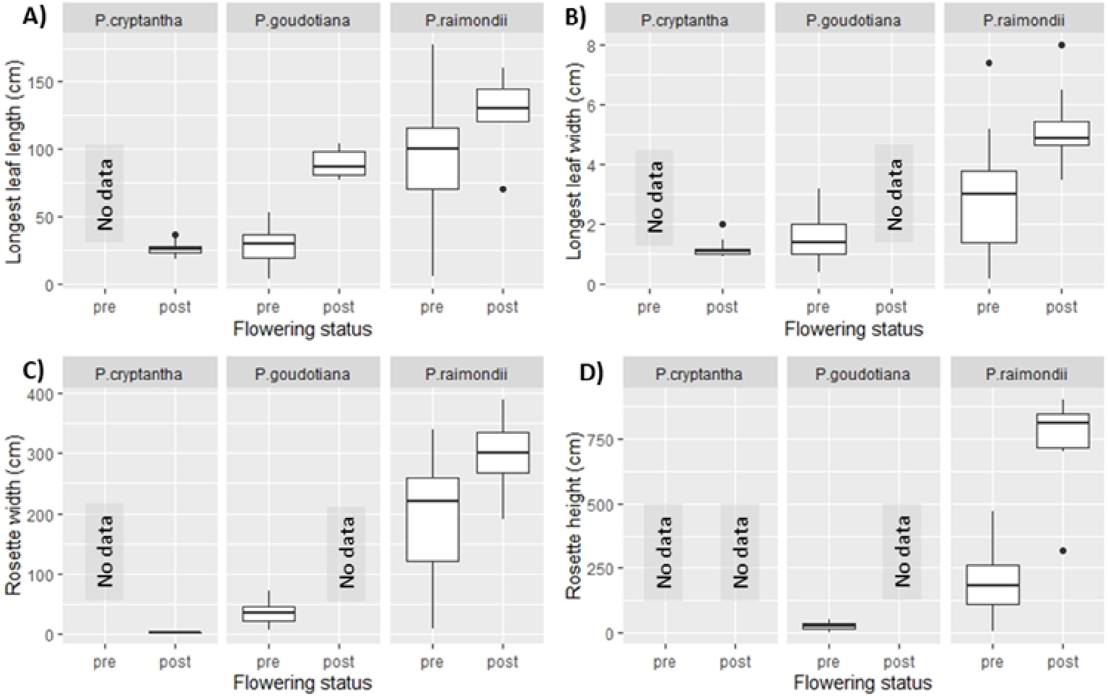

Figure 2. Boxplots showing size trait values for each species, divided by pre- and post-flowering individuals. **A.** Longest leaf length for all three species. **B.** Longest leaf width for all three species. **C.** Rosette width for all three species. **D.** Rosette height for all three species.

reproduction in *P. goudotiana* and *P. cryptantha*. The evidence for a threshold sexual reproductive size in the three studied *Puya* species differing in overall size, habitat, and life history, fits with a larger pattern of threshold size that has been described previously in other species (Augspurger 1985, Garcia Meneses & Ramsay 2014, Kuss et al. 2008, Mora et al. 2005, Young 1984). While a minimum size for flowering is an established phenomenon, reasoning for this threshold is less clear. This threshold may be due to meeting the minimum of stored fixed carbon, or the point when production of resources requires more energy than maintenance by the amount necessary to flower (Young 1984). Additionally, semelparous species' inflorescence size is more dependent on rosette size at reproduction than iteroparous species, which would make minimum rosette size particularly important for *P. raimondii* (Young 1984). Multiple studies have found semelparous species' reproductive output to be more sensitive to size at reproduction than that of iteroparous species (Schaffer & Schaffer 1977, 1979; Young 1990), but there is no evidence in our data that *P. raimondii* shows less variation in minimum flowering size than *P. cryptantha* or *P. goudotiana.* This may be because *P. raimondii* data were collected across a wider geographic range, or that *P. cryptantha* and *P. goudotiana* might be evolving towards semelparity.

Plants with larger flowers and less variable inflorescence size also tend to flower at larger sizes (Schmid et al. 1995). This finding may relate to *P. raimondii*, as it has large, open flowers like other members of *Puya* subgenus *Puya*, in contrast to the typical narrow flowers of most other species of the genus. Semelparous *Yucca whipplei* subsp. *whipplei* (Asparagaceae*)'*s reproductive output has been found to be highly responsive to increased photosynthate production from increased leaf surface area, while increased leaf surface area and photosynthate production had no impact on iteroparous *Yucca whipplei* subsp. *caespitosa*'s reproductive output (Huxman & Loik 1997). Although *P. cryptantha* and *P. goudotiana* are not entirely semelparous like *Yucca whipplei* subsp. *whipplei*, their apparent minimum size at flowering suggests their flowering may be similarly resource dependent (Mora et al. 2005, Young 1984).

Our data do not indicate a size threshold for clonal reproduction in *P. cryptantha*, although Mora et al. (2005) more extensively studied the species, and did find evidence of a threshold. A minimum size for branching was determined in iteroparous *Lobelia keniensis* (Young 1984). Because *Lobelia* and *Puya* are comparable in their growth forms and tropical high elevation habitats, a clonal reproduction size threshold in *Lobelia* could suggest a similar, convergently evolved pattern in iteroparous *Puya* species. *Puya cryptantha* individuals were very rare in our study area, and may be best studied in an area where they are more accessible for data collection.

Regardless of life history, all plants are partitioning their finite amount of energy towards competing goals of reproduction and individual growth, defense and

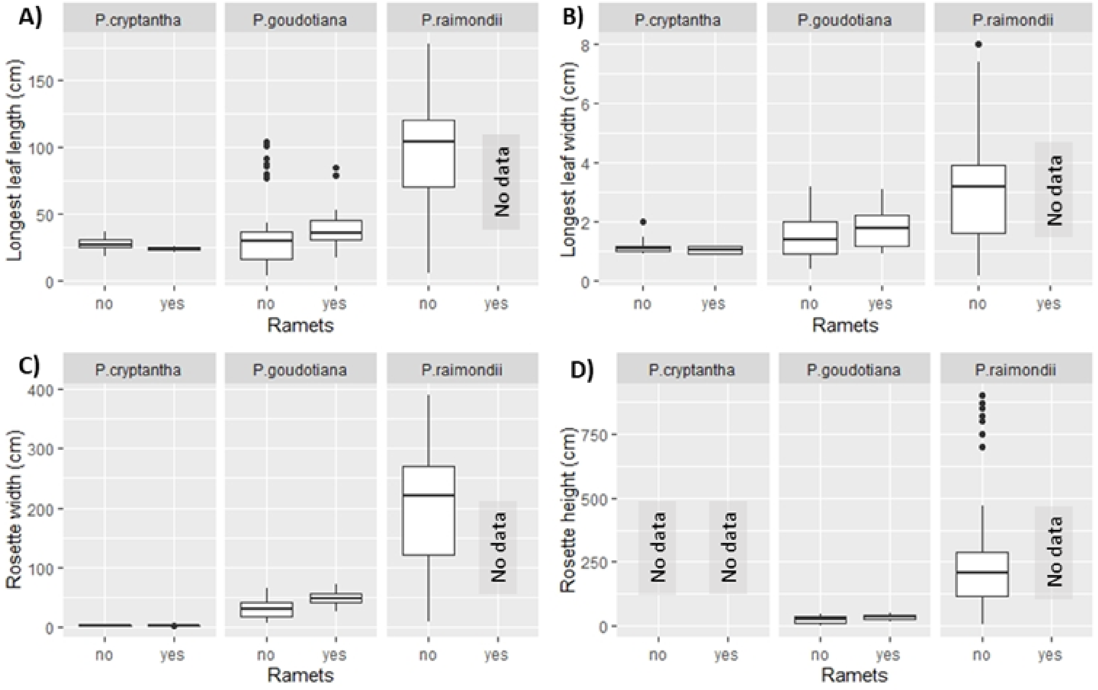

Figure 3. Boxplots showing each size trait for each species, divided by individuals with and without clonal ramets. **A.** Longest leaf length for all three species. **B.** Longest leaf width for all three species. **C.** Rosette width for all three species. **D.** Rosette height for all three species..

maintenance. Our data show evidence of this tradeoff in *P. cryptantha,* as individuals with clonal ramets tend to be smaller and produce fewer fruits, while larger individuals have no clonal ramets but more fruits. For this tradeoff to benefit the plant, the clonal ramets must compensate with sufficient reproductive output to offset the loss from the shorter inflorescence of the mother rosette; larger inflorescences are strongly correlated with higher reproductive success, partially due to increased pollinators and a higher portion of set seeds (Huxman & Loik 1997, Inouye & Taylor 1980, Schaffer & Schaffer 1977, 1979; Young 1990). It is unknown if the clonal ramets of *P. goudotiana* or *P. cryptantha* flower independently of the mother rosette, which would be important to consider when analyzing this potential tradeoff. Iteroparous *Lobelia keniensis* inflorescence size does not increase with higher soil moisture, but the number of rosettes per individual does, indicating that the clonal ramets are of significant importance to the plant, and are the preferable investment (Young 1990).

Puya raimondii is documented as a semelparous species, as it never reproduces clonally, and dies after flowering (Smith & Downs 1974). Our data match this expectation, as *P. raimondii* individuals that we visited had one terminal inflorescence and did not have ramets, and all with inflorescences appeared dead or senescing. *Puya cryptantha* and *P. goudotiana* both reproduce via ramets and flowers, but their life history strategies are harder to categorize as semelparous or iteroparous. The term "semi-semelparity," coined by Jabaily and Sytsma (2013), may be the correct categorization for both *P. cryptantha* and *P. goudotiana*, as both species have significantly reduced cloning ability compared to low-elevation *Puya* species and sympatric *P. nitida.* Some individuals of *P. goudoitana* and *P. cryptantha* were found flowering as a single rosette with no attached ramets. Additionally, we never saw either species' clonal ramets flower on their own, indicating that they may have lost the ability to flower while evolving towards true semelparity. It is hard to tell if a flowering rosette is the initial seed-grown mother, or if the flowering rosette was the product of clonal reproduction from a long-decayed mother.

While it has been established that *P. raimondii* is a semelparous species, there is currently no consensus of why this extreme life history strategy evolved in the species (Padilla 1973, Smith & Downs 1974). The evolutionary history of *P. cryptantha* and *P. goudotiana*'s transitional semi-semelparous life history strategies is similarly in need of further study. From other comparative studies, there is evidence of semelparity being associated with a drier site of one ecosystem, or the drier of two similar ecosystems (Young 1984). This mirrors the trend found in the three *Puya* species studied here, as the puna is significantly drier than the páramo and is the home of the only fully semelparous *Puya* species. Similarly, Young and Ausgsperger's (1991) bet-hedging model for semelparity evolution suggests that highly variable and unpredictable environments may favor semelparity, especially in habitats prone to unpredictable drought like the puna. This trend offers a plausible explanation for why so many it-

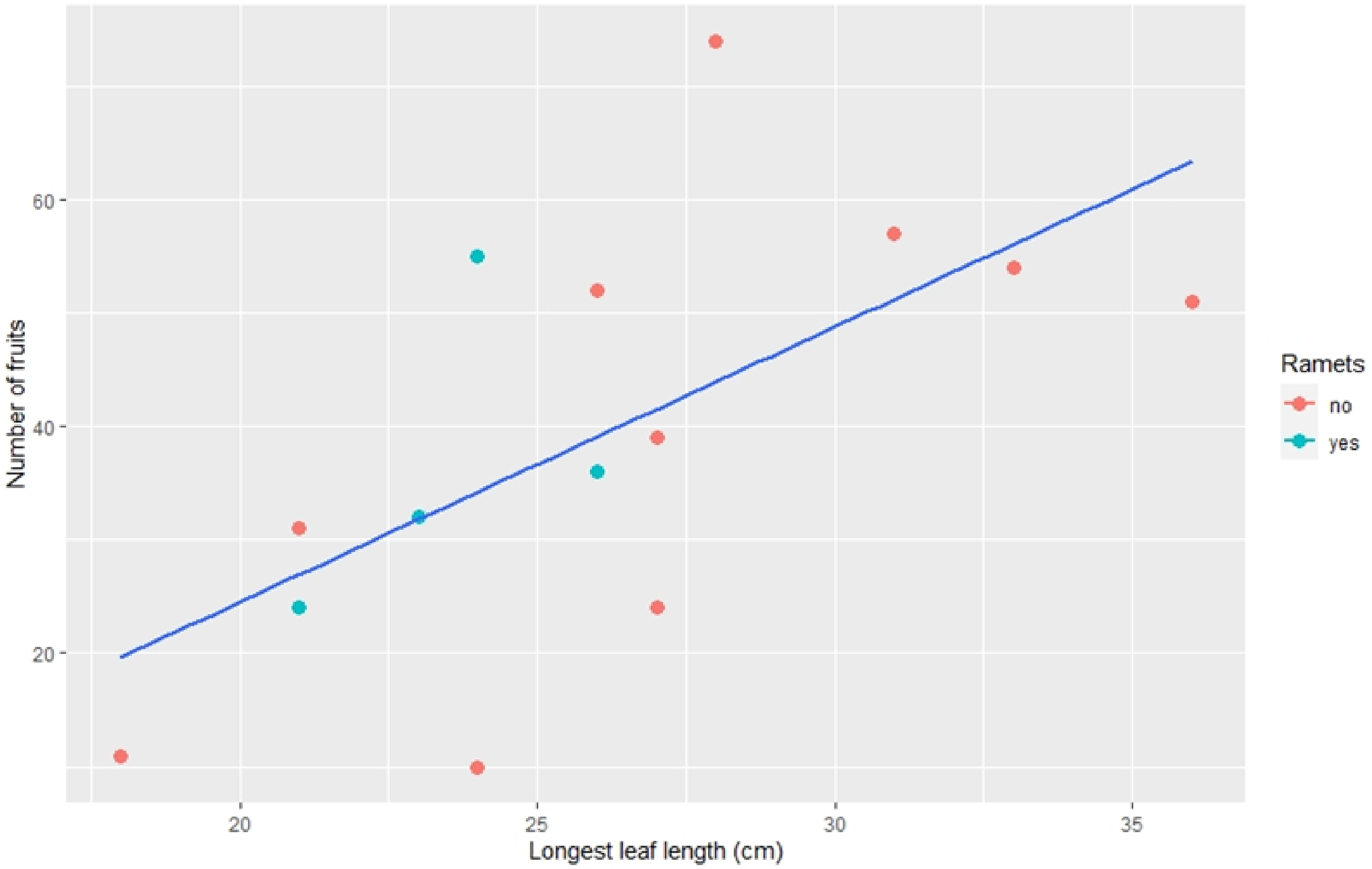

Figure 4. Regression between the estimated number of fruits per inflorescence and longest leaf length in *P. cryptantha* individuals (R^2=0.40, *P*=.01).

eroparous and non-fully semelparous species inhabit the páramo, as its rainfall is consistent throughout the year and experiences significantly less seasonality than the puna. Based on Young's 1990 study, plants with high survivorship, frequent reproduction and wet habitats require 13 times more reproductive output than iteroparous species to develop semelparity.

Plants in dry sites with low survivorship and less frequent reproduction only require five times the reproductive output to evolve semelparity (Young 1990). This finding is supported by the fact that semelparous plants are more resource-dependent than their iteroparous counterparts (Huxman & Loik 1997; Young 1984, 1990). For semelparous plants, resources are essential to building an inflorescence, which takes longer in the resource-limited environments where large semelparous plants are common (Smith & Young 1987, Young 1990). Giant inflorescences are predicted by Young and Augsperger's (1991) reproductive effort model of semelparity, which states that ever-increasing reproductive effort may favor semelparity, as larger inflorescences can be favored by pollinators and thus result in increased reproductive output (Rocha et al. 2005; Schaffer & Schaffer 1977, 1979). While pollinators have not been found to be major factors in the reproductive effort model (Young & Augspurger 1991), their presence and activity may be important in further determining how semelparity evolved in *P. raimondii*, and may be convergently evolving in the páramo lineages.

While our data **(see details in supplemental spreadsheet)** address important basic questions about the reproduction of *P. raimondii, P. cryptantha,* and *P. goudotiana*, there are still many areas for continued investigation. Specific age-class survivorship data for *P. raimondii* would allow for evaluation of the demographic and bet-hedging models of semelparity evolution. Data on pollinator preference and reproductive effort, output and success would also help to evaluate the reproductive effort model success would also help to evaluate the reproductive effort model and clarify habitat and pollinator role in life history evolution for the *Puya* genus. Comprehensive data on the environmental conditions of the puna and páramo would also be useful. Finally, reproductive output and success for semelparous and iteroparous species has been quantified in other genera, and would be interesting to analyze for *Puya* to test for evidence of the tradeoff between semelparity and iteroparity (Young 1990).

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DESCRIPTION OF LIFE HISTORY AND REPRODUCTIVE SIZE THRESHOLDS IN THREE HIGH ELEVATION *PUYA* (BROMELIACEAE)

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