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THE EFFECT OF THE LIGHT ENVIRONMENT ON POPULATION SIZE OF THE EPIPHYTIC HERB, *LEPANTHES RUPESTRIS* (ORCHIDACEAE)

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Introduction

The demographic dynamics of plant populations will depend on the relative role of density-dependent versus density-independent factors on population regulation. Density-independent factors (i.e. changes in climate, fire, hurricanes) will affect plant survival and reproduction within a population in a manner that is independent of the density of individuals. The amount of light that a plant receives is one such factor that will affect its mode of development, growth and reproduction independent of plant density. Life history traits may evolve when light requirements are a limiting factor in the survival of plant populations. Our research group has used the orchid *Lepanthes rupestris,* a common miniature orchid that inhabits riparian habitats mountain forests of Puerto Rico (Ackerman 1995, Tremblay 1997) as a model to understand the factors that affect the persistence of epiphytic orchids. In this study we were interested in determining if population size is affected by the amount of light perceived by the population.

Prior work on *L. rupestris* has studied demographic parameters and potential role of density-dependent effects in population regulation (Rivera-Gómez *et al.* 2006). At best, there was a positive (although very weak) relationship between the ratio of seedlings and juveniles to adults and population size, suggesting that some facilitation may be occurring. However, there was no relationship between the ratio of seedlings or juveniles to adults as population size regardless of substrate type (boulders or trees) suggesting that density dependence for population regulation in *L. rupestris* is likely to be rare. (Rivera-Gómez *et al.* 2006). Since density does not control the population size we sought to determine if the light environment affects population size. There are numerous studies on the effects of light environment on plant growth in orchids (Soontornchainaksaeng *et al.* 2001, Stancato *et al.* 2002), but not on population size.

We took advantage of a long-term census program of a metapopulation of *L. rupestris* in the Luquillo Mountains in Puerto Rico (Tremblay *et al.* 2006) to study the relationship between variation in light environment among plant patches (or subpopulations) and population size. As a preliminary study of the effect of the light environment on survivorship of populations we tested the following hypothesis. Under a theoretical light environment indicator distribution we expect that there should be an optimum light environment and that population size should reflect this distribution. Consequently there should be light environments where the indicator is in excess or below the required minimum, and thus populations size at these extremes should be generally small. A previous study investigating the relationship between light environments on growth rate of individuals has shown that growth rates in *L. rupestris* support this hypothesis (Fig. 1; Fernandez *et al.* 2003). Accordingly we should observe

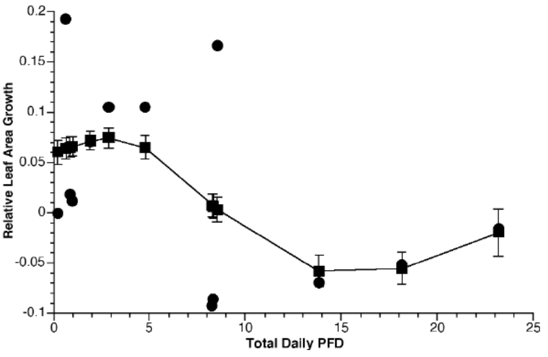

FIGURE 1: The cubic spline analysis of correlation between amount of light and growth rate is nonlinear and suggest maximum growth rate in the range of 1 to 5 Photon flux density (PFD), while higher PFD results in reduced growth rate. The data point are scattered below and above the best non-parametric fitness line suggesting that other environmental variables are likely to influence growth (Fernandez *et al*., 2003).

in an environment of too little or too much light small population sizes.

Plant species

Lepanthes rupestris is an orchid endemic to Puerto Rico that is commonly found along the riverbeds of the northwestern slopes of the Luquillo Mountains (Ackerman 1995, Tremblay 1997). It is common to find them on boulders, palms and trees (Fernandez *et al.* 2003). Plants are epiphytes and lithophytes (i.e., they anchor roots to the surfaces of trees or rocky boulders) and exhibit a maximum shoot height of 15 cm (Ackerman 1995). The populations of this species appear to behave as a metapopulation (Tremblay *et al.* 2006), which is defined as a set of subpopulations with asynchronous local dynamics occupying discrete patches (Hanski 1999, Hanski & Gaggiotti 2004).

Study site

The study was carried out along a 1000 m section of Quebrada Sonadora in the Luquillo Experimental Forest. Quebrada Sonadora is a steep first order tributary of the Espíritu Santo River, in northeastern Puerto Rico, latitude 18º 18'N, longitude 65º47'W (Tremblay *et al.* 2006). The section studied is between 400 and 500 m in elevation and runs through an area of secondary mature "Tabonuco" forest dominated by the tree species *Dacryodes excelsa* (Waide & Reagan 1996). Average annual precipitation is 3600 mm and somewhat seasonal, with a somewhat drier period between January and April (Brown *et al.* 1983, McDowell & Estrada Pinto 1988). Water discharge in these streams is highly variable and closely follows precipitation events (Johnson *et al.* 1998).

Materials and Methods

We examined a total of 191 subpopulations or plant patches. To estimate understorey light, we obtained hemispherical canopy photographs of the populations of Lepanthes rupestris, with a fisheye lens and digital camera. At each site photographs were taken above the highest concentration of individuals at about two inches above the plants. The objective was to capture the incoming light from the perspective of the population. Digital images were analyzed using HemiView Canopy Analysis Software (Version 2.1, Delta-T Devices, Cambridge, UK).

The light environment and canopy structure was characterized using the following indices: the direct site factor (DSF) and the indirect site factor (ISF), which represent the proportion of direct and diffuse radiation under the canopy relative to the levels outside the canopy, as well as the proportion of full sunlight penetrating the forest canopy (Global Site Factor, GSF). GSF combines direct radiation, by calculating the annual solar track, and diffuse radiation, based on a uniform overcast sky model (Clark 2003). In addition the proportion of visible sky (Visky) and the leaf area index (LAI) were estimated. LAI is the amount of projected leaf area in square meters above one-meter ground surface. We tested whether or not the distribution of this light environment indicators followed a normal distribution using a Shapiro-Wilkinson test.

We counted the number of individuals per each subpopulation in July 2006. We evaluated the relationship between light environment on five different life stages of the orchid as defined in Tremblay & Hutchings (2002) and Rivera-Gómez *et al.* (2006). The sum of the total number of all stages were correlated with the light indicator variables.

TABLE 1: Mean, standard error, median, 2.5 and 97.5 percentile of light environment indicators for 191 orchid populations. See methods and material for definition of indices.

Indicator	Mean	Standard Error	Median	Minimum 2.5 percentile	Maximum 97.5% percentile
Visky	0.082	0.003	0.073	0.023	0.179
ISF	0.123	0.004	0.108	0.025	0.296
DSF	0.156	0.007	0.130	0.020	0.414
GSF	0.152	0.007	0.127	0.020	0.401
LAI	2.93	0.053	2.81	1.95	4.94

It is expected that the variance in population size should increase as the quality of the light environment indicator reaches a maximum and that at the edge of this range population size variance should be smaller. Consequently we used a "Variability chart" to depict the variation in population size as a function of light environment indicator. All tests and analyses were conducted with the statistical program JMP (ver 6.0.0, SAS Institute Inc.). The square root of the population size was used for all analyses.

Results

The light environment indicators (Visky, DSF, ISF, GSF, LAI) show a non-normal distribution for all indices (Shapiro-Wilkinson W test for normality, all p's < 0.05). The amount of light perceived by the populations was generally low (Table 1) and in all cases skewed toward smaller values. For example, the proportion of visible sky above orchid populations is generally small with a mean of 8.2% (sd, 4.2%).

The light indicator indices do not predict any significant linear relationship to population size (all p's > 0.05; Table 2), except for leaf area index (LAI), where there is a positive relationship between total population size and leaf area index. Unfortunately the regression based on the LAI only explains 2% of the variation and consequently is inconsequential. Population size range and light indicators across all light variable index range showed in general a trend of smaller range of population size as the index of higher light indices increased in all light environment indicators except LAI (Fig. 2). However a pattern of the minimum threshold in the light indices on population size was not as clear, the two indices which might suggest this pattern are Visible sky (VisSky) and the indirect site factor (ISF), both of which show a reduced range in population size in the lower light indices categories.

Discussion

We found in general that the light environments where the populations of orchids are found are usually in the lower range of light index variables. Moreover, the only pattern that shows some consistency is a decrease in the variance in population size as light indices increase, suggesting a maximum threshold light environment for population growth rate. Clearly one may ask, how can we not have observed any stronger effect of the light environment on population size? On the other range of the light environment we found little evidence that limitation in light results in population size reduction. It is only logical for example that at some point too little light would bring about small populations. It is possible that the present extant populations are only in the environment where they growth more or less at their optimum. However, most populations were observed in only a subset of all light environments categories. It is likely that our sample sizes of too low and too high light environment were underrepresented and thus our ability to detect any effect was limited. An experimental design may be able to detect an effect

TABLE 2: Linear regression of light environment indicators as predictor of population size. Regression values, adjusted R squared and the Probability value for 191 orchid populations. See methods and material for definition of indices.

Indicator	Regression	Adj. R^2	P - value
Visky	6.26 - 5.32x	- 0.002	0.43
ISF	6.13- 2.54x	- 0.002	0.54
DSF	6.16 - 2.13x	-0.002	0.45
GSF	6.12- 2.24x	-0.002	0.45
LAI	3.39 + 0.82x	0.02	0.03

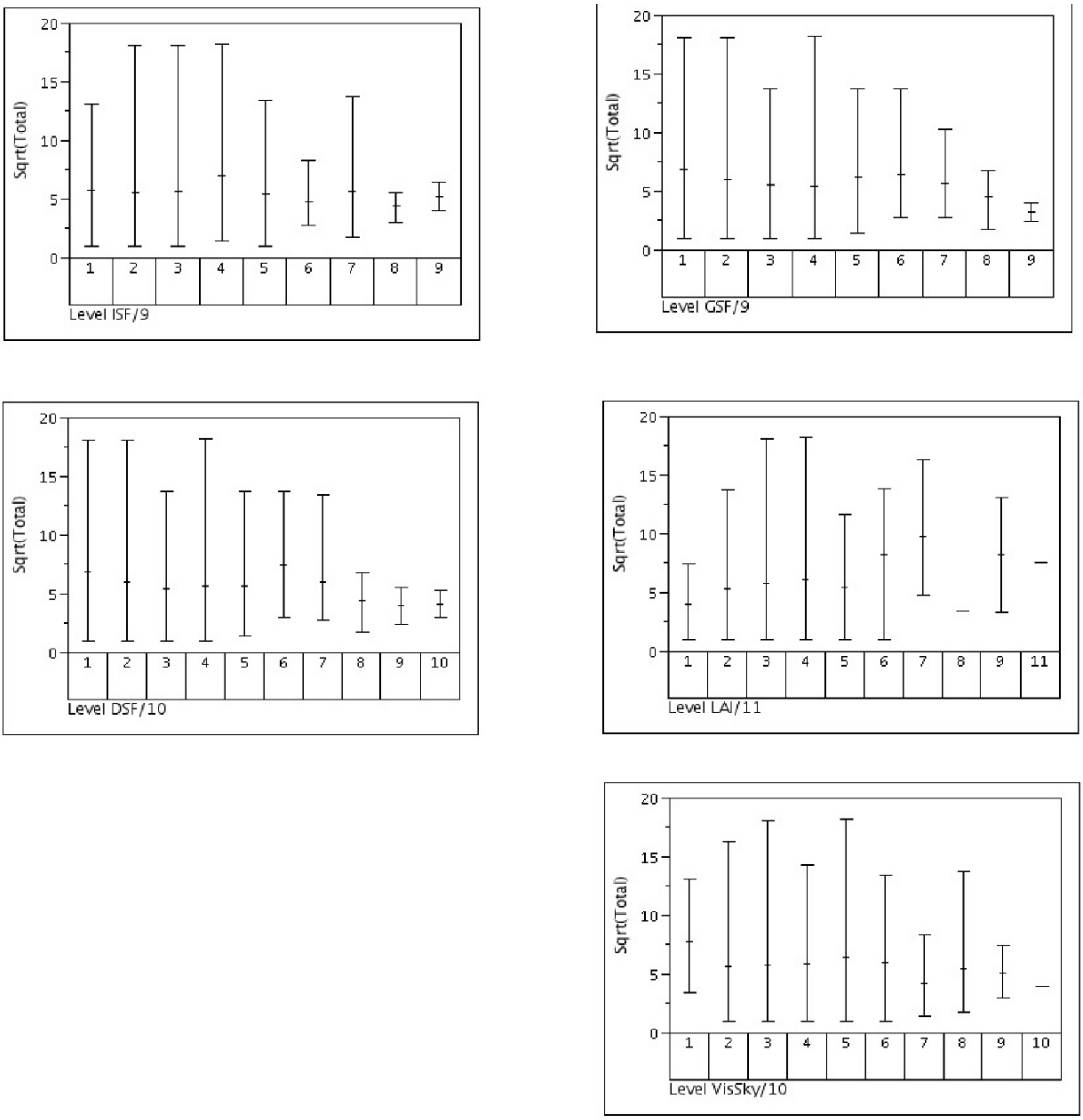

FIGURE 2: Variability Gage chart of the population size (sqrt) range and the varying categories of light indicators (Visky, DSF, ISF, GSF, LAI). The figure depict the range of the population size for low light levels (1) to high light levels (9-11) categories. The mean of each category is shown with a cross bar.

(if any) if conducted. To examine the real effect of exposure to light extremes in the population, there is a need for an experimental phase. In such experiment we can expose plants to extremes of light (a lot of light and practically no light) and observe the change in number (survival) and growth.

Another reason for the lack of difference between populations is the fact that these light measurements do not really measure the amount or quality of light perceived by plants, they are light indexes and they may not represent the actual light received by the plant. To make sure you are measuring photosynthetically important light and not relative light, light sensor could be installed in each population. In addition, light variability (measured as daily variance, for example), within a certain range of total radiation, may affect the population size instead of the actual total amount of light. The physiological basis for this hypothesis may be found in the capacity of the photosynthetic apparatus of this species to respond to rapid light changes. Not only may light variability in the population affect population size and growth, but also light variability within a population.

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LITERATURE CITED

Ackerman. J.D. 1995. An orchid flora of Puerto Rico and the Virgin islands, Mem. New York Bot. Gard. (73): 1-208.

Brown, S., A.E. Lugo, S. Silander & L.H. Liegel. 1983. Research Opportunities at the Luquillo Experimental Station General Technical Report SO-44, New Orleans, LA: 128.

Clark, J. S., J. Mohan, M. Dietze & I. Ibanez. 2003. Coexistence: How to Identify Trophic Trade-offs. Ecology (84): 17–31.

Fernández, D. S., R.l. Tremblay, J.D. Ackerman, E. Rodríguez & N. López. 2003. Reproductive potential, growth rate and light environment in *Lepanthes rupestris* Stimson. Lankesteriana (7):73-76

Hanski, I.A. 1999. Metapopulation Ecology. Oxford University Press, New York.

Hanski, I.A. & O.E. Gaggiotti. 2004. Ecology, Genetics and Evolution of Metapopulations. Elsevier Academic Press, San Diego, California, USA.

Johnson, S.L., A.P. Covich, T. Crowl, A. Estrada-Pinto, J. Bithorn & W.A. Wursbaugh. 1998. Do seasonality and disturbance influence reproduction in freshwater atyind shrimp in headwater streams, Puerto Rico? Int. Vereiningung Theor. Limnol. Verh (26): 2076-2081.

McDowell, W. H & A. Estrada Pinto. 1988. Rainfall at the El Verde Field Station, 1964-1986. University of Puerto Rico CEER T-228.

Rivera-Gómez, N., R.L. Tremblay & E. Meléndez-Ackerman. 2006. Distribution of Life Cycle Stages in a Lithophytic and Epiphytic Orchid. Folia Goebotanica (41):107-120.

Soontornchainaksaeng, P., S. Chaicharoen, M. Sirijuntarut & M. Kruatrachue. 2001. In vitro Studies on the Effect of Light Intensity on Plant Growth of *Phaius tankervilliae* (Banks ex L' Herit.) Bl. and *Vanda coerulea* Griff. ScienceAsia (27): 233-237.

Stancato, G.C., P. Mqzzafera & M.S. Buckeridge. 2002. Effects of light stress on the growth of the epiphytic orchid *Cattleya forbesii* Lindl. X *Laelia tenebrosa* Rolfe. Revista Brasil. Bot., 2 (25): 229-235.

Tremblay, R.L. 1997. Distribution and dispersion patterns of individuals in nine species of *Lepanthes* (Orchidaceae). Biotropica (29): 38-45.

Tremblay, R. L. & M. J. Hutchings. 2003. Population dynamics in orchid conservation: a review of analytical methods based on the rare species *Lepanthes eltoroensis*. Orchid Conservation (eds.) K. Dixon, S. Kell, R. Barrett & P. Cribb. Natural History Publications (Borneo) Sdn. Bhd. Kota Kinabalu, Sabah, Malaysia. Pp. 183-204.

Tremblay, R.L., E. Meléndez-Ackerman & D. Kapan. 2006. Do epiphytic orchids behave as metapopulations? Evidence from colonization, extinction rates and asynchronous population dynamics. Biological Conservation (I29):70-81.

Waide, R.B. & D.P. Reagan. 1996. The rainforest setting. In: Reagan, D.P., Waide, R.B. (Eds.), The Food Web of a Tropical Rainforest. The University of Chicago Press, Chicago, IL, USA: 1-16.

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