The Effects of Canopy Openings and Population Size on the Persistence of Southwest Columbines at Risk of Extinction

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Abstract: The habitat associated with riparian, understory, rare and endangered plant populations of the Southwest includes rocky places in high-altitude canyons, mostly along shady streams, pools, and dripping cliffs. The composition of these insular plant populations, which are separated by intervening desert, is influenced by several local environmental conditions. The understory light environment, which is influenced by canopy cover, is a key determinant of vegetation patterns; it varies spatially within and among populations, and is determined by intermediate closure and light availability. Light availability could directly affect individual fitness (via affecting photosynthetic, micro-climatic, and transpirational processes) and subsequently could indirectly affect plant population size and persistence. We examined the environmental influences of canopy cover and light availability in seven populations of herbaceous, perennial yellow columbines (genus *Aquilegia*) in the Southwest. *Aquilegia* populations exhibit many of the characteristics, particularly isolation and relatively small population size, associated with at-risk populations. For example, *Aquilegia chaplinei*, or Chapline's columbine, is currently protected under the New Mexico Endangered Plant Species Act. Canopy cover and understory light environments were quantified from the view each plant has of the sky, measured via vertical photography. These images were analyzed to investigate the percentage of sky versus canopy cover, as well as the relationship of canopy cover and within- and among-population traits. Overall, these ecological assessments will help expand our understanding of environmental influences and may be important in regard to the conservation, persistence, and recovery of small, isolated plant populations.

Historically, the main criterion for identifying threatened and endangered plant species has been the scarcity of individuals or populations. Recently, however, scientists and managers have recognized the need to assess rarity and vulnerability based on biological processes in addition to patterns of geographic distribution (Holsinger and Gottlieb 1991). Reduced geographical distribution or population size could be the result of, and could potentially be affected by, three important types of processes: genetic, demographic, and environmental. The performance of plant individuals and populations hinges on the integration of these types of processes. The focus here is on one environmental factor that potentially influences at-risk columbine (*Aquilegia*) populations in semiarid ecosystems of the U.S. Southwest. (For a discussion of the importance of understanding plant evolutionary genetics and demography see Milligan, and Stubben and Milligan, this volume).

Semiarid woodland ecosystems in the Southwest are especially sensitive to changes in vegetation due to habitat degradation (Schlesinger et al. 1990) and drastic climate changes (Neilson 1986). Climate change in particular has caused profound reductions in the ranges of Southwestern woody vegetation since the Pleistocene (Stephenson 1990). Changes in such overstory functional types directly affect the understory light environment. Previous studies have shown that woody overstory canopy patterns affect the understory by altering solar radiation and soil moisture (Breshears et al. 1997), seed germination and seedling performance (Caccia and Ballare 1998), ectomycorrhizal associations (Zhou and Sharik 1997), and species richness (Vetaas 1997), as well as desert grasslands being invaded by woody mesquite (Warren et al. 1996). Our study is unique in that it examines the direct relationship between overstory, woody canopy openings and the vegetative and reproductive outputs (directly or indirectly affecting fitness) of understory plant individuals whose populations are considered at risk of extinction.

Understory light (1) is influenced by canopy openings, (2) varies spatially within and among understory populations, (3) is often the most limiting factor, and (4) could influence vegetative and reproductive outputs for understory herbaceous plant functional types. Martens et al. (2000) clearly demonstrated the relatively strong, negative relationship between percent canopy cover and photosynthetically active radiation (PAR); as percent canopy cover increases, PAR decreases. Because PAR is the only light source available to plants,

fitness-related plant traits could be reduced as the degree of canopy opening becomes greater. Specifically, we predicted a negative relationship between overstory canopy gap and both vegetative and reproductive outputs for understory *Aquilegia* individuals.

To comprehend the relationship between light and understory plant distribution and performance, we must accurately quantify light availability through space. There are many techniques to measure the canopy, but photography of the overstory canopy closure, or the proportion of the sky hemisphere obscured by natural structures when viewed from a single point, is preferred for quantifying forest structure and its causal force on the understory light environment (Jennings et al. 1999, Robison and McCarthy 1999).

Methods

The genus *Aquilegia* (Ranunculaceae) is composed of at least 70 North Temperate herbaceous perennials (Munz 1946, Whittemore 1997). The *Aquilegia* populations in the Southwest exhibit many of the characteristics, particularly isolation and relatively small population size, associated with at-risk populations. This is exemplified by the conservation status of *Aquilegia chrysantha* var. *chaplinei* (Chapline's columbine) and its limited distribution within Eddy County, New Mexico. Chapline's columbine is currently protected at the state and federal levels, and is a U.S. Forest Service Sensitive Species.

The habitat associated with many Southwest *Aquilegia* consists of rocky places in canyons, mostly along streams and dripping cliffs; therefore, the biogeographical range of *Aquilegia* is among montane "islands." The woody overstory for such *Aquilegia* typically includes some combination of maple (*Acer* spp.), ash (*Fraxinus* spp.), and cottonwood (*Populus* spp.). The persistence of *Aquilegia* populations may depend on woody overstory; specifically, changes in the overstory structure could cause *Aquilegia* population size decline.

Previous genetic analyses of closely related Southwest *Aquilegia* suggest a limited among-population gene flow within and among mountain ranges in the Southwest (Hodges and Arnold 1994, Strand et al. 1996). As a result, the population structure of *Aquilegia* enables comparisons among geographically and genetically isolated "island" populations. Additionally, principal components analysis (PCA) for several floral traits of these *Aquilegia* implies indistinguishable taxonomic boundaries (unpublished data). This understanding of Southwest *Aquilegia* population isolation and of its possible dependence on woody overstory, regardless of historical taxonomic treatment, is fundamental for investigating the natural association between overstory canopy openings and understory *Aquilegia* population performance.

Study Sites

To empirically test our prediction that understory population size is affected by the degree of overstory canopy openings, we sampled populations that exhibit a range of numbers of individuals (Table 1). Population size estimates entailed counting the number of adult plants and estimating numbers of seedlings and juveniles. Sample sizes range from 20 to 160 individuals, depending on the population.

Vegetative and Reproductive Outputs

Data recorded for each individual plant consisted of stem height, rosette number, leaf number, and leaflet width for one of the basal leaves. Reproductive outputs quantified for each individual were the number of flowers and fruits produced per individual.

Canopy Opening

To assess the effect of the light environment on plant phenotypes, we quantified light availability from the view each plant has of the sky. Above each sampled plant, sky and canopy photographs were taken with an Olympus OM camera, a 28 mm, wide-angle lens, and Fuji 400 ASA black-and-white film. A blue filter (Tiffen 80B) was used to increase the contrast between foliage and sky. For each photograph, the camera was aligned with true north, and a level was used to ensure that the camera was positioned horizontally. A Hewlett Packard Scan Jet IIcx was used to scan the resulting images. Computerized image processing software (Open Visualization Data Explorer, available

Table 1. Sampled populations, locations, and estimated population sizes.

Aquilegia population	Location	Estimated population size
Caballero Canyon	Sacramento Mtns, NM	75
Pine Canyon	Chisos Mtns, TX	100
Cattail Falls	Chisos Mtns, TX	200
Dripping Springs	Organ Mtns, NM	235
McKittrick Can.	Guadalupe Mtns, NM	375
Maple Canyon	Chisos Mtns, TX	500
Ash Springs	San Andres Mtns, NM	3000

online at http://www.research.ibm.com/dx) was then used to express sky and foilage areas to calculate the fraction of open sky per image.

Data Analyses

All statistical analyses were performed with JMP IN7 statistical software (SAS 1996). The distribution of response variable data were checked for deviations from the normal distribution using the univariate procedure of a Shapiro-Wilks W test (a = 0.05; SAS 1996). In the event that these data possessed non-normal distributions or unequal variances, the data were log transformed or we used non-parametric statistical tests to rank responses for comparison (Pratt and Gibbons 1981, Sokal and Rohlf 1987, Sprent 1989). Further, to examine the relationships between the percent open canopy and a suite of plant traits, we used a regression of each of six traits, or response variables on the degrees of percent open sky (Sokal and Rohlf 1987). For statistical significance, the alpha level was set at $P < 0.05$.

Results

With regard to differences in canopy openings among populations, Figure 1 indicates that the distributions vary and the means differ across populations. However, there are possible *statistically* significant differences among the populations. The Wilcoxon/Kruskal-Wallis rank sums results (Table 2) show statistically significant differences in 16 of 21 total pairwise comparisons, prompting an investigation into whether the population-level differences in canopy opening played a role in influencing the number of surviving individuals in each population.

Because the degree of average canopy opening depends on the population, and because our sampled populations vary in the number of individuals, we investigated whether there is a direct, detectable relationship between the degree of open canopy and *Aquilegia* population size. The relatively low, non-significant Spearman's correlation coefficient value (rho = 0.1429; prob > |rho| = 0.7872) illustrates that *Aquilegia* population size is not directly dependent on the degree of open canopy. Although the degree of overstory canopy opening does not *directly* influence the numbers of individuals in the understory *Aquilegia* populations, it may have an *indirect* affect on *Aquilegia* population size if our data support a relationship between the degree of canopy opening and certain plant traits.

Ideally, we strove to determine whether differences in population-level averages of percent open canopy influence differences in population-level averages for a suite of plant traits. Table 3 shows the regression coefficients and describes the

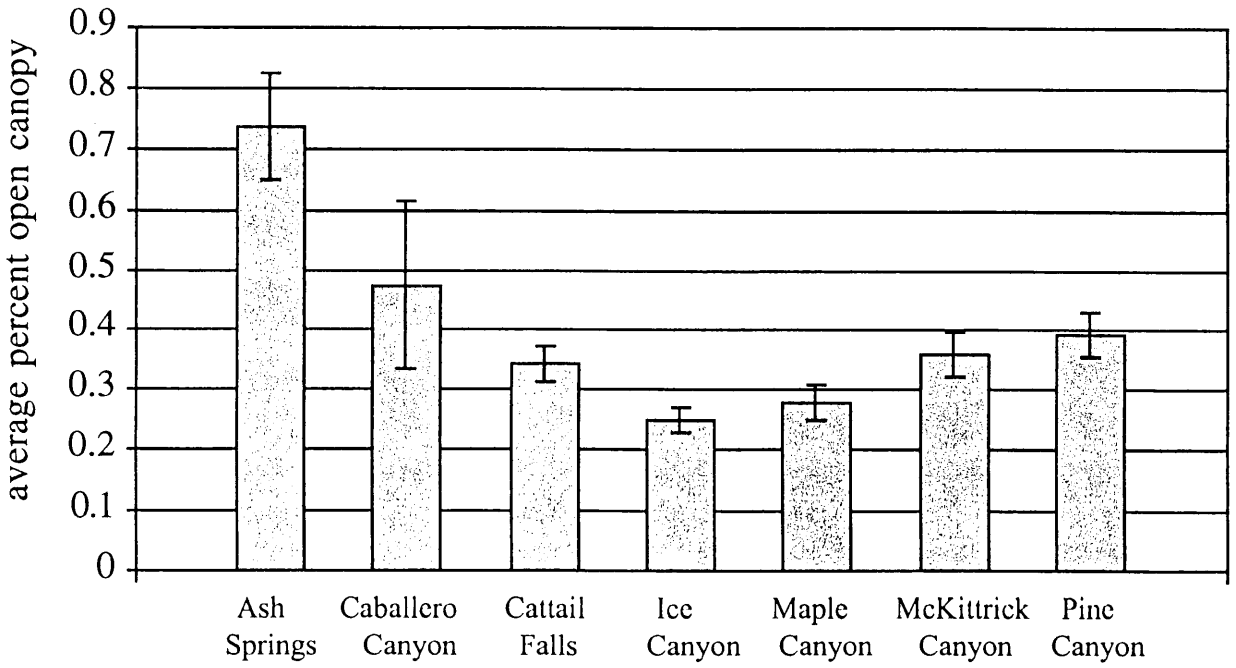

Figure 1. Population profile for average percent open canopy (with 95% confidence intervals).

Table 2. Wilcoxon/Kruskal-Wallis rank probabilities (Prob > χ^2).

	Ash Springs	Caballero Canyon	Cattail Falls	Ice Canyon	Maple Canyon	McKittrick Canyon	Pine Canyon
Ash Springs		0.045*	**	**	**	**	**
Caballero Canyon			0.087	**	0.011*	0.043*	0.387
Cattail Falls				**	0.012*	0.386	0.015*
Ice Canyon					0.547	0.002*	**
Maple Canyon						0.374	**
McKittrick Canyon							0.042*
Pine Canyon							

*prob < 0.05; **prob < 0.001.

Table 3. Regression coefficients describing the effect of open sky on a suite of fitness-related *Aquilegia* traits.

	Number flowers	Number fruits	Leaflet width	Number rosettes	Number leaves	Stem height	Stems
Ash Springs	0.1128*	0.1637*		0.0100	0.0242		0.0754
Caballero Canyon	0.0002	0.0507*	0.0161	0.0382	0.0301*	0.0705	0.0118
Cattail Falls		0.1439	0.2351*	0.0090	0.0042		
Ice Canyon	0.0270*	0.0420*	0.0258	0.0200*	0.0088*	0.1112*	0.1192*
Maple Canyon	0.0232	0.0005	0.0823	0.0177	0.0011	0.2548	0.0011
McKittrick Canyon	0.0274*	0.0009	0.0002	0.0082*	0.0005	0.0236	0.0006
Pine Canyon		0.1508*	0.2135*	0.0366	0.0149	0.3019	0.1357*

Empty boxes indicate missing data; *p < 0.05.

population-level relationships between the effects of open canopy and six plant traits per individual. We can then ask, if there are detectable relationships between the degree of canopy opening and plant traits, whether the regression coefficients, or slopes of the regression lines, differ across populations. In other words, does the expression of plant traits depend on the *interaction* between the population and canopy opening? The highly significant effect test results for five of the six plant traits (Table 4) illustrate that the influences of overstory canopy opening on these particular *Aquilegia* individual traits are remarkably dependent on the population.

Discussion

Our study represents a unique approach to account for the particular environmental influence of overstory canopy openings and estimates of light availability. Our results demonstrate that there exists considerable among-population differentiation in canopy openings, and that there is no detectable causal relationship between the degree of canopy opening and population size. Further, we gauged the impacts of open canopy on fitness-related traits of *Aquilegia* individuals within populations. Although our data for *Aquilegia* populations suggest that the degrees of canopy openings do slightly influence certain plant vegetative and reproductive outputs, this relationship may not be very strong, as evidenced by some of the weak regression coefficients. This is not surprising, given that variance in the mean understory light is often a curvilinear function of cover such that the photosynthetically active radiation (PAR) variance is highest at intermediate values of canopy and is dependent on the spatial pattern (Martens et al. 2000). Further, given the complex nature of the relationships between wavelengths of light affecting photosynthetic processes and the allocation of vegetative and reproductive outputs, there may be tradeoffs depending on the life histories of each population (Bazzaz 1996).

Another cause of the relatively weak relationships between percent open sky and certain plant traits may be due to time lags in understory response to changes in canopy cover, either within the lifetime of an individual or between generations. This phenomenon has been observed in other studies of this nature (e.g., Thomas et al. 1999) and is applicable to this study, especially due to the relatively long generation times of

Table 4. Effect test results for the expression of plant traits dependent on the interaction between the population and canopy opening.

Response variable (Y)	F Ratio	Prob > F
Number of flowers	1.767	0.105
Number of fruits	6.997	< 0.001*
Number of rosettes	3.554	< 0.001*
Number of leaves	3.951	< 0.001*
Stem height	5.376	0.003*
Lower leaflet width	3.536	< 0.001*

Aquilegia that would, in turn, cause a relatively slow rate of response to selection. Elucidation of a time lag could be resolved if demographic analyses are employed to determine plant growth rates (e.g., Pearcy 1983). Therefore, although most of the regression coefficients explaining the variation in traits due to canopy opening have low values, they afford potentially useful information for other analyses.

Future Objectives

Canopy images not only provide information regarding canopy openings, they also provide detailed quantitative descriptions of the forest canopy, such as leaf area index (LAI) , leaf angle distribution, and vertical distribution of leaves. These descriptions are necessary when studying the effects of overstory cover on the understory light environment (McIntyre et al. 1990). We intend to use our images to further characterize the structure of the overstory canopy and to quantify other environmental parameters such as the photosynthetically active radiation (PAR) available to *Aquilegia* individuals.

Although this paper focuses on one particular environmental process affecting at-risk plant populations, one of our aims is to integrate the environmental knowledge with our understanding of quantitative genetic factors that influence plant traits (Milligan, this volume). In particular, our quantitative genetic study seeks to determine the relative contributions of genetic versus environmental influences. Although the data presented in Table 2 suggest that vegetative and reproductive outputs for *Aquilegia* plant individuals are minimally influenced by one particular environmental parameter—the understory light environment—this information will play a significant role in our larger study.

In addition to the effects of open canopy on vegetative and reproductive outputs for perennial plants, the effect of open canopy is an integral factor in demographic processes. For example, theoretical (Pons 1992) and empirical (Caccia and Ballare 1998) studies have demonstrated that the understory light environment influences at least one particular demographic factor: seedling recruitment. Counts of recruited seedlings and of adult reproductive plants from ongoing studies on *Aquilegia* populations (Stubben and Milligan, this volume) provide essential demographic information, such as effective population sizes (Nunney and Elam 1994, Nunney 1995). Additionally, the precipitation available to each of the sampled *Aquilegia* populations has been quantified, showing that the amount of precipitation strongly influences fluctuations in population growth rate (Stubben and Milligan, this volume). Therefore, because we have obtained both demographic and environmental data, and considering that the associations of population size and persistence largely depend on the coupled effects of demographic processes and environmental influences, we have the potential to predict future population growth or decline. Therefore, the integration of genetic, demographic, and environmental influences could play a powerful role in the cause of understory *Aquilegia* population growth or decline.

Conclusion

This study evaluated overstory distribution patterns and the relationship between understory light environments and plant fitness. The importance of this project includes the utilization of photographic techniques and image analyses as powerful tools to estimate the degree of overstory canopy openings, as well as regression-based approaches to assess the relationship between the degree of canopy openings and quantitative traits in *Aquilegia*. Further, the overstory canopy data could be utilized to answer questions regarding other understory plant taxa associated with the Southwest *Aquilegia*, or the photographic methodology and image analyses could be widely applicable to gauging the effects of overstory, open canopy composition, or density on a variety of understory taxa. Ultimately, we intend to collectively examine the interrelationships among evolutionary genetics, demography, and the environment. This knowledge will elucidate a connection between the effects of open canopy and effective population size and persistence, and this will in turn aid our understanding and implementation of effective conservation strategies.

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