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RE-EVALUATION OF LIFESPAN IN A NEOTROPICAL ORCHID: AN ELEVEN YEARS SURVEY

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Lifespan as a variable of the total survivorship period of individuals is infrequently studied. When studied it is often limited to investigation of the effect of some environmental variable on the lifespan of short lived morphological unit of the plant such as leaves or flowers. However, it is of crucial importance for determining the likelihood of survival of populations (Calder 1983, Tremblay, 2000) and should be part of any population viability analysis (PVA). Moreover evaluation of the mean (or medium) life and variance (or quartile) in lifespan is a variable of vital importance when considered for analyses of the likelihood of natural selection and genetic drift (Barrowclough & Rockwell 1993, Merila & Sheldon 2000, Crognier 2003). Many parameters are correlated with lifespan such as effective population size and lifetime reproductive success. Lifespan has a positive correlation with reproductive success, which is a consequence that individuals with longer lifespan have a higher probability of having offspring. Moreover, the larger the variance in lifespan the larger the variance in reproductive success and consequently effects the effective population size (Barrowclough & Rockwell, 1993; Tremblay & Ackerman, 2001).

Tremblay (2000) published a three years survey of lifespan in four species of *Lepanthes* including *L. caritensis*, however, after the three years survey most juveniles and adults were still alive (64 and 91%, respectively), while most seedlings died during the survey period with only 25% still alive at the end of the survey. As a result, the survivorship curve only represented a partial life history of the species with a maximum possible lifespan as function of the survey period. Limited survey's can easily bias the results, which can

suggest smaller mean and variance in the projected lifespan. A second preoccupation with the previously published paper is that the number of seedling surveyed was very small and consequently the estimates could have been affected from random mortality and survivorship and not be a good representation of the typical lifespan of this life stage. Thus in this survey we present a continuation of the survey of one of the species, *Lepanthes caritensis* Tremblay & Ackerman and include a third population to the previously two studied with a total survey period of approximately eleven years for the first two populations.

Specifically we determined if mean and variance in lifespan from the surveyed populations and life stages are similar to the first 3 years survey. Secondly we evaluated if the survivorship among populations is equal. Thirdly, we investigated if the life stage and size (number of leaves) are determining factor in survivorship.

Methods

STUDY SYSTEM. *Lepanthes caritensis* is an endemic epiphytic, caespitose, and host specific orchid of 0.8 to 4.4 cm tall and its stems are appressed to the phorophyte. For description of the species and basic ecology refer to Tremblay & Ackerman 1993, Tremblay 1997a, 1997b, and Tremblay *et al.*, 1998.

STUDY AREA. This species occurs in a Subtropical Wet Forest of the Holdridge Life Zone System (Ewel & Wetmore 1973) and is found in the municipality of Patillas, Puerto Rico in the Carite Forest (Tremblay & Ackerman 1993). The plants are found at approximately 615m asl (maximum of Puerto Rico is 1100

TABLE 1. Sample size and sampled period for *L. caritensis* at three sites in the Carite Forest in Puerto Rico. Diameter at breast height (DBH) of the phorophyte (cm), and approximate sky visibility using a densiometer (% open sky).

Population	Number of individuals	Month survey started	Month survey ended	DBH of tree	Sky Visibility
1	184	September-94	August-06	43	36.40
2	111	September-94	August-06	45	32.24
3	222	May-02	August-06	67	26.00

asl) in an area that was apparently never logged. Annual mean temperature and rainfall are between 18 and 24°C, and 2200 mm respectively (Ewel & Wetmore 1973). Rain is more or less consistent throughout the year with a slight increase in the winter period.

DATA COLLECTION. We censored a total of 517 individuals on an irregular basis for over 11 years of which approximately six years were surveyed monthly (Table 1). We numbered all individuals with plastic tags as described in Tremblay 2000. At each survey period the number of leaves of each individual was counted and the stage of the individual was noted. Individuals from all populations were identified as seedlings, juveniles, and adults, where seedlings are small plants without lepanthiform sheets on the petioles of any of the leaves, juveniles are individuals with at least one lepanthiform sheath on the petiole without evidence of past or current reproduction, and adults encompassed individuals that are currently reproductive (active inflorescences) or have been in the past (inflorescences may persist for years after they have been active). The identification of plant stages follow previous studies (Tremblay 2000; Tremblay & Hutchings 2003; and Rivera Gomez *et al.*, 2006). The numbers of individuals alive at the end of the survey varied from 39 to 113.

The individuals from the three populations are all found on older individuals of the tree *Micropholis guyanensis* (A. DC.) Pierre 1891 (Sapotaceae). Orchids are only found on the largest individuals of this species (Tremblay *et al.*, 1998) and the three populations surveyed were on trees with DBH above 43 cm (Table 1).

INDICES MEASURED AND SOFTWARE USED. Comparison of the survivorship probability for all population and stages were evaluated by using proportional hazard

or Cox's model, methods that lets you define models having failure time as the response variable with right-censoring and time-independent covariates. All tests including for multiple samples and the Kaplan-Meier's equation estimates were analyzed using the statistical softwares Statistica and JMP (Kaplan and Meier, 1958; Statsoft, 1994; survival analysis model; SAS Institute Inc., 2004, JMP v.5.1.2).

Results

GENERAL PATTERN OF SURVIVORSHIP. Combining data from all three populations and stages the mean death rate per year in this specie is 5.1% per year. The mean lifespan (se) was estimated at 1388 ± 74.2 days (approx 3.8 yrs), and median lifespan at 846 days (approx. 2.3 yrs; Table 2, Fig.1).

DIFFERENCES IN LIFESPAN AMONG POPULATIONS. Mean death rate per year by populations ranged from 4.1% to 18.0% per year. The two populations that were surveyed for 11 years had similar death rates while the third population had a higher death rate (Table 1, 2). The mean (s.e.) expected lifespan by population ranged from 739 ± 39 to 1544 ± 119 days (Table 3). We found a significant difference in the lifespan between all populations (Log-rank Test, $\chi^2 = 9.2846$, $df = 2$, $p = 0.0096$). Population two had the longest estimated lifespan while population three had the shortest estimated lifespan (Fig.2).

DIFFERENCES IN LIFESPAN AMONG LIFE STAGES. Summing the individuals from the different stages of the three populations we found that the shortest mean lifespan (se) was observed in seedlings (286 ± 35.7) and the longest for adults (2037.1 ± 111.3 ; Table 2, Fig.3). The lifespan of the different stages were significantly different (Log -rank test, $\chi^2 = 260.2715$, $df = 2$, $p < 0.0001$). Seedlings are more at risk from failing than juveniles or adults.

TABLE 2. Total numbers of days surveyed, cumulative proportion surviving at the end of the survey, number of all individuals alive at the end of the survey, median, mean, and the standard error of the mean lifespan for all population and stages. (* = bias mean estimates as a result of censored observation (individuals still alive) in the final survey time, for this reason estimates are a lower bound for the true mean).

Population	Number of days surveyed	Cumulative proportion surviving (%)	Number of individuals of the mean	Median survivorship alive at the end of the survey	Mean	Standard error
1	4346	10.2	53	728	1544*	119
2	4346	7.4	39	1246	1244*	114
3	1567	26.7	113	653	739*	39
Combined		9.04	205	846	1388*	74
Stage						
Seedling		7.9	32	154	287	36
Juvenile		1.2	79	688	783	71
Adult		17.2	94	1246	2037*	111

THE EFFECT OF NUMBER OF LEAVES ON THE SURVIVORSHIP OF INDIVIDUALS. The number of leaves affected the survivorship within stage categories. The mean lifespan is dependent on the number of leaves in juveniles ranging from 539 to 1080 days and for adults we found that the mean lifespan (se) varies from 1653 to 2196 (Table 4). The median lifespan varied from 485 to 688 days for juveniles and 1120 to 1246 for adults, noting that the median for individuals with five or more leaves do not have an estimated value because more than 50% of individuals were still alive at the end of the 11 years survey.

Discussion

We found that in general that the mean lifespan of *Lepanthes caritensis* is approximately 3.8 years, which

denotes that most of the individuals we’ve been studying had die in our 11 years survey. After the 3 yrs survey the lifespan for *L. caritensis* had been estimated at 1245 days (3.4 yrs; Tremblay 2000), which is clearly very close to the eleven yrs survey. The main effect on the length of the lifespan comes from the short lifespan of seedlings that influences the length of the species lifespan. The life history curve is a typical type two curve where the rate of change is fairly constant. Type one curve is for organisms living out their full physiological lifetime, for example *Rhododendron maximum*, and type three curve is for organisms experiencing high mortality and low survivorship in early stages like *Spergula vernalis* (Smith 1990).

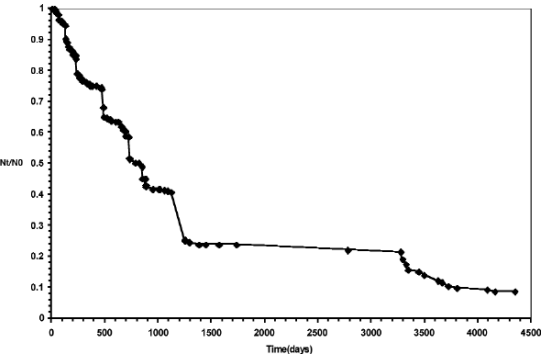


FIGURE 1. Survival curve of *Lepanthes caritensis* from an 11 yrs survey from 571 number of individuals. All populations and stages combined. Nt/No = the number of individuals at time t over the number of individual at the beginning of the survey.

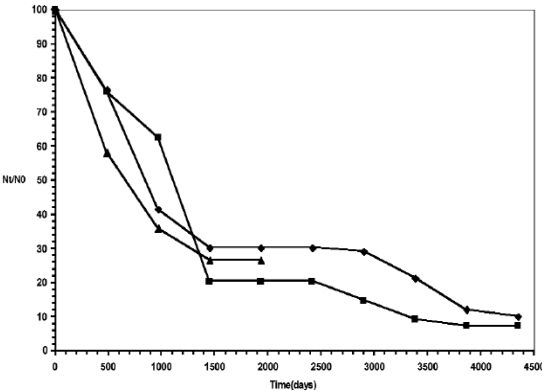


FIGURE 2. Cumulative proportion surviving for all populations of *L. caritensis*. Population 3 survey period was shorter. Nt/No = the number of individuals at time t over the number of individual at the beginning of the survey. Diamonds = pop. 1, squares = pop. 2, triangles = pop. 3.

TABLE 3. Percent death and mean lifespan (year) of *Lepanthes caritensis* and the sample size for estimating the parameter.

Population	Percent death/year	Mean lifespan (yrs)	Sample Size
1	7.5	4.2	184
2	7.9	3.4	111
3	18.0	2.0	222
Combined	7.7	3.8	517
Stages			
Seedling	45.3	0.8	96
Juvenile	9.5	2.1	197
Adult	7.0	5.6	224

TABLE 4. The lifespan of individuals with varying number of leaves and life stages, mean lifespan (se) and median time for individuals by stage (J = Juveniles, A = Adults). (* = Bias estimate as some individuals still alive at the end of the survey).

Number of leaves	Stage (N)	Sample size	Mean	Standard Error	Median Time
1	J	38	539	62	688
2	J	69	718	118	530
3	J	65	877	125	728
4	J	18	988	303	689
≥ 5	J	7	1080	502	485
1	A	34	1653*	285	1120
2	A	68	1978*	189	1246
3	A	63	1841*	178	1246
4	A	30	2023*	277	1246
≥ 5	A	20	2196*	265	--

The behavioral pattern of survivorship between the three populations demonstrates that the two longest surveyed populations behave similarly while the newly added site had a shorter lifespan. In the previous study the median survivorship (1245 days) in the second population was the same as in this analysis (1246 days), while the median lifespan in population one was much lower (1245 days as compared to 728 days after the 11 yrs survey). The newly added population has a lower median lifespan as compared to population one (653 days). The reduce survivorship in this population could be influenced by the light availability; the proportion of visible sky in the third population is reduced, consequently higher shaded area (Table 2).

The life stages (seedling, juvenile or adult) are informative in determining the plant's lifespan. Seedlings have short lifespan as compared to juveniles (2.7 times longer lifespan than seedlings), while

adults also differ from juveniles (2.6 times longer lifespan). In the previous survey estimates of lifespan were not available because too few individuals had perished during the survey period (Tremblay 2000). The increase survey period allowed for gathering estimates on the mean and median in lifespan of the different stages of this species.

The numbers of leaves in *Lepanthes caritensis* makes a significant difference in the plants lifespan. There is a correlation between lifespan and the number of leaves held by an individual. The number of leaves is related to the total leaf area and consequently these individuals are more likely to survive environmentally stressful period or partial herbivory (rare in this species).

The addition of 8 more years to the survey for estimating *Lepanthes caritensis* survivorship had little effect on the estimators of seedlings, however the addi-

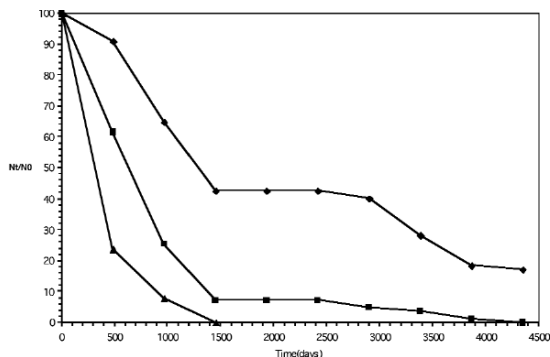


FIGURE 3- Cumulative proportion surviving for all three stages of *L. caritensis*. N_t/N_0 = the number of individuals at time t over the number of individual at the beginning of the survey. Diamonds = Seedlings, squares = Juveniles, triangles = Adults.

tional survey suggest that juveniles and adults have a longer lifespan than predicted from the three year survey. Moreover, the number of leaves has a large impact of survivorship probabilities and thus could also be used a surrogate method for predicting lifespan instead of stages. Assuming constant mortality of adults at 7% mortality *per annum* and a Weibull survivorship distribution it is expected that 10% of adults survive 12.2 yrs and 1% will survive 21.5 yrs. Consequently a few individuals will likely have a very long lifespan as compared to most individuals and likely leave an excess of progeny as compared to most adults, resulting in a high variance in reproductive success.

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