

Competitive ability of an epilithic moss, *Thuidium tomentosum* Schimp., under different light treatments in a subtropical lower montane forest in Puerto Rico

By

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A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

BIOLOGY

UNIVERSITY OF PUERTO RICO,

MAYAGÜEZ CAMPUS

2007

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ABSTRACT

Bryophyte competition in tropical vegetation has been considered a weak shaping drive in the assembly of the communities. Studies on tropical bryophytes considered that changes in species composition are originated mainly by direct interactions with abiotic factors rather than by inter-specific interactions. Here I investigated the competitive ability of *Thuidium tomentosum*, as well as the importance of its flagelliform branches and the competitive hierarchy with two epilithic bryophyte species: *Ceratolejeunea cornuta* and *Leucoloma cruegerianum*. Relative growth rate (RGR) of *T. tomentosum* was compared across three species combinations, three levels of light (full light, intermediate light and full shade), and two clipping levels (clipped and non-clipped flagelliform branches) during a nine months in a secondary forests of the Ciales municipality. Bryophyte hierarchies were estimated using standardized growth rates during three months in the Toro Negro Commonwealth Forest. Changes in RGR and relative competitive performance (RCP) were analyzed with a mixed model ANOVA for repeated measures. The combination of *T. tomentosum* with only one of the species showed an effect coherent with the resource competition hypothesis, but the combination of the three species together showed a positive interaction coherent with facilitation hypothesis ($F = 8.62$, $p < 0.001$). Light intensity modified the competitive ability of *T. tomentosum* with higher growth rates under full light and intermediate light than in complete shade ($F = 2.76$, $p = 0.0076$). Flagelliform branches seemed to have a role in the lateral expansion of *T. tomentosum* under different light conditions ($F = 3.73$, $p = 0.025$) but did not enhance its competitive ability ($F = 0.08$, $p = 0.98$). The competitive ability of *T. tomentosum* was favored by the presence of *C. cornuta* and *L. cruegerianum* and at the same time was reduced in the presence of a sole species. *Thuidium tomentosum* showed the

best competitive performance and was at the top of the hierarchy. *Ceratolejeunea cornuta* and *L. cruegerianum* interchanged their role under different light conditions ($F = 11.7$, $p = 0.001$) indicating that competition is an important element structuring the epilithic bryophyte communities of mountain forests in Puerto Rico. Changes in the competitive hierarchies across environmental gradients are a new approach to explain the coexistence of numerous bryophyte species in tropical mountains.

RESUMEN

La competencia en briofitos tropicales ha sido considerada una fuerza débil en la conformación de las comunidades. Los estudios realizados han resaltado la interacción con los factores abióticos más que las interacciones interespecíficas. En este estudio investigue la capacidad competitiva de *Thuidium tomentosum*, la importancia de sus ramas flageliformes en su capacidad competitiva y la jerarquía competitiva con otras dos especies de briofitos epilíticos, *Ceratolejeunea cornuta* y *Leucoloma cruegerianum*. La tasa de crecimiento relativo (RGR) de *T. tomentosum* fué comparada en tres combinaciones de especies, tres niveles de luz (iluminación completa, iluminación intermedia y sombra), y dos niveles de poda (poda y no poda de las ramas flageliformes) durante nueve meses. Las jerarquías de las tres especies fueron establecidas luego de tres meses de mediciones. Cambios en RGR y desempeño competitivo relativo (RCP) fueron analizados con una ANOVA mixta para medidas repetidas. Las combinaciones de *T. tomentosum* con solo una de las especies mostró una respuesta acorde a la hipótesis de competencia por recursos con valores inferiores de RGR a los monocultivos, sin embargo la combinación de las tres especies estuvo acorde a la hipótesis de facilitación con tasas de crecimiento similares a los monocultivos ($F = 8.62$, $p < 0.001$). La intensidad de la luz afectó el desempeño de *T. tomentosum* con valores un mejor desempeño en iluminación completa e intermedia que en sombra ($F = 2.76$, $p = 0.0076$), evidenciando a *T. tomentosum* como una especie de zonas abiertas. Las ramas flageliformes aparentemente tienen un papel en la expansión lateral de *T. tomentosum* ($F = 3.73$, $p = 0.025$) pero no incrementan su capacidad competitiva ($F = 0.08$, $p = 0.98$). *Thuidium tomentosum* tuvo siempre un mejor desempeño que las otras dos especies, sin embargo *C. cornuta* y *L. cruegerianum* intercambiaban posiciones en su desempeño en diferentes niveles de luminosidad ($F = 11.7$, $p = 0.001$), indicando la competencia como un

factor importante en la determinación de la composición y estructura de las comunidades de briofitos epilíticos de montaña. Los cambios en las jerarquías competitivas a lo largo de gradientes ambientales son un acercamiento novedoso para explicar la coexistencia de numerosas especies de briofitos en las montañas tropicales.

ACKNOWLEDGEMENTS

I want to thank my wife Jenny Urbina for her continuous support and unbeatable faith. I also want to express my gratitude to the following persons: Dr. D. China who kindly allowed the use of the GIS laboratory to process the digital images, MSc Donato Segui for his help and valuable comments during the work, Aurora Sastre that let us use a small area in her farm “Hacienda Niña Grande” to set the experiments, and all the people of the Bryology Lab in Mayagüez. I also thank the Department of Biology in Mayagüez that supported the transportation and the facilities to successfully complete the work, and the program MARK/SLOAN that funded part of the experimental setting. And finally I want to thank Prof. Inés Sastre-De Jesús for her guidance and friendship during the last years and who guide me in this first steps of the quantitative ecology of tropical bryophytes.

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INTRODUCTION

In contrast with vascular plants, the composition and structure of bryophyte communities has been considered to change almost exclusively in response to environmental modifications (Holz & Gradstein 2005) and only in few cases the role of biotic interactions has been taken into account in the dynamics of bryophyte communities (Mulligan & Gignac 2002, Zamfir & Goldberg 2000). In recent years the relevance of biotic interactions in bryophyte communities has been evidenced in different temperate habitats: peatlands, fens, heathlands, mires, and boreal forests (Määkisaari & Heikkinen 2003; Heijmans et al. 2002; Mulligan & Gignac 2002; Gignac 1992; Scandrett & Gimingham 1989). Hypothetically, the structure and composition of bryophyte communities are the result of environmental conditions such as substrate availability, temperature and humidity; together with the positive and negative interactions with other bryophyte colonies or vascular plants (Mulder et al. 2001). However, the nature of these species-specific interactions has been poorly studied and the mechanisms behind the structure of many bryophyte communities remain uncertain (Zamfir & Goldberg 2000).

Biotic interactions in tropical bryophyte communities have been neglected in the literature and only in a few studies indirect evidence of their relevance have been asserted. For example in managed *Theobroma cacao* plantations, the dominance of small bryophytes and crustose lichens was considered to result from stripping off bromeliads and mosses--the larger competitor species--from the trees (Krautz & Gradstein 2001). The coexistence of numerous intermixed bryophyte species in tropical mountains regions has been explained by a low interspecific competition and a high specialization on different available microhabitats such as leaf surfaces and tree trunks (Zartman 2003, Kürschner & Parolly 2005, Holz & Gradstein 2005).

However, descriptive data can only give circumstantial evidence of the role of competition (Rydin 1997, Keddy 1990).

Bryophytes are excellent models for competition experiments because they lack roots and are sporadically attacked by herbivores, avoiding two of the main hidden factors in competition experiments, below ground competition and herbivory (Rajaniemi et al. 2004; Mulligan & Gignac 2002). Since bryophytes have a low vertical development their changes in cover can be used as a measure of bryophyte performance (Braun-Blanquet 1932). A particular feature of bryophytes is that they are poikilohydric plants therefore their metabolic rate is related to water and light availability (Proctor & Tuba 2002). Their sensibility to water loss has been considered to be compensated by behavioral responses, like growth forms and water retention properties (Pedersen et al. 2001).

Due to their small size and low growth rate bryophytes have not been considered strong competitor species (Rydin 1997). However, the competitive strategy of bryophytes has been observed in several experiments, evidencing the presence of negative and positive interactions as well as the existence of competitive hierarchies among the different species (Mulder et al. 2001, Rincon & Grime 1989). According to Grime (1974) plants can be classified into three different strategies: 1. competitive –where plants are supposed to control a high amount of the resources; 2. stress tolerant– where plants remain small and show a slow potential growth rate; and 3. ruderal– where plants have short life span and high reproductive effort. Following this definition bryophytes were previously considered both stress tolerant or ruderal, however evidence from studies including only bryophytes revealed the presence of competitor species among them (Rydin 1997).

The water retention properties of bryophytes are related, among other characteristics, to plant architecture; i.e., growth form. Growth forms are characterized by morphological changes in the branching pattern, direction and exposure of shoots and canopy structure (Gimingham & Birse 1957, Rice et al. 2004). Changes in growth forms have been associated to environmental gradients, and the distribution of the different growth forms in a particular environment may help to predict the characteristics of the habitat (Bates 1998). Different bryophyte growth forms have been recognized: turfs – plants with parallel upright shoots, smooth mats – with dense and interwoven shoots extending horizontally, and wefts- with loose inter-twining shoots often ascending (Gimingham & Cunningham 1957). Species also have exclusive traits such as flagelliform branches that may be used as predictive tools of the species performance in particular environments (Kürschner & Parolly 2005); but the role of the traits may change with the environment, modifying the performance of the species (Suding et al. 2003).

The intensity of competition may be defined as the ability of a plant to evade growth suppression from other species or competitive ability (Mulligan & Gignac 2002), but this competitive ability only tells about the competitive performance of a particular species. Another approach is to determine the existence of competitive hierarchies, to detect such hierarchies species are grown in pairs to compare its relative performance, thus providing a ranking of the species according to their relative competitive ability (Keddy et al. 2002, Zamfir & Goldberg 2000). However, competitive hierarchies may not be constant along environmental gradients and changes in the competitive hierarchies of different species are an indication that competition is an important factor regulating the assembly of the communities (Novoplansky & Goldberg 2001). Competitive hierarchies among bryophytes have been evidenced in peatlands with a clear dominance of *Sphagnum* species over the subordinated feather mosses (Mulligan & Gignac

2002). Changes in the hierarchies of the species across environmental gradients have been used as evidence of strong competition in plant communities where species are finely adjusted to particular conditions (Novoplansky & Goldberg 2001, Keddy 1990).

Despite of their great importance, our understanding about competition processes in bryophytes is almost completely absent in tropical regions (Rydin 1997, Mulligan & Gignac 2002). Bryophyte importance in tropical countries is highlighted by their participation in water retention processes (Bruijnzeel & Veneklaas 1998), soil cover for erosion protection (Kok et al. 1995), incorporation of atmospheric nutrients in the ecosystems (Hietz et al. 2002) and biodiversity component (Acebey et al. 2003). The predictability of the outcome in bryophyte interactions may be used in restoration projects where particular species arrangements of bryophytes are desired to promote a mild microclimate and vascular epiphytic colonization. For example Nadkarni and Solano (2002) found that tree branches stripped of bryophytes have shown a higher temperature and a lower humidity reducing the colonization and growth of vascular epiphytes. This study will provide information about the degree of competitive interactions of bryophytes in a controlled environment, and will supply information about the dynamics and possible restoration strategies in tropical mountains where bryophytes play an important role.

This work is centered in the competitive ability of *Thuidium tomentosum* Schimp. a moss that frequently covers rocks and almost any substrate in the forest floor in mountain forests suggesting that it could be considered a competitive species sensu Grime (1974). *Thuidium tomentosum* is frequently found with two other bryophyte species, *Ceratolejeunea cornuta* (Lindenb.) Schiffner, a liverwort, and *Leucoloma cruegerianum* (Müll. Hal.) A. Jaeger, a moss I addressed the following questions to evaluate the competitive ability of *T. tomentosum*

and to determinate how epilithic bryophyte communities are structured in mountain forest of Puerto Rico.

1. Is the performance of *T. tomentosum* affected in the presence of competitor species? Despite the fact that *T. tomentosum* may be considered a dominant species due to its large size and high vertical development, smaller bryophytes such as *C. cornuta* and *L. cruegerianum* with contrasting growth forms may interact with *T. tomentosum* and effectively affect its growth.
2. Is the competitive ability of *T. tomentosum* the same across a light gradient? Since *T. tomentosum* may be considered a sun tolerant species, it will dominate the other species in full light treatments.
3. How do particular morphological traits such as the flagelliform branches in *T. tomentosum* affect its performance? Since traits may be considered a compromise between growth limitations and ecological performance (Suding et al. 2003), trait modification may affect positively or negatively the bryophyte response across environmental gradients.
4. Is the light regime a driving factor in the structure of rock bryophyte communities affecting the species hierarchies? *Thuidium tomentosum* is frequently found in open and forested habitats while *C. cornuta* and *L. cruegerianum* are in illuminated areas inside the forest (Dauphin 2003, La Farge-England 1998). The dominance of different species across the light gradient may be explained by changes in the competitive hierarchies of these three species since they are not limited by environmental conditions, they grow across the light gradient, or

substrate availability.

Our knowledge about bryophyte ecology in tropical countries has a remarkable absence of experimental studies. During the last century, nearly 80% of the studies conducted had a geo-ecological approach (Sastre-de Jesús 2004) and even more studies have been “mensurative” without control of the factors under study (Hulbert 1984). However, manipulative experiments have a stronger predictive power when compared with mensurative experiments, because the effects in the experimental procedure can be separated (Hulbert 1984). Thus, the influence of space and resource competition in the species performance may be separated or controlled in properly designed experiments. Also the use of non-destructive yield methods allows inferences from continuous studies, with a higher predictive power than destructive methods that are based only in initial and final estimates (Pedersen et al. 2001). In this particular case, the simulation of the rock environment with controlled conditions of light, substrate age, topography, and the subsequent nutrient availability generate powerful information about the interspecific processes regulating the bryophytes communities of rocks in tropical mountains.

METHODS

The four questions formulated above were tested in two different localities in the *Cordillera Central* of Puerto Rico (Figure 1). Below are the descriptions, characteristics, and experimental setting for each of them. The data gathering protocol –image processing– was the same for both experiments.

Species selection

Thuidium tomentosum has a weft growth form and flagelliform branches that creep over

the substratum. Two other epilithic species are observed in mountain forest of central Puerto Rico: *Leucoloma cruegerianum* and *Ceratolejeunea cornuta*. *Leucoloma cruegerianum* is an acrocarpous turf forming moss (La Farge-England 1998). *Ceratolejeunea cornuta* is a liverwort with a smooth mat growing form with completely horizontal branches and abundant vegetative gemmae (Dauphin 2003).

Study area

Two experiments were located respectively in the North and South facing slopes of the *Cordillera Central* of Puerto Rico. The climate in the area is humid and the life zone has been classified as Subtropical Moist Forest (Ewel & Whitmore 1973). The first experiment was located at the northern slopes of the *Cordillera Central* in the Ciales municipality in the farm *Hacienda Niña Grande*; therefore referred as the Ciales experiment. This experiment was setup at 650 m.a.s.l., the total annual rainfall was nearly 2000 mm/yr during the study and the mean temperature was 24 °C (Anon. 2006). The second experiment was setup in the Toro Negro Commonwealth Forest in the Orocovis municipality at the South face of the *Cordillera Central*; therefore referred as the Toro Negro experiment. This second experiment was at 850 m.a.s.l., with a yearly rainfall reaching the 2570 mm/yr and a mean temperature of 18.4 °C. The climatic data correspond to mean temperature and rainfall for the period 1999 to 2005 (Anon. 2006). The temperature and relative humidity was measured in situ using HOBOTM data loggers, the data were recorded with two hour intervals during the nine months of the study.

Experimental design

The experiment was a split block design with the light as complete plot treatment and the species mixtures the sub plot treatment. The three bryophyte species were collected

from the Toro Negro Commonwealth Forest; the collections were mixed to avoid particular genetic effects and unwanted species were removed. Bryophytes were planted on 25 x 25 cm clay tiles and randomly distributed in PVC scaffoldings. The clay tiles were porous non-glazed and without herbicides or chemical agents. The tiles were used to control additional sources of variation in bryophyte epilithic communities such as available area, isolation, microtopographic heterogeneity and successional age of the substratum (Kubesova & Chytrý 2005, Kimmerer & Driscoll 2000, Pharo & Vitt 2000). Each of the scaffoldings had three light levels: full light – with no shade, intermediate light – with a single shade net providing an effective 50% reduction in luminosity, and full shade – with a double layer of shade netting providing an 80% reduction in light intensity (Figure 2). Due to the relevance of abiotic factors in bryophyte growth, the relationship between mean monthly temperature, rainfall and relative humidity were evaluated with simple regressions. And since bryophytes were transplanted to a foreign substrate, temperature in natural rocks and clay tiles were compared by measuring rock and tile temperatures simultaneously in 8 sites each hour during.

Ciales experiment. Bryophyte cover on 108 clay tiles was measured once per month from September 2005 to June 2006. The objective was to assess: (a) the competitive ability of *T. tomentosum*, (b) the variation of its competitive ability across the three light levels, and (c) the role of the flagelliform branches in its competitive ability across the light regimes. This experiment was replicated 6 times with light as a whole plot treatment with the three luminosity levels. And the species combination was the subplot treatment. To evaluate the competitive ability of *T. tomentosum*, its growth rate was compared across the next species combinations in the three light levels: (1) monocultures of *T. tomentosum*, (2) *Thuidium tomentosum* growing with *C. cornuta*, (3) *Thuidium tomentosum* growing with *L. cruegerianum*, and (4) *Thuidium*

tomentosum growing with *C. cornuta* and *L. cruegerianum*. To evaluate the role of the flagelliform branches in the competitive ability of *T. tomentosum* an additional treatment of plants with the branches clipped was included. The latter test had two species mixtures: (1) monocultures of *T. tomentosum*, and (2) mixtures of *T. tomentosum* with *C. cornuta* and *L. cruegerianum*. Each species combination had a clipping treatment comparing the performance of *T. tomentosum* between plants with the flagelliform branches clipped and non clipped. The presence of the monocultures in the test as positive controls was necessary to ensure the assumption that clipping the flagelliform branches did not affect the growth rates of *T. tomentosum*.

Toro Negro experiment. Bryophyte cover was estimated monthly from April to July of 2006 in 72 clay tiles. The objective was to establish the competitive hierarchies among *T. tomentosum*, *L. cruegerianum* and *C. cornuta* under the three light levels. The setup of the experiment included the same species combination as in the Ciales experiment plus monocultures of *C. cornuta* and *L. cruegerianum*.

Bryophyte cover and growth rates

Bryophyte cover was estimated monthly during 9 months in the Ciales experiment and during 3 months in the Toro Negro experiment. The bryophyte cover was estimated from serial images processed with the IDRISI Kilimanjaro GIS software (Eastman 2003). The cover was extracted from digital photographic images using a combination of manual drawing of the bryophyte profiles and automatic identification of bryophyte areas using pixel clustering, with the CLUSTER module. Successive images were aligned using the RESAMPLE module, allowing for direct comparisons between the areas. Pixels were converted to cm² and the relative

growth rates were calculated. Relative growth rate was calculated as: $RGR = \frac{(A2 - A1)}{t}$ with A1– area in time 1, A2– area in time 2, and t- time in days between successive measurements (Mulligan & Gignac 2002).

The ability of the neighbor species to suppress the growth of different species was calculated as relative competitive performance: $RCP = \frac{RGRa - RGRn}{RGRn} * 100$. $RGRa$ is the relative growth of the species in monocultures and $RGRn$ is the relative growth in mixtures. The strategy is analogous to that used by Keddy et al. (2000) and Mulligan and Gignac (2002). The RCP index offers a direct interpretation of the interaction outcomes. Positive values indicate a better performance of the species growing in monocultures and negative values indicates synergic interactions with higher growth rates of the species in mixtures.

Statistical analysis

The relationship between humidity and temperature with *T. tomentosum* RGR was estimated by linear regression, to evaluate the relevance of climate on the overall experiment. Temperature differences between the rocks and the tiles were calculated using a paired t test, with the site used as the nested factor.

The competitive ability of *T. tomentosum* was evaluated across the three light levels using a mixed model ANOVA, comparing bryophyte RGR changes during the study period. The serial correlation between successive measurements was taken into account by using a Toeplitz covariance matrix and the tiles were used as random nested factors in the repeated measures ANOVA. Mixed models have a higher power allowing inferences from data with departures from normality and asymmetrical variances (SAS Inc. 2002). The interactions between species

arrangements and light levels were tested in order to interpret only the main effects of the treatments, species combinations and light intensity. The ANOVA analyses were performed using the SAS MIXED procedure for repeated measures experiments (SAS Inc. 2002) as well as the glm library of the R package (R Core development team 2006, Lindsey 1993). The ANOVA model $RGR = \text{time} * \text{tower}(\text{shade}) + \text{time} * \text{tower}(\text{arrangement})$. Linear mixed models were selected after fitting the data to more general models as linear, logarithmic, or exponential functions (Lindsey 1993). The residuals of the model were analyzed after extracting the serial correlation (Venables & Ripley 2002). The third question was also evaluated using the Mixed ANOVA procedure but in this case the model was of the form $RGR = \text{time} * \text{tower}(\text{shade} * \text{clipping}) + \text{time} * \text{tower}(\text{arrangement} * \text{clipping})$.

The second experiment addressed the fourth question and was based only in the RCP of the three species. The RCP of the three species in the different light levels was evaluated using a nested ANOVA for split plot designs with two repeated measures. The RCP of each species was compared across the different species and light combinations. The R and SAS code for all the analysis are listed in Appendix 1.

RESULTS

The climate during this study had a moderate seasonality with slightly higher temperatures from July to September and lower from December to March. Relative humidity at noon was lower (40%) during the dry periods February-April, and reached its maximum at 100% during all day during the humid season. Temperature recorded was between 14 and 34 °C with the 95% of the values between 17 and 25 °C (Figure 3). Rainfall distribution showed a dry period from January to March and a humid period from August to November (Figure 4). The mean

RGR of *T. tomentosum* was directly related to humidity (R^2 adj = 0.39, df=8, F=5.5, p=0.04) and inversely to temperature (R^2 adj = -0.43, df=8, F=6.1, p=0.03). Differences in temperature were found between rocks and tiles with higher temperatures in the clay tiles ($t = 3.41$, $n = 40$, $p < 0.001$) (Fig).

Ciales experiment

Overall growth of *T. tomentosum* was negative with a mean rate of $-0.02 \text{ cm}^2 / \text{month}$. The RGR of *T. tomentosum* showed significant differences across the 4 species combinations. Comparisons made with a priori contrasts showed higher values of RGR in *T. tomentosum* monocultures and mixtures of the three species than in combinations of *T. tomentosum* either with *L. cruegerianum* or *C. cornuta* (Figure 6, Table 1). The interaction of species arrangement versus light intensity was explored but it was found non significant ($F = 0.82$, $df_1 = 6$, $df_2 = 60$, $p = 0.55$).

The competitive ability of *T. tomentosum* changed with changes in light intensity. The RGR of *T. tomentosum* was lower in the full shade treatment; but there were no differences between the full light and intermediate light treatments ($F = 1.41$, $p = 0.016$) (Figure 6, Table 1).

The clipping of the flagelliform branches of *T. tomentosum* had a significant effect on its RGR. The RGR of clipped *T. tomentosum* plants was lower than non clipped plants; however, the effect was more noticeably in monocultures than in species mixtures, and in the full light treatment than in the shade treatment (Figure 7, Table 2). Specific comparisons showed that there were no significant differences in the RGR of *T. tomentosum* mixtures among clipped and non

clipped plants ($F = 3.69$, $DF \text{ num} = 1$, $DF \text{ den} = 48$, $p = 0.06$).

Toro Negro experiment

Overall growth of the 3 species was generally higher in the monocultures than in mixtures, showing a competitive effect (Table 3). The differences in RCP between species showed a hierarchical arrangement with *T. tomentosum* having higher values of RCP than *C. cornuta* and *L. cruegerianum* under the three light conditions (Figure 8). However for the secondary species the RCP was higher for *L. cruegerianum* than for *C. cornuta* in full light and the opposite pattern under full shade.

DISCUSSION

Environmental conditions as temperature and relative humidity showed a clear effect on bryophyte performance, it was less affected by warm temperatures and high relative humidity. Such results agree with a study that monitored bryophyte dynamics during 20 years which showed that growth of *Hylocomium splendens* was closely related to temperature (Callaghan et al. 1997). Since bryophytes are poikilohydric plants, it is expected that water availability, regulated by temperature and relative humidity, plays a main role in bryophyte metabolic rates (Wiklund & Rydin 2004, Proctor & Tuba 2002).

Bryophytes inhabiting rock surfaces are specially adapted to dry periods and low nutrient income, and the negative growth rate of *T. tomentosum* may be explained by the excessive heat reached by the tiles during the day; however the results of this study reveal the importance of biotic interactions even in extreme environments as the surface of a clay tile. Excessive heat has

been reported to produce cell damage and shoot death in the moss *Plagiomnium acutum* with a notorious increment of cell damage at temperatures over 45°C (Liu et al. 2004). Bryophyte leaves can reach up to 10°C over the temperature of the surrounding air, including the heat transmitted from the substrate (Liu et al. 2004). During this study temperatures over 35°C were seldom recorded; however, during the dry months – January through March – some dead shoots were observed in *T. tomentosum* indicating that in conditions of low humidity and high temperatures a high level of cell damage may take place.

The suppression of *T. tomentosum* growth observed during the experiment may result from two different processes: biotic interactions among the species involved in the experiment and abiotic responses. The limited growth observed in *T. tomentosum* suggests a reduced performance of this species in the presence of *C. cornuta* or *L. cruegerianum* which corresponds to a competitive strategy: some species allocate more resources than others and finally overgrow the species with reduced growth rate (Rydin 1997). Otherwise, the differences in performance may reflect also a better adaptation of *L. cruegerianum* and *C. cornuta* to the transplant conditions. However, when the three species were planted together the performance of *T. tomentosum* was similar to the performance in monocultures indicating the presence of non-negative or even positive interactions. The existence of non-negative interactions among bryophytes has been considered an explanation of the commonness of positive density dependence particularly in mixed stands (Mulder et al. 2001, Rydin 1997). Mixed stands may promote non-negative interactions that ultimately would promote an increment in the water retention ability due the interaction among different species (Økland 1994, Rydin 1985).

Since *T. tomentosum* has been found growing in full light (I. Sastre-De Jesús pers. comm.), it was expected to have a better performance in the full light treatment. However, the

higher performance was found in intermediate light. The later result may be explained by the extreme heat that the tiles can reach during the day. The clay tiles where *T. tomentosum* was planted have higher heat/mass transfer than the rocks, and thus the small mass of the clay tiles have a slow rate of heat dissipation overheating the bryophytes growing over them. It has been reported that bryophytes exposed to temperatures over 40°C and full light have a considerably increment in cell damage (Liu et al. 2004) and thus treatments that reduce the amount of sun light and heat will have a positive impact on bryophyte performance as observed in this experiment. On the contrary, the metabolic rates of bryophytes are extremely reduced when the radiation levels are extremely low as in the full shade treatment (Rincon & Grime 1989) and thus intermediate levels of light are favored.

Morphological traits may be considered trade offs between species evolutionary constraints and ecological performance (Suding et al. 2003). They may help the plant under particular conditions but in a different environment they may not provide any advantage. The flagelliform branches of *T. tomentosum* are a characteristic of all the Thuidiaceae; they presumably allow the plant to physically grow over the substrates covering other bryophyte species (Rincon & Grime 1989). However, the long flagelliform shoots are completely exposed to the wind and desiccation may be an important factor limiting their growth. Romero, Putz and Kitajima (2006) evidenced that shoot exposition is an important factor in the water economy of the plant, with longer shoots more exposed to desiccation than shorter ones. The subtraction of the flagelliform branches in *T. tomentosum* clearly reduces its performance, but its competitive ability seems to be unaffected by the clipping. Thus, the flagelliform branches may be viewed as expanding shoots responsible of a foraging growth pattern (Rydgren et al. 2001, Rincon and Grime 1989) more than a trait enhancing its competitive ability.

Different studies have shown that plant competitive strategies remain the same even if the environment changes (Keddy et al. 2002). However studies focused in bryophyte interactions reveal the existence of different responses of bryophytes in different environments. For example, Mulligan and Gignac (2002) found that in bogs site characteristics has a significant effect on the relative competitive performance of bryophytes, with changes in the hierarchies of the secondary species, feather mosses, among different sites but not among the dominant ones, *Sphagnum* species. Our results showed a hierarchical organization among the three species studied with a dominance of *T. tomentosum* followed either by *C. cornuta* or *L. cruegerianum*. Then it is expected that rocks in montane forest of Puerto Rico will become covered by *T. tomentosum*, however *C. cornuta* and *L. cruegerianum* have been observed dominating on rocks in the study area. A possible explanation for this contradiction is substrate inclination that may affect the establishment and posterior growth of the three species. In fact, *Ceratolejeunea cornuta* was frequently found on rocks with inclined surfaces in shaded places and *L. cruegerianum* was found on rocks completely exposed to the sun. *Ceratolejeunea cornuta* is a liverwort with rhizoidal discs that firmly attaches the smooth mat plant to the rock (Dauphin 2003), and *L. cruegerianum* is also an epiphyte and is usually attached to vertical trunks under full light. Another factor explaining the presence of different species on the same rock comes from the perturbations of the rock surface that allow recolonization by different species. Weibull & Rydin (2005) showed that rock inclination is an important factor explaining the overall bryophyte diversity on siliceous boulders, inclination may affect not only sun exposure but also attachment ability of the plant.

Competitive hierarchies indicate how strong is the competition as the force organizing the assembly of plant communities (Keddy et al. 2002, Novoplansky & Goldberg 2001). Even so,

competition hierarchies may explain how plant competition controls the distribution of the different species across gradients. The dominance of *T. tomentosum* in the hierarchy may indicate that resource competition in rocks is not a main force structuring the rock communities in montane forests of Puerto Rico, because *Thuidium tomentosum* is always the species with the highest competitive performance of the three species along the different environmental conditions. Mulligan and Gignag (2002) showed changes in the competitive hierarchy of five mosses along an environmental gradient where resource competition was easily observed between individuals. The changes were particularly observed in secondary species with a clear dominance of *Sphagnum magellanicum* along the gradient. Conversely, some particular traits are considered to have a predictive power in the hierarchical arrangement of the species. Keddy et al. (2002) showed size as one of the best predictors in the hierarchical positions of 63 herbaceous species with larger species having a dominant role over the other species. *Thuidium tomentosum* is considered large for mosses and forms carpets that may have up to 20 cm high and the branches may reach up to 20 cm long and have long flagelliform branches (Churchill & Linares 1995). Because of the larger size of *T. tomentosum* it is possible to predict a dominant position in the competitive hierarchy of bryophytes in montane forests of Puerto Rico (Freckleton & Watkinson 2001).

The changes in the hierarchies showed by the secondary species *L. cruegerianum* and *C. cornuta* along the light gradient is an indication of their competitive relationship. Even so, the community is dominated by *T. tomentosum* the relative abundances of the subordinated species are regulated by the interactions among them under the particular environmental conditions; i.e., light intensity (Novoplansky & Goldberg 2001). The changes in the hierarchy guarantee that a species turnover originated by biological interactions observed along the environmental gradient.

Nonetheless, there are other factors not included in this study that have been shown to affect bryophyte distribution on rocky surfaces as inclination, size, tree cover and litterfall amount (Weibull & Rydin 2005).

The high diversity of tropical mountain bryophytes has been explained by the rather stable temperature, high humidity and short desiccation intervals (Leerdam et al. 1990). And the species coexistence has been explained by terms such as ecological equivalence (Wolf 1993) or mass effect (Kessler 2000). However a more subtle explanation is provided by species interaction and the changes in competitive hierarchies across climatic gradients will be expressed as changes in community composition. As exemplified here, changes in the competitive hierarchies of bryophytes are common and bryophyte coexistence is supported by a mixture of positive and negative interactions.

Bryophyte competition has been largely exemplified in northern temperate forests almost completely dominated by bryophytes and almost always including *Sphagnum* species (Rydin 1997, Mulligan & Gignac 2002). Conversely, bryophyte competition in tropical ecosystems has been only mentioned as a secondary factor and considered a weak force in the shaping of bryophyte communities and factors like environmental tolerance are considered to be more important (Kürschner & Parolly 2005). However, competition may be considered an important factor influencing the present bryophyte communities in the tropics since the interaction observed in this experiment is a compelling evidence of competition among tropical bryophytes. Acknowledgment of competition as a strong force in tropical bryophytes communities had been superficially explored; i.e., Andersson and Gradstein (2005) found that trees “stripped” of epiphytes show a high cover of smooth mats and crustose lichens. They conclude that the high cover of these two life forms is explained by the absence of resource competitors; instead, the

dominance of these growth forms may be explained by the dispersal limitation of the bigger epiphytes that were removed from the area. This observation indicates that detecting competition requires explicitly manipulative experiments to separate the effects of dispersion, colonization, and resource competition (Rydin 1997).

FUTURE WORK AND RECOMMENDATIONS

This study was focused in an extremely modeled environment and in this way several sources of variability were controlled: topography, microclimate, water and nutrient distribution, light, and wind. But the modeling also limited the growth of the species, since the tiles have a small size and a lower heat/mass transfer rate than the natural rocks. The next step should be aimed to more complex communities like epiphytes and include a larger number of species with combinations of all the possible pairs of interacting species or with the inclusion of phytometers.

Another relevant item is related with the experimental setting. I suggest in next experiments to place the tiles directly over the ground, to ensure the heat dissipation by transfer to the soil. Increasing the contact between the tiles and the ground will moderate the temperature reducing cell damage and increasing bryophyte growth. I also suggest to measure bryophyte dominance in different ways: a – include bryophyte height; because acrocarpous species as *Leucoloma cruegerianum* has a predominantly upward growth and lateral measurements as cover do not represent accurately the dominance of these species; however, some studies have shown that bryophyte cover is an appropriate indicator of bryophyte dominance patterns in peatland ecosystems (Rydin 1997); b – include values of bryophyte true dominance with biomass and carbon content estimates, should be noticed that these measurements are destructive and the appropriate experimental design should be used.

According to the results of this project, restoration projects that want to propagate *T. tomentosum* are encouraged to do so in open areas in close proximity with bryophyte species of different growth forms. The bryophytes should be placed in surfaces with enough mass to dissipate the heat or in close contact with the ground. It is also suggested to remove the litterfall and organic debris that may fall over the plants and intercept the sun light.

LITERATURE CITED

- ACEBEY, A., S. R. GRADSTEIN & T. KROMER. 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *Journal of Tropical Ecology* 19: 9–18.
- ANDERSSON, M. S. & S. R. GRADSTEIN. 2005. Impact of management intensity on non vascular epiphyte diversity in cacao plantations in Western Ecuador. *Biodiversity and Conservation* 14: 1101–1120.
- ANONYMOUS. 2006. Climatological data summary Puerto Rico and Virgin Islands. National Oceanic and Atmospheric Administration – Department of Commerce – United States of America. URL: www5.ncdc.noaa.gov/pdfs/cd/prvr.
- BATES J.W. 1998. Is ‘life–form’ a useful concept in bryophyte ecology? *Oikos* 82: 223–237.
- BRAUN–BLANQUET, J. 1932. *Pflanzensociologie*. Translated to English by Fuller, G. D. & H. S. Conard. Starcher–Hafner Service Agency Inc. NY. Pp. 439.
- CALLAGHAN, T.V., CARLSSON, B.Å., SONESSON, M. & TEMESVÁRY, A. 1997. Between–year variation in climate–related growth of circumarctic populations of the moss *Hylocomium splendens*. *Functional Ecology* 11 157–165.

- CHURCHILL, S. P. & C. E. LINARES. 1995. Prodrromus Bryologiae Novo Granatensis. Bibliot. José Jerónimo Triana 12: 1–924.
- DAUPHIN, G. 2003. Ceratolejeunea. Flora Neotropica Monograph 90: 1–87.
- EASTMAN, J. 2003. Idrisi Kilimanjaro: Guide to GIS and Image Processing. Manual Version 14.00. Clark Labs, Clark University, Worcester, Massachussets.
- EWEL, J. L. & J. L. WHITMORE. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. USDA For. Serv. Res. Pap. ITF–18.
- FRECKLETON, R. P. & A.R. WATKINSON. 2001. Predicting competition coefficients for plant mixtures: reciprocity, transitivity and correlations with life–history traits. Ecology Letters 4: 348–357.
- GIGNAC, D. 1992. Niche Structure, Resource Partitioning, and Species Interactions of Mire Bryophytes Relative to Climatic and Ecological Gradients in Western Canada. The Bryologist 95: 406–418.
- GIMINGHAM, C.H. & E.M. BIRSE. 1957. Ecological studies of growth–form in bryophytes: I Correlations between growth form and habitat. Journal of Ecology 45: 533–545.
- GRIME J.P. 1974 Vegetation classification by reference to strategies. Nature 250: 26–31.
- HEIJMANS, M. M. P. D., H. KLEES & F. BERENDSE. 2002. Competition between *Sphagnum magellanicum* and *Eriophorum angustifolium* as affected by raised CO₂ and increased N deposition. Oikos 97: 415–425.
- HIETZ, P., W. WANEK, R. WANIA & N. NADKARNI. 2002. Nitrogen–15 natural abundance in a montane cloud forest canopy as an indicator of nitrogen cycling and epiphyte

- nutrition. *Oecologia* 131: 350–355.
- HOLZ, I. & S.R. GRADSTEIN. 2005. Cryptogamic epiphytes in primary and recovering upper montane oak forest of Costa Rica – species richness, community composition and ecology. *Plant Ecology* 178: 89–109.
- HULBERT, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211.
- KEDDY, P. A. 1990. Competitive hierarchies and centrifugal organization in plant communities. In J. Grace and D. Tilman (eds.) *Perspectives on Plant Competition*, Academic Press, New York, pp. 262–290.
- KEDDY, P. A., C. GAUDET, & L. H. FRASER. 2000. Effects of low and high nutrients on the competitive hierarchy of 26 shoreline plants. *Journal of Ecology* 88: 413–423.
- KEDDY, P., K. NIELSEN, E. WEIHER & R. LAWSON .2002. Relative competitive performance of 63 species of terrestrial herbaceous plants. *Journal of Vegetation Science* 13: 5–16.
- KESSLER, M. 2000. Altitudinal zonation of Andean cryptogam communities. *Journal of Biogeography* 27: 275–282.
- KIMMERER R.W. & M.J.L. DRISCOLL. 2000. Bryophyte species richness on insular boulder habitats: the effect of area, isolation, and microsite diversity. *The Bryologist* 103: 748–756.
- KOK K, P.A. VERWEIJ & H. BEUKEMA.1995. Effects of cutting and grazing on Andean treeline vegetation. In S.P. Churchill, H. Balsev , E. Forero and J.L. Luteyn (eds).

- Biodiversity and Conservation of Neotropical Montane Forests, New York Botanical garden, New York, pp 527–539.
- KRAUTZ, T. & S. R. GRADSTEIN. 2001. On the ecology and conservation of *Spruceanthus theobromae* (Lejeuneaceae, hepaticae) from Western Ecuador. *The Bryologist* 104: 607–612.
- KUBESOVA, S. & M. CHYTRY 2005. Diversity of bryophytes on treeless cliffs and talus slopes in a forested central European landscape. *Journal of Bryology* 27: 35–46.
- KÜRSCHNER, H. & G. PAROLLY. 2005: Ecosociological studies in Ecuadorian bryophyte communities. III. Life forms, life strategies and ecomorphology of the submontane and montane epiphytic vegetation of S Ecuador. *Nova Hedwigia* 80: 89–113.
- LA FARGE-ENGLAND, C. 1998. The Infrageneric Phylogeny, Classification and Phytogeography of *Leucoloma* Brid. (Dicranaceae, Bryopsida). *The Bryologist* 101: 181–220.
- LEERDAM, A. VAN, R. J. ZAGT & E. J. VENEKLAAS. 1990. The distribution of epiphyte growth-forms in the canopy of Colombian cloud-forest. *Vegetatio* 87: 59–71.
- LINDSEY, J. K. 1993. *Models for repeated measurements*. Oxford, New York. 413pp
- LIU, Y., Z. LI, T. CAO & J. M. GLIME. 2004. The influence of high temperature on cell damage and shoot survival rates of *Plagiomnium acutum*. *Journal of Bryology* 26: 265–271.
- MÄÄKIPÄ, R. & J. HEIKKINEN. 2003. Large-scale changes in abundance of terricolous bryophytes and macrolichens in Finland. *Journal of Vegetation Science* 14: 497–508.

- MULDER, C. P. H., D. D. ULIASSI & D. F. DOAK. 2001. Physical stress and diversity–productivity relationships: The role of positive interactions. *PNAS* 98: 6704–6708.
- MULLIGAN, R. C. & L. D. GIGNAC. 2002. Bryophyte community structure in a boreal poor fen II: interspecific competition among five mosses. *Canadian Journal of Botany* 80: 330–339.
- NADKARNI, N. & R. SOLANO. 2002. Potential effects of climate change on canopy communities in a tropical cloud forest: an experimental approach. *Oecologia* 131: 580–586.
- NOVOPLANSKY, A. & D. GOLDBERG. 2001. Effects of water pulsing on individual performance and competition hierarchies in plants. *Journal of Vegetation Science* 12: 199–208.
- ØKLAND, R. H. 1994. Patterns of bryophyte associations at different scales in a Norwegian boreal spruce forest. *Journal of Vegetation Science*: 5: 127–138.
- PEDERSEN, B., H. M. HANSLIN & S. BAKKEN. 2001. Testing for positive density–dependent performance in four bryophyte species. *Ecology* 82: 70–88.
- PHARO E.J. & D.H. VITT. 2000. Local variation in bryophyte and macrolichen cover and diversity in montane forests of western Canada. *The Bryologist* 103: 455–466.
- PROCTOR, M.C.F. & Z. TUBA. 2002. Poikilohydry and homoihydry: antithesis or spectrum of possibilities? *New Phytologist* 156: 327–349.
- R DEVELOPMENT CORE TEAM. 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL

<http://www.R-project.org>.

- RAJANIEMI, T., V. J. ALLISON & D. E. GOLDBERG. 2004. Root competition can cause a decline in diversity with increased productivity. *Journal of Ecology* 91: 401–416.
- RICE, S. K., C. GUTMAN & N. KROUGLICOF. 2004. Laser scanning reveals bryophyte canopy structure. *New Phytologist* 166: 695–704.
- RINCÓN, E. & J. P. GRIME. 1989. Plasticity and light interception by six bryophytes of contrasted ecology. *J. Ecology* 77: 439–446.
- ROMERO, C., F.E. PUTZ & K. KITAJIMA. 2006. Ecophysiology in relation to exposure of pendant epiphytic bryophytes in the canopy of a tropical montane oak forest. *Biotropica* 38: 35–41.
- RYDIN, H. 1985. Effect of water level on desiccation of *Sphagnum* in relation to surrounding *Sphagna*. *Oikos* 45: 374–379.
- RYDIN, H. 1997. Competition among bryophytes. *Advances in Bryology* 6: 135–168.
- RYDGREN, K., H. DE KROON, R. ØKLAND & J. VAN GROENENDAEL. 2001. Effects of fine-scale disturbances on the demography and population dynamics of the clonal moss *Hylocomium splendens*. *Journal of Ecology* 89: 395–405.
- SAS INSTITUTE, INC. 2002. SAS/STAT® User's Guide, vol. 1, Version 9. SAS Institute Inc., Cary NC.
- SASTRE-DE JESÚS, I. 2004. Ecología de briofitos en América Latina: de presuposiciones florísticas a la práctica ecológica. *Memorias VIII Congreso Latinoamericano de Botánica*.
- SCANDRETT, E. & C. H. GIMINGHAM. 1989. Experimental investigation of bryophyte

- interactions on a dry heathland. *Journal of Ecology* 77: 838–852.
- SUDING, K. S., D. E. GOLDBERG AND K. M. HARTMAN. 2003. Relationships among species traits: separating levels of response and identifying linkages to abundance. *Ecology* 84: 1–16.
- VENABLES, W. N. & B. D. RIPLEY. 2002. *Modern applied statistics with S*, 4th edition. Springer–Verlag, New York. 501pp.
- WEIBULL, H. & H. RYDIN. 2005. Bryophyte species richness on boulders: relationship to area, habitat diversity and canopy tree species. *Biological Conservation* 122: 71–79.
- WIKLUND, K. & H. RYDIN. 2004. Colony expansion of *Neckera pennata*: Modelled growth rate and effect of microhabitat, competition, and precipitation. *The Bryologist* 107: 293–301.
- WOLF, J. H. D. 1993. Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Annals of the Missouri Botanical Gardens* 80: 928–960.
- ZAMFIR, M. & D.E. GOLDBERG. 2000. The effect of initial density on interactions between bryophytes at individual and community levels. *Journal of Ecology* 88: 243–255.
- ZARTMAN, C. E. 2003. Habitat fragmentation impacts on epiphyllous bryophyte communities in central Amazonia. *Ecology* 84: 948–954.

APPENDIX 1

1. SAS code for Mixed model ANOVA for repeated measures of the competitive ability of *T.*

tomentosum

```
data test1;
input id torre cob$ arreglo$ t1 t2 t3 t4 t5 t6 t7 t8 t9;
      t=t1; month=1; output;
      t=t2; month=2; output;
      t=t3; month=3; output;
      t=t4; month=4; output;
      t=t5; month=5; output;
      t=t6; month=6; output;
      t=t7; month=7; output;
      t=t8; month=8; output;
      t=t9; month=9; output;
drop t1-t9;
datalines;
.....•
DATA
proc mixed method=ml covtest;
class id torre cob arreglo month ;
model t = cob arreglo cob|arreglo/s ;
random torre cob*torre;
repeated month / type=toeb subject=id r;
contrast 'arreglo'
         arreglo 1 1 1 -3;
         cob 1 1 -2;
lsmeans arreglo;
run;

quit;
```

2. SAS code for Mixed model ANOVA for repeated measures of effect of clipping flagelliform

branches sin the competitive ability of *T. tomentosum*.

```
data test1;
input id torre cov$ clip$ spec$ t1 t2 t3 t4 t5 t6 t7 t8 t9;
      t=t1; month=1; output;
      t=t2; month=2; output;
      t=t3; month=3; output;
      t=t4; month=4; output;
      t=t5; month=5; output;
      t=t6; month=6; output;
      t=t7; month=7; output;
      t=t8; month=8; output;
      t=t9; month=9; output;
drop t1-t9;
```

```

datalines;

proc mixed method=ml covtest;
class id torre cob arreglo month clip;
model t = cob arreglo clip cob|arreglo*clip/s ;
random torre cob*torre;
repeated month / type=toeb subject=id r;
lsmeans arreglo*clip;
contrast 'clip'
        arreglo*clip 1 -1 1 -1;
run;

quit;

```

3. SAS code for Mixed model ANOVA of RCP of three different bryophyte in three light levels and pairwise species interactions.

```

data test RCP thuidium;
input id torre cob$ arreglo$ month rcp;

datalines;

227 7 Doble Thuid_Leuco 0.127318495
... ..
...

proc mixed ;
class id torre cob arreglo rcp;
model rcp = cob arreglo cob*arreglo;
repeated month / subject=id r;
random torre cob*torre;
lsmeans arreglo*cob;
run;
quit;

```

4. SAS code for non parametric Kruskal Wallis or Wilcoxon two rank test

```

data test6 RGR;
input Torre cob$ arreglo$ especie$ RGR;
datalines;

proc npar1way wilcoxon ;
    class arreglo;
    var RGR;
run;
quit;

```

5. Code for non linear modeling in R package for repeated measures with different species arrangements.

```
>t6<-read.csv("tt6.csv",header=TRUE)
>names(t6)
>lme2<-lme(rgr ~species*ordered(time) + light*ordered(time), random=~1|id,
data=t6)
>aov2<-aov(rgr ~ species*ordered(time) + light*ordered(time)+
Error(tiempo/id),data=t6)
>summary(aov2)
>write.table(lme2$fitted,"lme2fit.txt")

>summary(lme2)
>summary(aov2)
```

6. Code for linear regression in R package. Analysis of the relationships between the RGR of *T. tomentosum* and the environmental variables.

```
>clim<-read.csv("climate.csv",header=TRUE)
>names(clim)
>is.vector(clim$temperature)
>is.vector(clim$RH)
>
>lm1<-lm(RGR~temperature,data=clim)
>aov1<-aov(RGR~temperature, data=clim)
>summary(aov1)
>
>aov2<-aov(RGR~RH, data=clim)
>summary(aov2)
```

7. Code for ANOVA test in R package. Analysis of the RCP of *T. tomentosum*, *C. cornuta* and *L. cruegerianum* in different light conditions and under different species interactions.

```
crcp<-read.csv("crcp.csv")
> lrcp<-read.csv("lrcp.csv")
> trcp<-read.csv("trcp.csv")
```

```

> aov3<-aov(RCP~arr+ cob+ arr*cob ,data=crp)
> summary(aov3)

          Df Sum Sq Mean Sq F value Pr(>F)
arr          2   75.64    37.82  1.2338 0.31572
cob          2  239.71   119.86  3.0079 0.03916 *
arr:cob      4   90.19    22.55  0.7356 0.5797
Residuals   18  551.76    30.654
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

> aov1<-aov(RCP~arr+ cob+ arr*cob ,data=trcp)
> summary(aov1)

          Df  Sum Sq Mean Sq F value  Pr(>F)
arr          4  39.750   9.938  1.5304 0.21856
cob          2  54.819  27.410  4.2211 0.02425 *
arr:cob      8  60.678   7.585  1.1681 0.35000
Residuals   30 194.804   6.493
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

> aov2<-aov(RCP~arr+ cob+ arr*cob ,data=lrcp)
> summary(aov2)

          Df  Sum Sq Mean Sq F value Pr(>F)
arr          2  24.397  12.198  1.2429 0.3122
cob          2  43.402  21.701  2.2111 0.1385
arr:cob      4  33.961   8.490  0.8651 0.5036
Residuals   18 176.661   9.815

```

7. SAS code for paired t test comparing clay versus rock temperatures.

```

data tile_temp;
input time tratam$ id ttile trock;
datalines;

proc univariate normal plots;

var ttile trock;

probplot /square pctlminor;

output out=pctscore median=Median pctlpts=98 50 20 70
pctlpre=Pctl_ pctlname=Top Mid Low;

proc ttest data=tile_temp;
paired ttile*trock;
run;

```

FIGURES



Figure 1. Study sites in Ciales (A) and Toro Negro (B) in the *Cordillera Central* of Puerto Rico

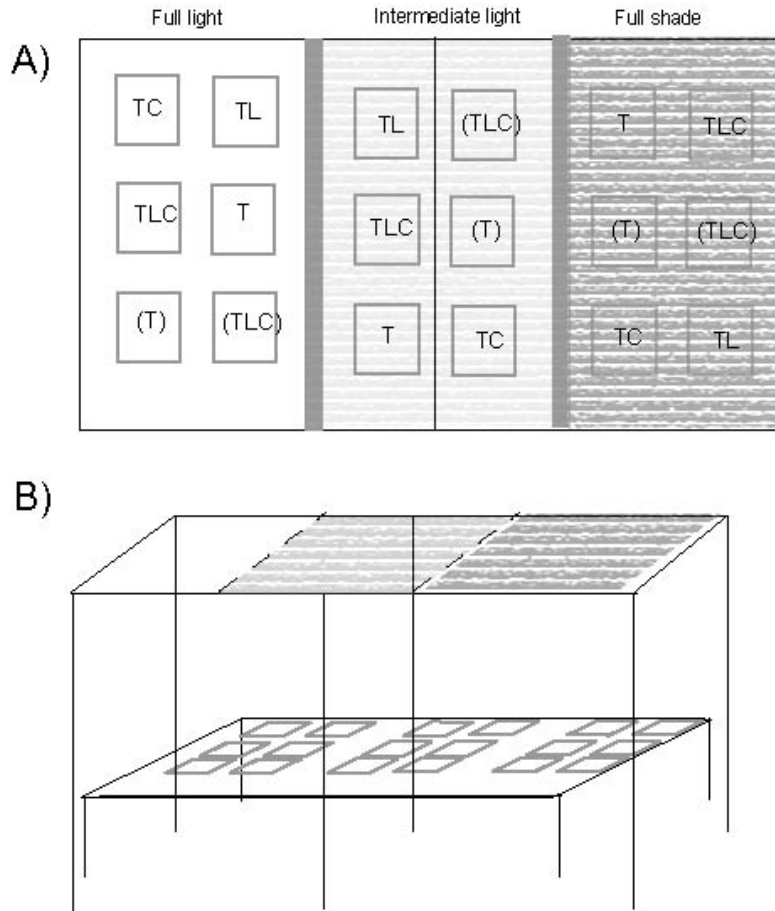


Figure 2. A - Bryophyte combinations and light treatments distribution in the scaffoldings. Initials follow: T – monocultures of *Thuidium tomentosum*, TC – *T. tomentosum* and *Ceratolejeunea cornuta*, TL – *T. tomentosum* and *Leucoloma cruegerianum*, TLC – *T. tomentosum* with *C. cornuta* and *L. cruegerianum*, (T) and (TLC) indicates species mixtures with clipped branches. B – Sketch of the PVC scaffolding with two layers: lower layer holding the tiles and upper layer holding the black gardening netting.

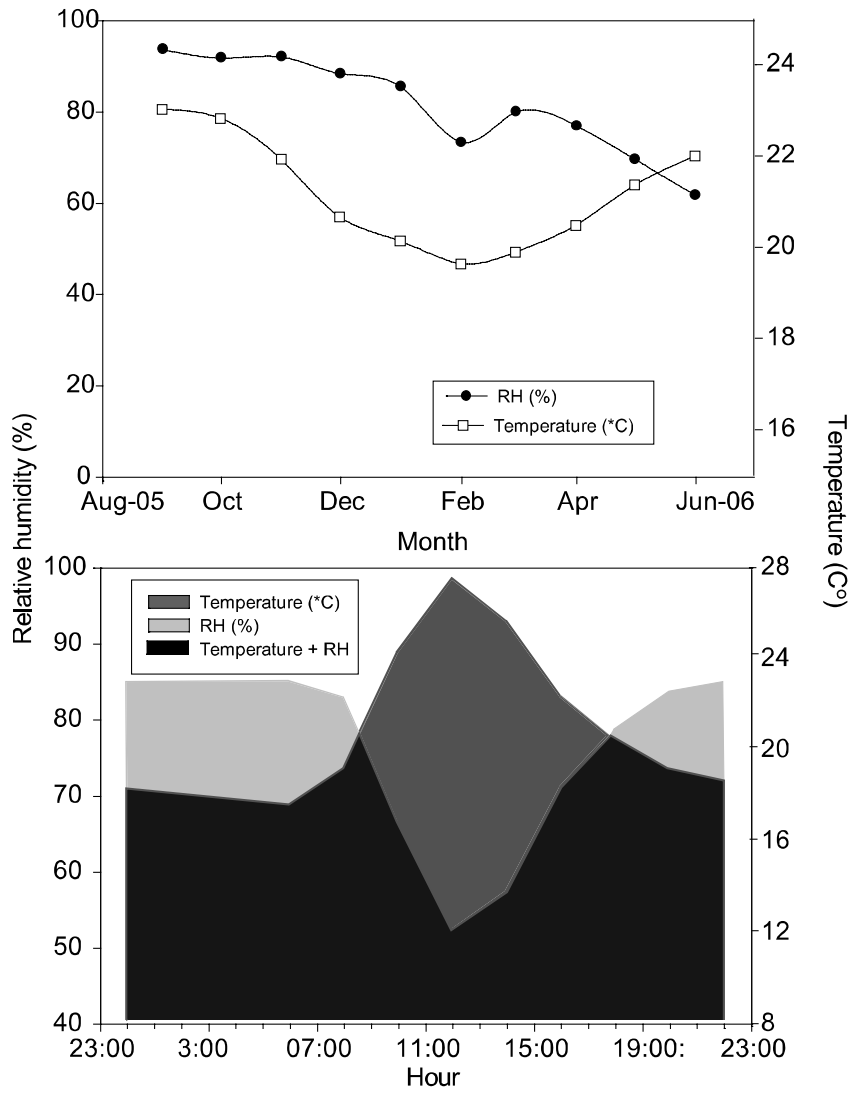


Figure 3. Monthly (top) and daily (bottom) variation in temperature and relative humidity in Ciales. Data gathered with HOBO © data loggers.

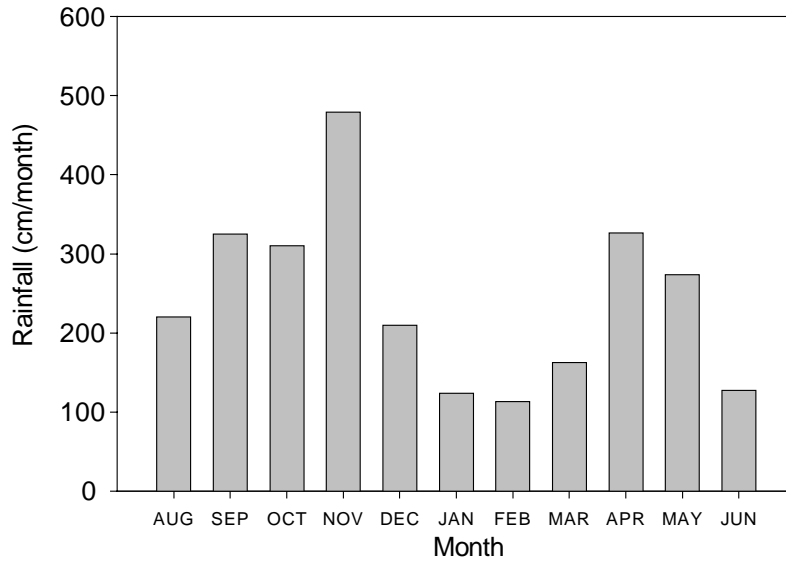


Figure 4. Variation of annual precipitation in Toro Negro Commonwealth forest, values are averages from January 1999-December 2005 (Anon. 2006)

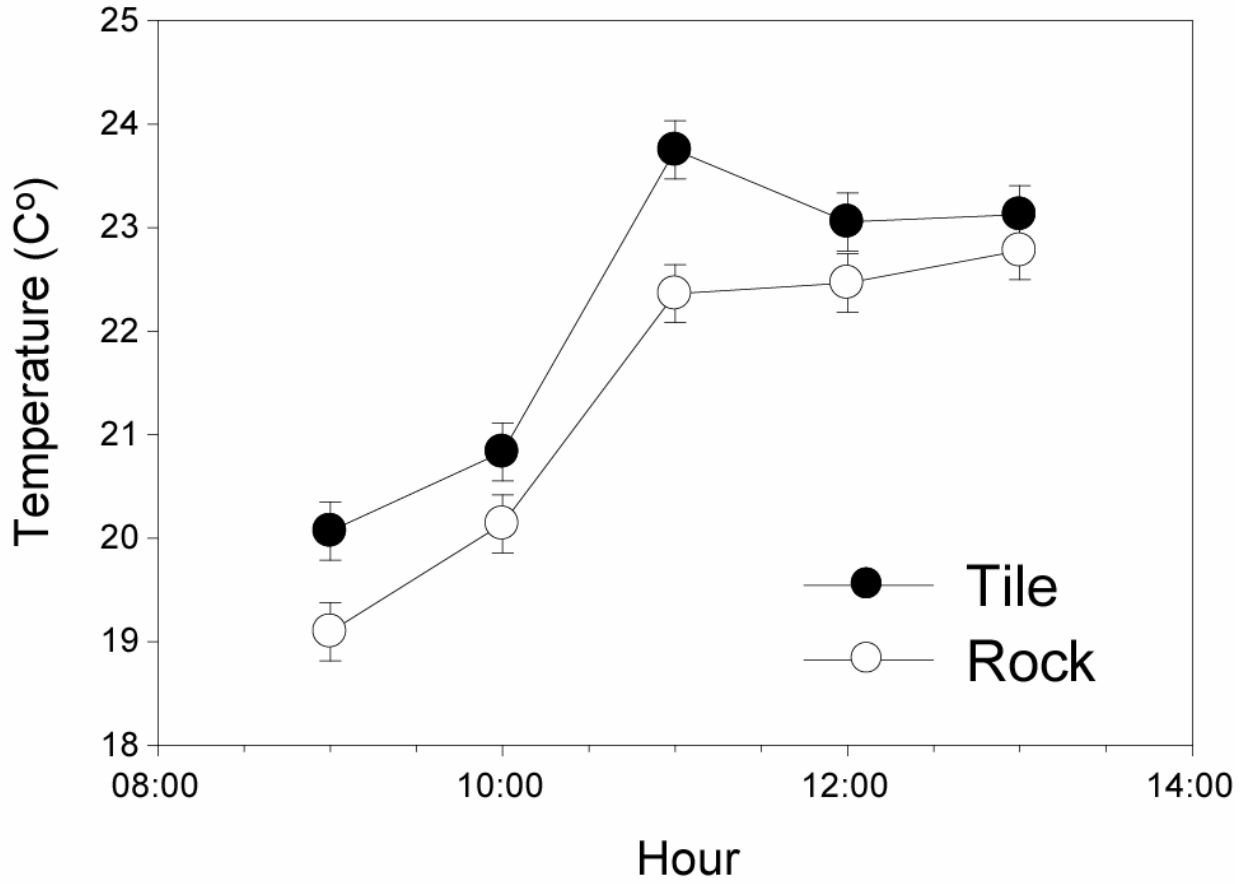


Figure 5. Average temperature for clay tiles (black circles) and rocks (white circles) during 5 hours in 8 sites in a lower montane subtropical forest. Bars in SD.

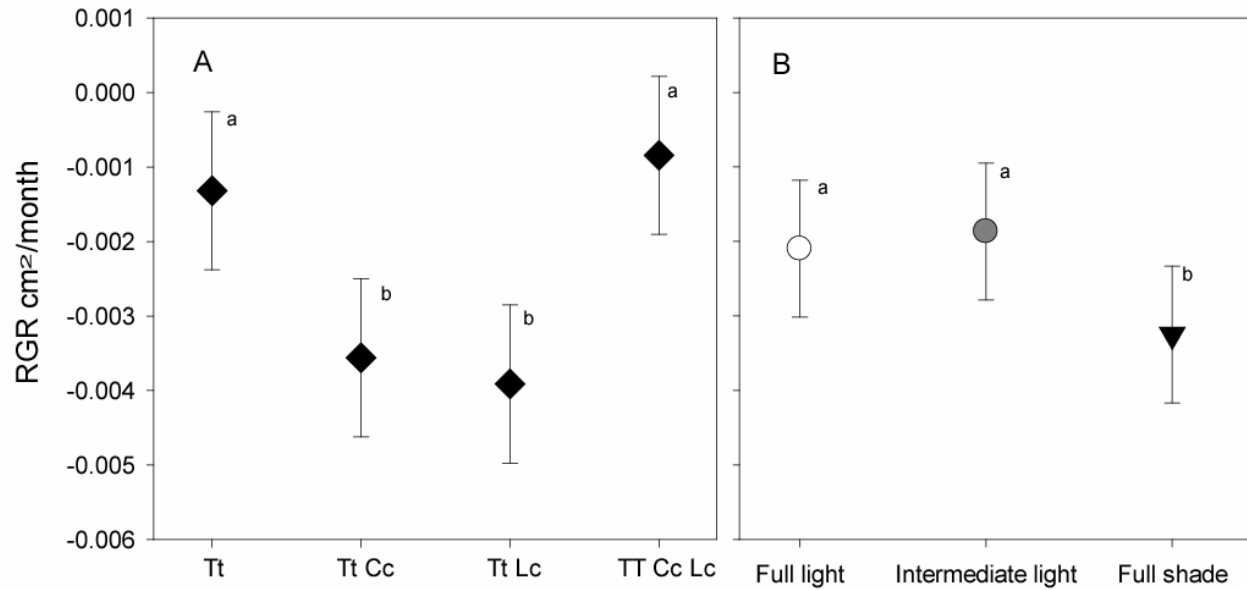


Figure 6. A – Mean Relative Growth Rate (RGR) of *T. tomentosum* in four species arrangements. Tt– Monocultures of *T. tomentosum*, Tt Cc – *T. tomentosum* and *C. cornuta*, Tt Lc – *T. tomentosum* and *L. cruegerianum* and Tt Cc Lc *T. tomentosum*, *L. cruegerianum* and *C. cornuta*. B: Mean RGR of *T. tomentosum* under three different light treatments. Bars in SD and points marked with the same letter have homogeneous means.

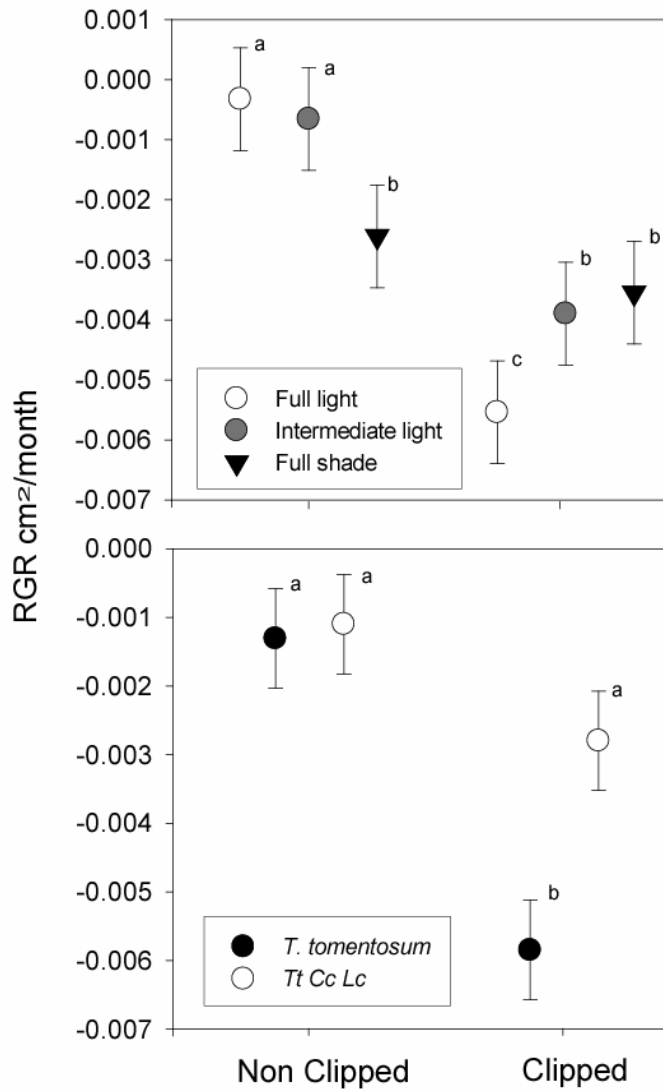


Figure 7. Effect of clipping the flagelliform branches of *T. tomentosum* on its competitive ability under three light treatments. Top: RGR of *T. tomentosum* in non clipped and clipped treatments under different light conditions. Bottom: RGR of monocultures of *T. tomentosum* (Tt) and mixtures with *C. cornuta* (Cc) and *L. cruegerianum* (Lc) in clipped and non clipped treatments between *T. tomentosum* monocultures and mixtures. Bars in SD.

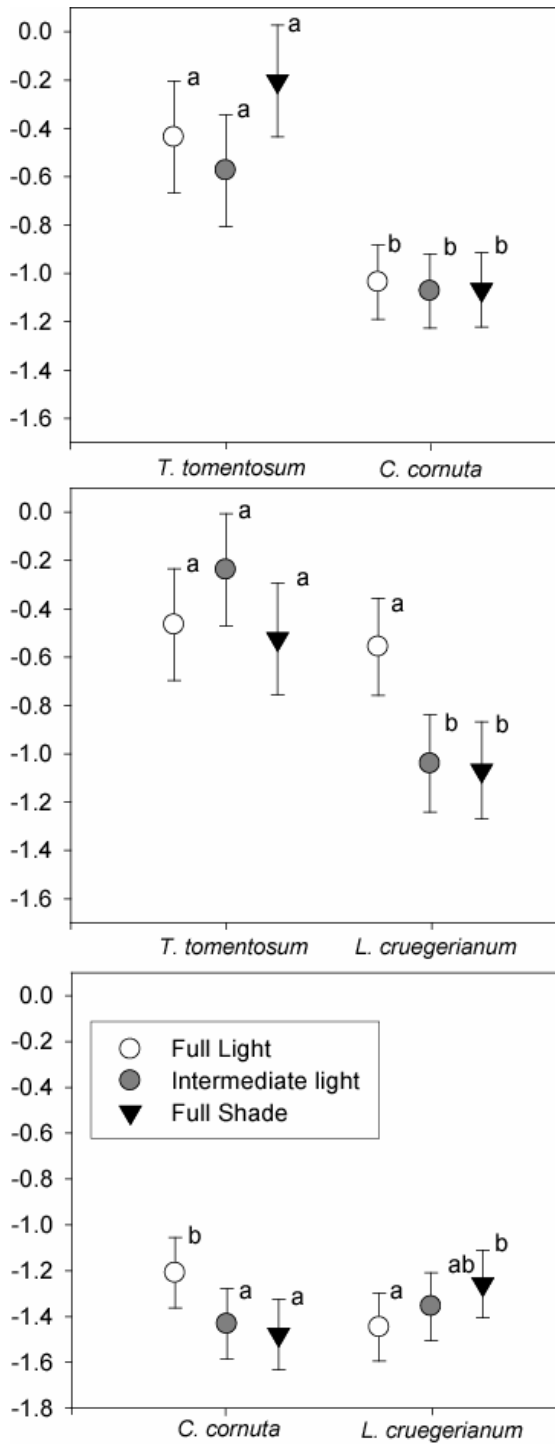


Figure 8. Effect of different neighbor species grown under different light treatments in the RCP of *T. tomentosum*, *C. cornuta* and *L. cruegerianum*. Top: RCP of *L. cruegerianum* in the presence of *T. tomentosum* and *C. cornuta*. Middle: RCP of *C. cornuta* in the presence of *T. tomentosum* and *L. cruegerianum* in mixtures. Bottom: RCP of *T. tomentosum* in the presence of *C. cornuta* and *L. cruegerianum*. Bars in SD and points marked with the same letter have homogeneous means.

TABLES

Table 1. Effect of species combination and light intensity on the RGR of *Thuidium tomentosum*. Mixed model ANOVA of RGR for 4 species arrangements (*T. tomentosum*, *T. tomentosum*-*C. Cornuta*, *T. tomentosum*-*L. Cruegerianum* and *T. tomentosum*-*C. Cornuta*-*L. ruegerianum*) across three light treatments (full light, intermediate light and full shade). * Significance codes Pr (F) < 0.05.

Source	Numerator DF	Denominator DF	F Value	Pr > F
Light intensity	2	10	2.76	0.0076*
Species	3	621	8.62	<0.001*
Light * Species	6	621	0.95	0.45

Table 2. Mixed model ANOVA of RGR for clipped and non clipped plants of *T. tomentosum* in monocultures of *T. tomentosum*, and *T. tomentosum* mixed with *C. cornuta* and *L. Cruegerianum*. * Significance codes Pr (F) < 0.05.

Source	Numerator DF	Denominator DF	F Value	Pr > F
Light intensity	2	10	0.6	0.5694
Species mixtures	1	621	6.5	0.011 *
Clipping	1	621	23.95	<.0001 *
Light*clipping	2	621	3.73	0.0245 *
Species*clipping	1	621	4.94	0.0266 *
Light*species*clipping	4	621	0.08	0.9896

Table 3. ANOVA table comparing the relative competitive performance of *T. tomentosum*, *L. cruegerianum* and *C. cornuta* in different light treatments. * Significance codes Pr (F) < 0.05.

Variable		<i>C. cornuta</i>	<i>L. cruegerianum</i>	<i>T. tomentosum</i>
Light intensity	DF treatments	2	2	2
	DF residuals	4	4	4
	F value	1.07	0.67	2.25
	Pr > F	0.42	0.55	0.22
Species mixtures	DF treatments	1	1	2
	DF residuals	42	42	57
	F value	11.88	11.7	3.89
	Pr > F	0.0013*	0.0014*	0.02*
Light x species mixtures	DF treatments	2	2	4
	DF residuals	42	42	57
	F value	0.62	2.46	0.8
	Pr > F	0.54	0.09	0.53