THE EFFECTS OF SOIL MOISTURE, PH, AND LIGHT AVAILABILITY ON SPORE PRODUCTION BY A COMMON FERN

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Abstract. We examined the relationship between spore production by a common fern species and three abiotic variables (soil water, soil pH, and light) in the Monteverde Cloud Forest. High soil water could lead to generally rapid growth and high spore production, or spore production could be highest in areas with more sunlight (if ferns are light limited or if sexual reproduction is triggered by water stress). Ferns with fertile fronds occurred in wetter soils than ferns without fertile fronds. However, among individuals with some spore production, there was no relationship between soil moisture and number of fertile fronds or abundance of sori. There was no relationship between sori production and either light availability or soil pH. The production of fertile fronds and sori is positively correlated with natural variation in soil moisture.

Key Words: fern viability, Thelypteris, *tropical premontane forest*

INTRODUCTION

As with any understory plant, fern populations experience spatial variation in moisture and light that is related to variation in canopy cover. Many fern species are restricted to shaded environments with high soil moisture and a limited range of soil pH (Foster 1985). Individuals of one abundant fern species at Monteverde seemed to vary greatly in the extent to which they were producing spores. The production of fertile fronds could either be an indicator of rapid growth and a generally favorable environment or of a fern under environmental stress. We hypothesized that spore production would be related to natural gradients in light and soil water. It could be that high soil water leads to rapid growth and high sori production. We would also predict high sori production in moist microsites if the reproduction by fern sporophytes is linked to the ecological requirements of fern gametophytes (fern gametophytes require free water for spore germination, prothallus growth and fertilization by flagellate sperm; Raven et al. 1986). Alternatively, if ferns are frequently light limited, or if sexual reproduction is triggered by water stress, spore production may be highest in relatively sunny sites. We evaluated these hypotheses by examining the production of fertile fronds and sori in relation to soil moisture, light availability, and soil pH.

METHODS

We sampled 39 individuals of a common species of fern (probably *Thelypteris* sp.) in the forest of the Estación Biológica in Monteverde, Costa Rica. Individuals were at least 5 m apart and haphazardly chosen. All sampling took place on 21 January 1998 on several trails above the Estación (1540 - 1810 m asl). For each fern, we scored presence or absence of fertile fronds. For all ferns with fertile fronds, we counted the proportion of fronds with sori and the number of sori per pinnule (from a subsample of 5 pinnulae). Within a 25 cm radius of each fern we measured soil pH and percent moisture (average of 3 measurements taken with a DEMETRA E.M. System Soil Tester) and percent open canopy (using a spherical densiometer, average of 4 readings).

We used t-tests to test for differences in soil moisture, light availability, and soil pH between ferns with and without sori. We used correlations to examine relationships between the three environmental parameters and the proportion of fronds with sori and the number of sori produced per frond. All proportional data were arcsin transformed prior to analysis.

RESULTS

Soil moisture measurements ranged from 0.3 - 30%, openness of canopy ranged from 2 - 14%, and soil pH ranged from 3.7 - 6.4. Of the 39 ferns sampled, 17 had fertile fronds with sori. Ferns with fertile fronds occurred in wetter soils more

often than those without fertile fronds ($t_{37} = 2.80$, $P = 0.008$; Fig 1). Among individual ferns with fertile fronds, the proportion of fronds with sori and the number of sori per pinnule were not correlated to soil moisture ($r = 0.11$, $P = 0.66$ and $r = -0.20$, $P = 0.43$ respectively; $n = 17$). There was little variation in sori per pinnule (mean ± SE = 4.39 ± 0.47) and much of that variation was probably an artifact of pre-sampling dispersal of spores from some older ferns. Neither light availability nor soil pH were related to the number of sori produced (Table 1).

DISCUSSION

Fern reproduction, as indicated by the presence of fertile fronds with sori, was strongly associated with high soil moisture. Ferns in areas of low soil moisture areas were less likely to invest in sori production. However, the proportion of fertile fronds and number of sori per pinnule were not related to soil moisture, indicating that water availability does not influence the extent of spore production, even though it may influence whether or not spore production occurs at all. These two aspects of sori production may be developmentally constrained and have only limited phenotypic variation.

There was no obvious relationship between sori production and light availability. This may be because the forest had a relatively homogeneous canopy and the variability in canopy cover was not large enough to impact fern physiology. We also did not find a relationship between sori production and soil pH. This suggests that the fern species we sampled is able to tolerate a considerable range of soil pH. Different species of fern may have varying environmental requirements for growth and reproduction, and a similar study across several species might reveal such patterns.

There are two possible explanations as to why ferns produce more sori in wet environments then in dry. It is possible that ferns in wet and dry habitats allocate the same proportion of their total reproductive investment towards sori and vegetative growth but simply have more resources to invest toward reproduction in a wet environment. Alternatively, ferns may allocate more of their reproductive investment toward

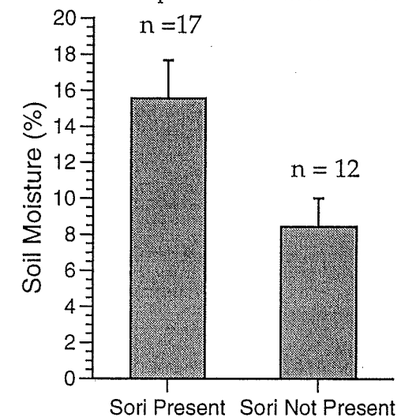

FIG. 1. Soil Moisture beneath ferns with and without sori (means ± 1 SE).

spores in environments that favor success of gametophytes. These alternatives could be separated by a study that compares spore production and vegetative growth across environmental gradients.

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TABLE 1. Results of analyses (t-tests and correlations) comparing three measures of sori production with light availability and soil pH.

	Light Availability		Soil pH	
Sori Present vs. Not Present (n = 29)	t = 0.06	P = 0.95	t = 0.06	P = 0.95
Proportion of Fronds with Sori (n = 17)	r = 0.06	P = 0.71	r = -0.04	P = 0.79
Number of Sori per Pinnule (n = 17)	r = 0.10	P = 0.55	r = 0.01	P = 0.93