MADROÑO, Vol. 53, No. 1, pp. 60–64, 2006

OBSERVATIONS OF FROND GROWTH AND DEVELOPMENT IN *PENTAGRAMMA TRIANGULARIS* SUBSP. *TRIANGULARIS* (PTERIDACEAE) OF SOUTHERN CALIFORNIA

GARY B. PERLMUTTER
North Carolina Department of Environment and Natural Resources, Raleigh Regional Office, 3800 Barrett Drive, Raleigh, NC 27609
gary.perlmutter@ncmail.net

ABSTRACT

Frond growth and development of *Pentagramma triangularis* subsp. *triangularis* was examined in canyon populations in Ventura County, California during the winter growing season of 2003. Fronds developed from emerging croziers to full size within 35 days and reached sexual maturity by 70 days. Frond growth occured in two stages with stipe elongation nearly complete when the crozier began to unfurl, about a week before full maturation of the entire frond. Discernable developmental stages are described as well as their respective ages. Fern growth occurred both prior to and after the study frond monitoring period, indicating multiple growth flushes throughout the growing season, possibly related to rain events. Based on these preliminary results, suggestions are offered for further study.

Key Words: frond growth, *Pentagramma triangularis*, phenology, Pteridaceae, southern California.

Pentagramma triangularis (Kaulf.) Yatsk., Windham & E.Wollenw. (Pteridaceae) grows in western North America (Yatskievych and Windham 1993) inhabiting rock crevices within a variety of habitats including woodlands, chaparral and deserts (Smith 1998). Plants of this species complex, commonly called goldback and silverback ferns, produce 10–35 fronds (7–40 cm) from a short, slender rhizome. Each frond consists of a brown to black stipe and a deltate-pentagonal, 1–2 pinnate-pinnatifid blade as wide as long (4–9 cm). The abaxial surface of blades are covered with silver or gold farina, hence their common names. Plants are winter-green perennials producing fronds at first rains, which persist until hot weather, when their blades curl due to drought (Yatskievych et al. 1990; Smith 1998).

The ecology and life history of these ferns are largely unexplored. Except for having a growing season that coincides with winter rains, frond phenology of *P. triangularis* is largely undocumented. This lack of knowledge regarding frond phenology is representative of the pteridophytes in general, with few studies reported in the literature (e.g., Sato 1982; Willmot 1989; Sharpe and Jernstedt 1990; Johnson-Groh and Lee 2002).

The objectives of this study were to measure the growth and to describe the developmental stages of *P. triangularis* subsp. *triangularis* fronds. This report presents the first detailed phenological description for *Pentagramma* and lays a foundation for further study of *P. triangularis* life history, which could provide a better understanding of this fern's adaptation to its seasonally dry habitat.

METHODS

Pentagramma triangularis subsp. *triangularis* ferns were monitored in two small populations along the Cozy Dell Trail in Sheldon Canyon, Ventura County, California (34°28′39″N, 119°17′09″W). The study area, located 22 km from the coast at an elevation of 427 m, is in the Transition Climate Zone and is influenced by a mixture of maritime and continental air masses with hot, dry summers and mild, rainy winters (Bailey 1966; Hickman 1993). Total rainfall for the 2002–2003 rainy season (from October through April) in Stewart Canyon, 3.2 km ESE of the site, was 454 mm with most falling in November, December and March. Temperatures taken at Matilija Dam, 2.4 km WNW of the study site for the same period, included a winter minimum of 6.3°C in December and spring maximum of 22.8°C (Ventura County Watershed Protection District, unpublished data). However, this rainy season was atypical in being warm, with a dry spell in January (Fig. 1).

The study area is a steep, north-facing slope with cobble and boulder talus of sedimentary rocks (Norris and Webb 1990) in coastal oak woodland/mesic chaparral dominated by a patchy canopy of *Quercus agrifolia* Née (Fagaceae) with a dense shrub layer of *Ceanothus cuneatus* (Hook.) Nutt. (Rhamnaceae) and *Heteromeles arbutifolia* (Lindl.) M. Roem. (Rosaceae). Understory seed plants included *Toxicodendron diversilobum* (Torr. & A. Gray) Greene (Anacardiaceae), *Diplacus* (=*Mimulus*) *longiflorus* Nutt. (Phrymaceae), and undetermined grasses and forbs. Other ferns in this area included *Polypodium glycyrrhiza* D.C. Eaton (Polypodiaceae),

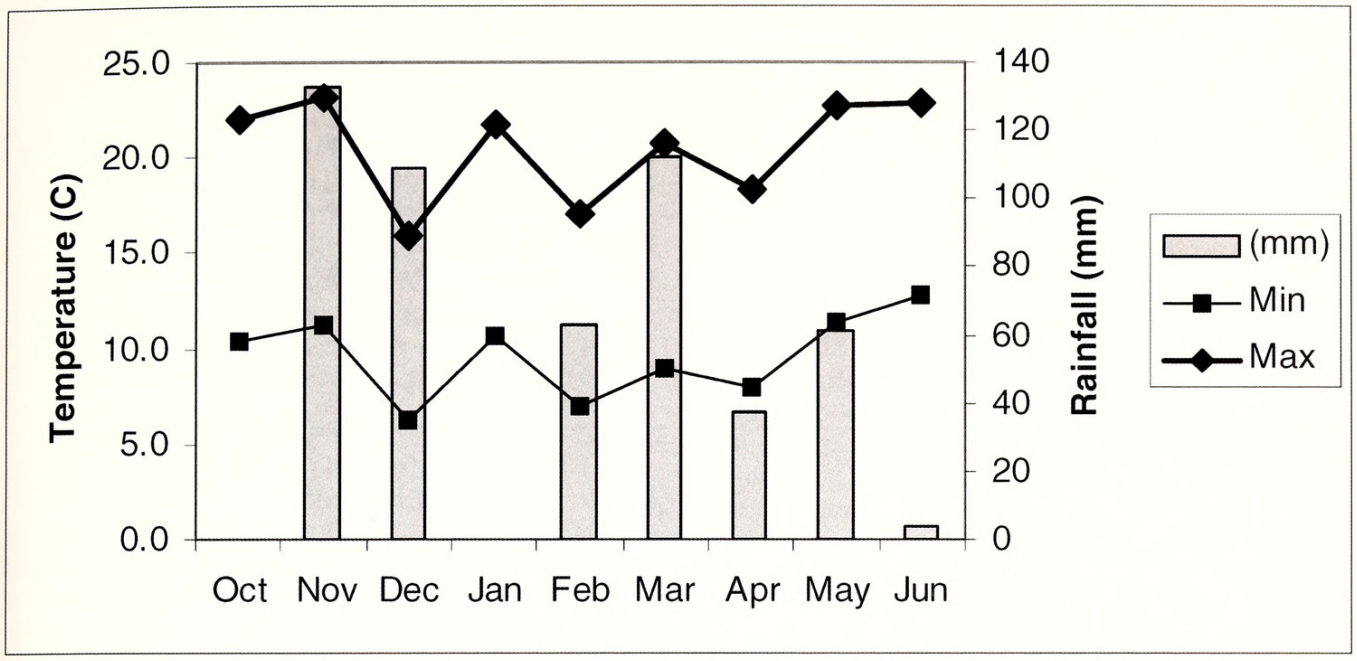

FIG. 1. Rainfall and temperature patterns for the October 2002–April 2003 rainy season, extended to June 2003, at Stewart Canyon and Matilija Dam meteorological stations, respectively (data source: Ventura County Watershed Protection District).

Pallea andromediflora (Kaulf.) Fée (Pteridaceae), and *Dryopteris arguta* (Kaulf.) Maxon (Dryopteridaceae). Exposed rock surfaces harbored *Selaginella bigelovii* Underw. (Selaginellaceae) plus foliose and crustose lichens.

The study populations, separated by 0.2 km, consisted of 24 and 25 ferns each, with densities of approximately 1.6 and 6.3 ferns m^{-2}, respectively (densities appeared determined by amount of rocky edge microhabitat). Ten ferns per population were haphazardly selected for study. Data from the two populations were lumped for analysis because no significant differences were observed between them.

On 5 January 2003, I selected for study the crosier on each fern that was closest to the soil surface (≤10 cm height), and thus recently emerged, and marked its stipe with correction fluid for growth monitoring. Weekly measurements of marked fronds included stipe and rachis lengths (while in crozier, head diameter was measured to represent this variable); for developmental stage classification, the frond's development (i.e., shape, color, farina, and presence of sporangia) was also described. Lengths were measured until fronds had reached their full size (i.e., no increase for three consecutive measurements), but developmental observations continued until the frond senesced. Three fronds failed to grow and develop completely, and for these a replacement crosier on the fern was marked and monitored. Two of these were on one plant that senesced prematurely, in March; this fern was on an exposed rockface.

Growth curves were developed from the stipe and rachis length means. Other phenological observations of these plants were also made at irregular intervals, including after the period of frond growth monitoring. Voucher specimens were deposited at Santa Barbara Botanic Garden Herbarium (SBBG).

RESULTS

Frond Growth and Development

From 5 January through 26 March 2003 development of study fronds passed through seven discernable stages from crozier to mature sporophyll. Growth curves are shown in Figure 2, while the mean (±1 SD) frond sizes and their respective percent mature sizes for each developmental stage are listed in Table 1 and included in the text below. Frond stages are described below.

(1) Young Crozier (YC): Fronds first appeared light green, with stipe lengths from emergence (0 cm) to 5.5 cm. Crozier diameters averaged 0.32 ± 0.11 cm.

(2) Mature Crozier (MC): Stipe lengths averaged 9.3 ± 3.7 cm or 64 ± 16% of the full length and darkened from the base toward the tip. Croziers grew to 0.44 ± 0.14 cm diameter with pinnae visible. Fronds were in this stage for 7–14 days.

(3) Unfurling Frond (UF): Blade development began with croziers opening at 14–28 days after emergence, lasting seven days or less. Stipes elongated on average to 94 ± 4% of their mature length and rachises reached a mean of 30 ± 9.5% of mature size.

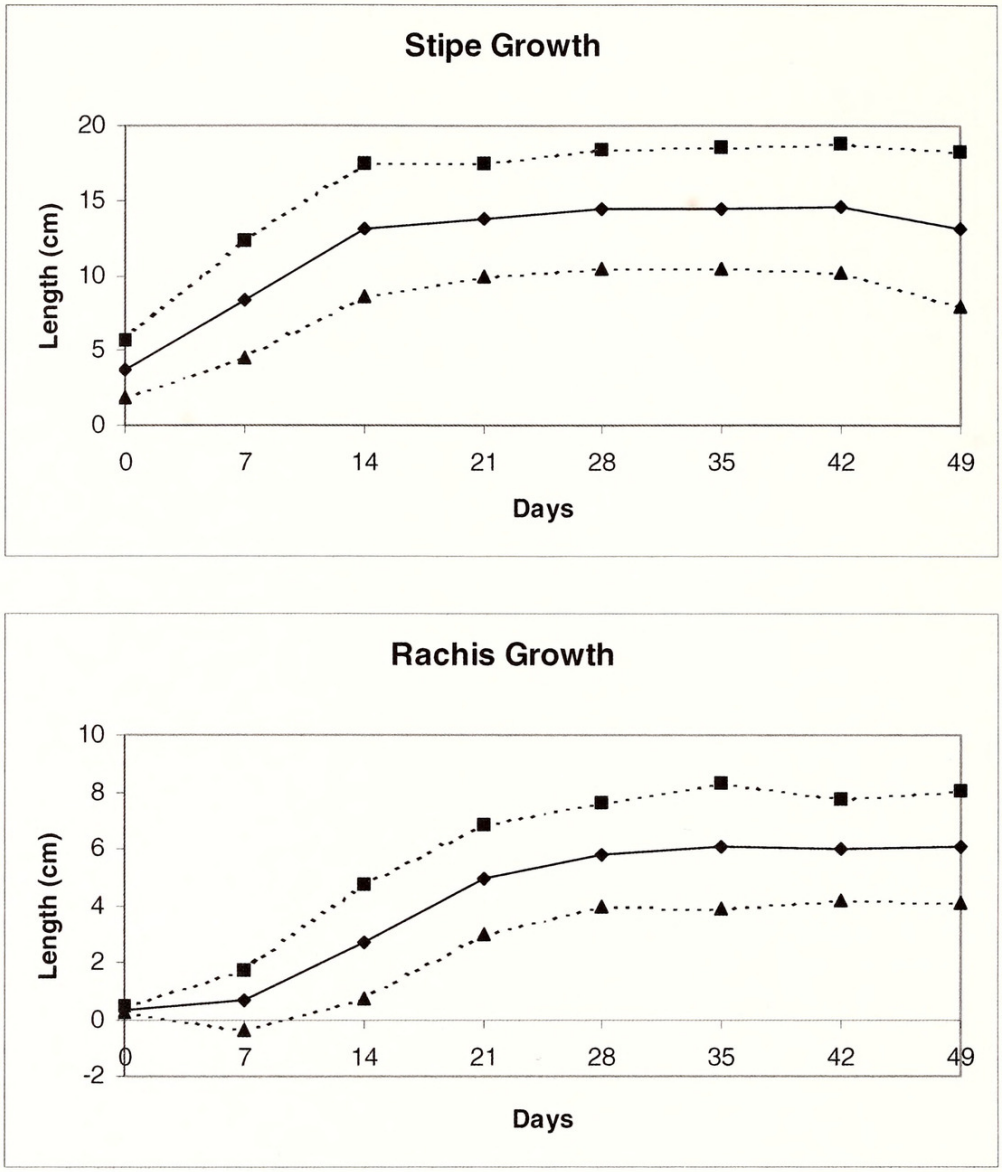

FIG. 2. Mean (± 1 SD) growth curves of frond stipes and rachises from 18 *Pentagramma triangularis* subsp. *triangularis* ferns monitored in Sheldon Canyon, California, USA during 05 January–16 March, 2003.

(4) Immature Frond (IF): By 7–21 days, blades were fully open at this stage with thin shiny, yellowish green pinnae and pinnules that expanded as the blade developed. Stipes reached their full length while rachises elongated to an average of 80 ± 15% (range 53–100%) of full size.

TABLE 1. MEAN ± 1 SD LENGTHS PLUS PERCENT OF MEAN MATURE SIZES OF *PENTAGRAMMA TRIANGULARIS* SUBSP. *TRIANGULARIS* FROND DEVELOPMENTAL STAGES. Observations made in Sheldon Canyon, Ventura County, California, USA, 05 January–16 March with Sporophyll Observations until 01 June 2003. Number of observations included multiple examinations of 18 monitored ferns (one frond per plant). Monitoring of stipe growth ceased once fronds reached full size. See text for stage definitions.

Stage	Frond age (Days)	Stipe		Rachis		No. Observations
		Length (cm)	% Mature	Length (cm)	% Mature	
YC	0–7	3.3 ± 1.6	26 ± 9	0.3 ± 0.1	6 ± 1	8
MC	< 7–14	9.3 ± 3.7	64 ± 16	0.4 ± 0.1	8 ± 2	16
UF	14–28	13.1 ± 4.3	95 ± 6	2.0 ± 1.1	30 ± 9	8
IF	14–35	14.7 ± 3.5	100	5.0 ± 1.5	81 ± 16	25
MF	21–63	14.4 ± 4.3	100	5.9 ± 1.8	100	56
IS	63–77	N/A	N/A	N/A	N/A	14
MS	70+	N/A	N/A	N/A	N/A	48

(5) Mature Frond (MF): Blades developed a dull green color with light farina abaxially by 21–35 days. During frond maturation some stipes developed a bent stature.
(6) Immature Sporophyll (IS): Sporangia were first observed at 56–70 days as a light brown dusting on the abaxial surface.
(7) Mature Sporophyll (MS): Fronds appeared dark green adaxially; farina were mixed with dark brownish sporangia on the abaxial surface. Growth-monitored fronds were first observed in this stage by 63–77 days.

Not all crosiers were of equal length at the start of monitoring, thereby lowering precision of this growth study. By 26 July, 175 days after monitoring began, all study fronds had curled adaxially in senescence, exposing the farinose abaxial surface.

Duration of frond (i.e., stipe and rachis) growth averaged 19.8 ± 5.7 days. Stipe elongation averaged 12.4 ± 5.3 days, which was a significantly shorter growth period than for the frond entire (t-test, $P = 0.0004$). Growth duration of the rachis was equivalent to growth duration of the frond entire, because it included rachis growth while in the crosier head.

Phenology

At the onset of this study (5 January 2003), ferns had young as well as older fronds, the latter already in the mature sporophyll stage. On 15 December 2002, ferns in the area also were observed exhibiting the full range of frond developmental stages from young crosier to mature sporophyll. During this study, crosiers appeared on the study plants as late as 23 March, when most of the growth-monitored fronds were already in the mature sporophyll stage. Young crosier observations appeared to follow rain events of >50 mm within approximately 14 days, but data were insufficient for statistical analysis. By 26 July, however, all fronds on plants in the study area had senesced.

Discussion

The growth of monitored fronds was completed within 35 days; reproductive maturation of fronds was completed within 70 days. Frond development passed through a series of discernable stages, which are useful for describing a frond's growth and reproductive state. Observations of older fronds at later stages growing concurrently with younger fronds indicated that frond production and growth occurs in successive flushes. Determining how many flushes of new fronds can occur within a season and how they are triggered will probably require observations over several years, especially considering the variable nature of the southern California climate (Nilsen and Muller 1981).

While this note describes the frond growth, development and phenology in *P. triangularis* subsp. *triangularis*, the results are based on observations at a single site during only part of one year; thus, further study is needed to confirm and elaborate on these findings. In particular, populations should be monitored for consecutive years, and observations of reproductive development should include microscopic examination of freshly collected sporophylls. Questions for future investigation include: 1) what environmental factors (e.g., rain, temperature, daylength) trigger onset of fern growth and how quickly do ferns respond to these factors; 2) do flushes of growth coincide with periodic rain events within a season, and if so, how many flushes can occur in a year; 3) how long is the growing season for this species, and how long do individual fronds live before senescence;, 4) what triggers sporulation, and how long is sporangial development prior to sporulation; 5) how does habitat and microhabitat affect the phenology; and 6) how does the phenology of *P. triangularis* subsp. *triangularis* compare with that of co-occurring fern taxa.

Acknowledgments

I thank Ruth Kirkpatrick, John C. Hunter and two anonymous reviewers for their helpful comments on earlier drafts of this manuscript. David Laak of the Ventura County Watershed Protection District provided climatic data for the study period.

Literature Cited

Bailey, H. P. 1966. Weather of southern California. University of California Press, Berkeley, CA.

Hickman, J. C. (ed.). 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, CA.

Johnson-Groh, C. L. and J. M. Lee. 2002. Phenology and demography of two species of *Botrychium* (Ophioglossaceae). American Journal of Botany 89:1624–1633.

Nilsen, E. T. and W. H. Muller. 1981. Phenology of the drought-deciduous shrub *Lotus scoparius*: climatic controls and adaptive significance. Ecological Monographs 51:323–341.

Norris, R. M. and R. T. Webb. 1990. Geology of California, 2nd ed. John Wiley and Sons, Inc. New York, NY.

Sato, T. 1982. Phenology and wintering capacity of sporophytes and gametophytes of ferns native to northern Japan. Oecologia 55:53–61.

Sharpe, J. N. and J. A. Jernstedt. 1990. Leaf growth and phenology of the dimorphic herbaceous fern *Danea wendlandii* (Marattiaceae) in a Costa Rican rain forest. American Journal of Botany 77:1040–1049.

Smith, C. 1998. A Flora of the Santa Barbara region, California, 2nd ed. Santa Barbara Botanic Garden and Capra Press, Santa Barbara, CA.

WILLMOT, A. 1989. The phenology of leaf life spans in woodland populations of the ferns *Dryopteris filix-mas* (L.) Schott and *D. dilatata* (Hoffm.) A. Gray in Derbyshire. Botanical Journal of the Linnean Society 99:387–395.

YATSKIEVYCH, G., M. D. WINDHAM. 1993. Pentagramma. Pp. 149–151 *in* Flora of North America Editorial Committee (ed.), Flora of North America, north of Mexico, Vol. 2. Pteridophytes and gymnosperms. Oxford Univeristy Press, New York, NY.

———, ———, AND E. WOLLENWEBER. 1990. A reconsideration of the genus *Pityrogramma* (Adiantaceae) in western North America. American Fern Journal 80:9–17.