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Life History and Environmental Factors Influence Population Density and Stage Structure in Hydrophyllum brownei

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ABSTRACT.—*Hydrophyllum brownei* is a rare endemic species restricted to the Ouachita Mountains of Arkansas. One objective of this study was to model *H. brownei* population density by investigating the influence of sun exposure, soil characteristics and crowding. The most parsimonious model including shade alone best predicted population density, in which increasing shade was correlated with greater population densities. Reproductive capacity of different parts of the root was tested and individuals of the species were found to produce vegetative shoots from all portions of the root. This indicates that individuals are prolific vegetative reproducers, especially in circumstances of intense physical soil disturbance that break apart root systems. Leaf number was strongly correlated with number of root swellings and was determined to be a good predictor of individual plant stage. It was found that populations were structured either "normally," with about equal numbers of individuals in all stage classes, or "dynamically," skewed to a greater number of early stage individuals. Levels of shade relate to population density and site disturbances likely influence the density and stage structure of populations due to the life history trait of extensive vegetative reproduction from the roots. Further questions about genetic diversity and the ability to colonize new sites should be investigated to gain a better understanding of limits to *H. brownei*'s distribution.

INTRODUCTION

Hydrophyllum brownei Kral & Bates (Hydrophyllaceae) is a rare endemic plant species known to grow only in eight Arkansas counties in the Ouachita Mountains Natural Division. Kral and Bates (1991) described this species as distinct from its closest morphological congener, *H. macrophyllum*, based primarily on distinctive rootstock attributes. The U.S. Fish and Wildlife Service expressed interest in this species as a possible addition to the federal Endangered Species Act and contracted FTN Associates to conduct a status survey in 2001 (FTN Associates, pers. comm.). As research continued on the species in 2002, previously unknown populations were discovered and recommendations were made to lower the rarity ranking of *H. brownei* (Marsico, 2003). In addition, quantitative measures were taken about location and characteristics of landscapes in which the populations grow (*e.g.*, proximity to streams, amount of shade, associated plant and canopy species) (Marsico, 2003).

In 2002 it appeared that populations varied in size and density and that size of plants and proportion of flowering individuals also differed among sites. The causes of these observed differences are investigated in the present study. The most likely environmental factors affecting growth of individuals in populations were amount of shade, soil texture properties and interspecific competition (Kral and Bates, 1991; FTN Associates, pers. comm.).

Shade is an important factor for species in the genus *Hydrophyllum* (Beckmann, 1979). FTN Associates (pers. comm.) noted that although the amount of shade is variable at

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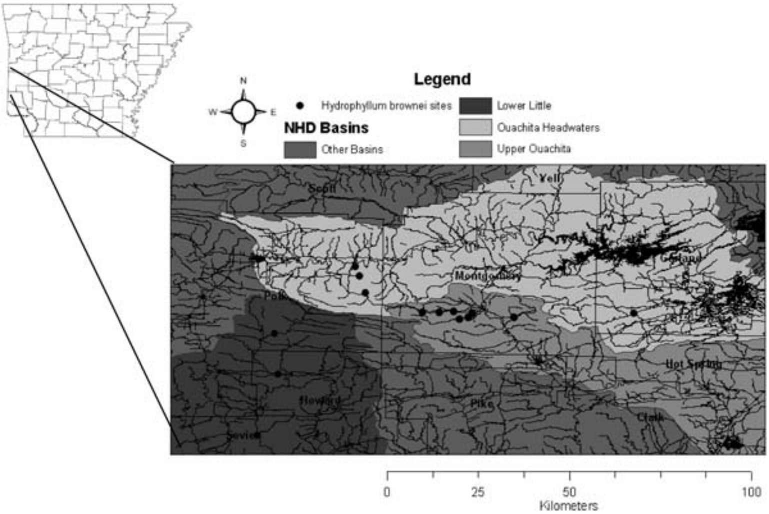

FIG. 1.—Map of *Hydrophyllum brownei* study sites showing Arkansas counties and National Hydrography Database basins

H. brownei sites, all populations grow under riparian hardwood shade. Soil texture also seemed important because both Kral and Bates (1991) and FTN Associates (pers. comm.) noted that populations grow in silt-loams with varying fractions of sand and clay. Soil texture may be a single measurement for the complicated relationship between soil moisture and mineral content because soils high in clay hold more minerals (due to clay particle composition and negative charge of the particles) and more moisture (due to the small size of the particles and pores and the large surface area of the particles) (Brady and Weil, 2000). Kral and Bates (1991) and FTN Associates (pers. comm.) discussed the frequency with which *H. brownei* is found growing in a rocky or gravelly substrate and suggested that this species was well adapted to rocky soils. Several populations considered (subjectively) vigorous in 2002 were found rooted in soil lacking gravel. Therefore, investigating the role of gravel in population density was thought to be important. *Hydrophyllum brownei* plants appeared to be less vigorous and in fewer number in areas where they were crowded by other species, indicating that interspecific competition may play a role in the species' distribution and abundance.

The purpose of this research was to investigate those factors thought to be important in explaining *Hydrophyllum brownei* population density and gain an understanding of the population structure and capacity for vegetative reproduction. Understanding stage structure in plant populations may provide insight on population dynamics of the species, indicating whether the species is expanding, stable or declining (Aguraiuja *et al.*, 2004). The results provide state and federal agencies with information for monitoring *H. brownei* populations and managing land.

METHODS

Field research.—The study area is located in the Ouachita Mountains region of west-central Arkansas (Fig. 1). Study populations were located near with the Cossatot River (Howard, Polk and Sevier counties), Big Fork Creek (Polk County), Caddo River (Montgomery County), Polk Creek (Montgomery County), Collier Creek (Montgomery County) and Mazarn Creek (Garland County) (Fig. 1). The six streams were classified into three basins based upon the National Hydrography Dataset: the Lower Little Basin, Ouachita Headwaters Basin and Upper Ouachita Basin (Fig. 1). In 2003 field data were gathered on eight days between 25 April and 8 May. Thirteen populations were randomly selected (in addition to one non-randomly selected pilot site in Sevier County) to be visited in the 2003 season (Fig. 1). Upon arrival to an *Hydrophyllum brownei* site, the population was located and assessed for its approximate boundaries. Once population boundaries were identified, a starting point for a transect was determined using a randomly generated value. Afterward, numbered flags were placed along a transect parallel to the stream course. Flags were placed so that 0.5-m^2 rings centered on adjacent flags would not overlap (*i.e.,* no closer than approximately 0.8 m apart). However, flags were not placed in a uniform manner because there were often gaps in the population, and every flag needed to be centered on a set of *H. brownei* individuals. One hundred flags were placed along the transect(s) in most populations. If the end of the population was reached before all 100 flags were placed, a random number was used to step farther away from the stream to establish additional transects until all 100 flags were used, unless the site was too small to support placement of all 100 flags.

The method described above was followed until a maximum number of flags was placed. Since some sites were larger and thus received more flags, a proportional sampling scheme was developed such that if 2 to 25 flags were placed, two randomly selected flags were sampled; if 26 to 50 flags were placed, three were sampled; if 51 to 75 were placed, four were sampled; and if 76 to 100 were placed, five samples were taken. The first set of non-repeating randomly generated numbers was used to choose which numbered flags would be sampled.

A 0.5-m^2 ring was centered on a selected flag to create a study plot. Within a plot, all *Hydrophyllum brownei* individuals were counted, along with the number of leaves of each. Flowering status was recorded also. After 22 plots had been sampled (five populations), it was decided that the number of root swellings on each plant would provide valuable information about the population. It was impossible to collect the rootstock on every individual as the substrate was sometimes gravelly or the plants were deeply rooted. However, great care was taken when removing plants from the soil to avoid losses of root swellings and allow for accurate counts. Except for a few individuals taken from one population for the vegetative reproduction experiments (*see* below), all individuals were returned to the sampling area after counts were made. This allowed for the possibility of survival of the sampled individuals of this perennial species, since regrowth from rootstock is likely in the subsequent season (*see* vegetative reproduction results).

In addition to measurements on plants, a measure of physical parameters was also taken. A concave spherical densiometer was used at approximately one meter above the ground to determine the percent canopy cover at a given plot. The herbaceous cover in each plot was visually estimated for the percent bare ground, *Hydrophyllum brownei* and other species. A 2000-ml soil sample was collected at the center of each plot. The soil sample was sifted on-site to separate out the gravel portion (if any) and the sifted portion was placed in a standard labeled soil box for later physical (soil texture) analysis. The gravel portion was taken to the adjacent stream and fully sifted and washed of organic debris and fine earth fraction. The remaining gravel was placed into a container filled with water, and the water that spilled over was collected. Displaced water was poured into a 500-ml graduated cylinder to provide a measure of gravel volume in a 2000-ml soil sample. The measure was used to estimate percent gravel in each soil sample.

Soil particle size analysis was determined by following the standard procedure for the hydrometer method (Ashworth *et al.*, 2001). The method uses a dispersing solution to break up conglomerated soil particles. The soil and dispersing agent was filled up to one liter with distilled water. The mixture was then shaken and a hydrometer, which measures solution density, was inserted into the solution 40 s and then again 6 h after end-over-end mixing. The 40 s reading provided a raw measure for the amount of sand in the mixture and the 6 h reading provided the amount of clay. Percent silt was determined by subtracting the percent sand and clay from 100. A blank solution was used to standardize readings. Except for use of sodium hexaphosphate as a dispersing agent, the methods in Ashworth *et al.* (2001) were closely followed. Sodium hexaphosphate, used in this analysis, has been used in the past (Day, 1965; Gee and Bauder, 1986) and is a similar dispersing agent to the tetrasodium pyrophosphate decahydrate suggested by Ashworth *et al.* (2001).

Modeling.—Before fieldwork commenced, an *a priori* set of models was developed to evaluate differences in population density. Models were based on *Hydrophyllum brownei* life history (Kral and Bates, 1991; FTN Associates, pers. comm.) and the life histories of other *Hydrophyllum* species (Constance, 1942; Beckmann, 1979). The variables used in the modeling were: (1) percent shade over each plot, (2) percent gravel in a substrate sample, (3) percent sand in the substrate sample (clay values were similar for all sites), (4) percent cover of non- *H. brownei* species in each plot and (5) the stream basin in which the populations were growing. The global model used to evaluate population density included all main effects and a single interaction term. Candidate models were nested within the global model, and each contained one or more main effects and one model included the interaction between canopy shade and the cover by other species. Candidate model selection using Akaike's Information Criterion (AIC) is more appropriate for this type of observational study than is null hypothesis testing. For the analysis of the data, AIC_c [Akaike Information Criterion AIC adjusted for small sample size] was employed to rank the candidate models. In SAS (SAS Institute, 1999), PROC GENMOD was used to determine the log-likelihood of each model. A negative binomial distribution was used when modeling number of plants to account for overdispersion. The values obtained were then used in the formula $AIC_c = -2l + 2K\ [n/(n - K - 1)]$, in which $l =$ the log-likelihood of the parameter given the data and model, $K =$ the number of estimable parameters and $n =$ number of populations. Δ_i values, representing the difference in the minimum AIC_c and the AIC_c for each model, were then ranked to determine the best of the candidate models. The Akaike weight (w_i) was obtained to provide a measure of the weight of evidence in favor of the best model (of the candidates developed) being selected, and then the evidence ratio was solved for, allowing for the best model to be compared to the others (Burnham and Anderson, 2002).

Population stage structure.—Root swelling number may be the best indicator of an individual's age, in which older individuals have a greater number of swellings (Kral and Bates, 1991). However, an exact relationship between root swelling number and plant age is unknown; therefore, plant "stage" was the metric used to compare populations (Gurevitch *et al.*, 2002). Further evidence that the perennial habit of *Hydrophyllum brownei* is documented in its rootstock is found in the morphology of root swellings themselves. Root swellings can be differentiated into two age classes. It was determined that dark colored swellings have developed a compact periderm layer (secondary growth). It was observed that this secondary growth darkens the swellings lower on the root axis. Flesh-colored swellings, which develop on the highest fascicle of the rootstock, are younger than the darker swellings. Root swellings were counted with the understanding that swelling number increases with and individual's age/stage. However, the number of root swellings was obtained on less than one-half of the individuals measured. Correlation analysis was used to determine that the number of leaves per individual was an acceptable substitute for root swellings in classifying plants into stages. The proportion of plants at each site with a given leaf number was plotted to determine how individuals were distributed within and among sites. A chi-square test was used to assess differences in population stage structure.

TABLE 1.—Summary table of measurements taken on the 14 populations studied. Values shown are population mean estimates followed by the standard deviation. Codes for basins are as follows: OH = Ouachita Headwaters, UO = Upper Ouachita, LL = Lower Little

Density (plants*m^{-2})	% shade	% gravel	% sand	% cover (by other spp.)	Basin	No. leaves	No. root swellings	% flowering
22.4 ± 14.8	99.0 ± 1.2	5.6 ± 5.3	61.4 ± 12.5	62.4 ± 25.7	OH	2.4 ± 7.3	3.9 ± 2.2	0.0
38.4 ± 23.6	99.8 ± 0.2	23.9 ± 15.2	76.8 ± 8.4	42.4 ± 24.9	OH	2.2 ± 1.6	5.7 ± 3.2	14.6
18.0 ± 2.8	99.3 ± 1.3	0.0 ± 0.0	56.6 ± 4.2	82.5 ± 3.5	OH	2.3 ± 1.2	5.9 ± 5.6	5.6
13.6 ± 10.4	95.4 ± 5.5	3.4 ± 3.7	63.0 ± 11.4	70.6 ± 28.9	UO	1.8 ± 1.1	5.3 ± 3.2	5.9
22.8 ± 7.3	95.0 ± 9.9	37.6 ± 13.3	71.2 ± 9.4	58.4 ± 12.1	UO	2.4 ± 1.6	NA	14.0
55.0 ± 43.8	97.7 ± 2.2	12.3 ± 6.7	60.9 ± 6.4	45.0 ± 14.1	UO	2.0 ± 1.2	NA	1.8
31.5 ± 21.4	84.1 ± 4.1	4.5 ± 3	39.6 ± 5.5	43.3 ± 31.7	UO	3.3 ± 2.1	6.9 ± 4.3	20.6
38.0 ± 24.6	96.7 ± 4.2	18.7 ± 12.7	56.2 ± 9.4	40.6 ± 28.8	UO	2.0 ± 1.3	NA	3.2
21.2 ± 20.3	98.8 ± 1.5	9.3 ± 5.9	70.2 ± 7.6	43.0 ± 31.1	UO	3.1 ± 1.9	5.7 ± 3.2	13.2
17.5 ± 9.3	98.6 ± 1.5	0.8 ± 1.2	59.5 ± 21.1	48.8 ± 8.5	UO	4.9 ± 5.5	6.2 ± 3.7	28.6
30.4 ± 21.4	95.7 ± 2.9	0.0 ± 0.0	53.0 ± 1.8	54.0 ± 23.0	LL	3.0 ± 1.9	NA	6.6
133.6 ± 116.4	98.4 ± 2.6	0.0 ± 0.0	68.7 ± 2.0	20.0 ± 36.4	LL	1.7 ± 1.2	2.7 ± 2.1	2.4
59.2 ± 19.0	93.2 ± 3.6	0.05 ± 0.1	60.6 ± 1.8	61.6 ± 18.7	LL	2.3 ± 1.5	NA	0.0
24.4 ± 19.0	99.3 ± 0.9	0.5 ± 0.9	61.2 ± 8.9	54.4 ± 36.3	OH	2.2 ± 1.8	4.9 ± 2.9	6.6

Vegetative reproduction.—For the purpose of determining the ability of *Hydrophyllum brownei* to reproduce vegetatively from its rootstock and root swellings, several individuals were collected from one of the sampled populations to use in a growth experiment. Roots were assigned to one of five treatments and were planted in experimental pots. The treatments included: (1) a single large rootstock with root swellings attached, (2) four or five sets of two root swellings joined by roots but without main rootstock, (3) six rootstocks stripped of their root swellings, (4) 15 individual flesh-colored root swellings or (5) 20 individual dark brown or black root swellings. The two different root swelling color types (in treatments 4 and 5) are based upon epidermis morphology as described above and they represent swellings in two different age classes. None of the experimental rootstocks had associated stem or leaf material at the time of planting in mid-May. The pots were placed outside and watered regularly. The pots were left outside throughout the next year, and only covered with straw for extra protection from cold during the winter months. Plants emerged in March 2004 and were counted and assessed in April.

RESULTS

Field research.—Table 1 summarizes measurements obtained in the field. Environmental factors differed in their variability within and among populations. Levels of gravel and sand were highly variable among sites. Some populations grew on substrates containing no gravel, whereas other localities had areas where the soil was very rocky. Percentages of sand were more differentiated among sites than within them, though all localities ranged from ~40–80% sand in the soil. The percent cover by other species, a metric for interspecific competition, varied widely within and across sites. The amount of shade was high at all sites (a minimum of 84% canopy shade) and values varied little within sites. Population density mean estimates ranged from 14 to 134 plants/m^2, with the majority of the populations having between 20 and 40 plants/m^2. Two populations had none of the sampled individuals attempting sexual reproduction and most of the populations had flowering estimates under

TABLE 2.—Notation, form and description of candidate models used to evaluate *Hydrophyllum brownei* population density

Model notation	Model form	Model description
Global	$\beta_0 + \beta_1(\text{shade}) + \beta_2(\text{gravel}) + \beta_3(\text{sand}) + \beta_4(\text{cover}) + \beta_5(\text{shade*cover}) + \beta_6(\text{basin})$	Responses differ by % shade, % gravel in substrate, % sand in substrate, % coverage of other species, the interaction between % shade and % coverage of other species, and the stream basin
Shade	$\beta_0 + \beta_1(\text{shade})$	Responses differ by % shade
Shade, Cover	$\beta_0 + \beta_1(\text{shade}) + \beta_4(\text{cover})$	Responses differ by % shade and % cover
Shade*Cover	$\beta_0 + \beta_5(\text{shade*cover})$	Responses differ by the interaction between % shade and % cover
Shade, Sand	$\beta_0 + \beta_1(\text{shade}) + \beta_3(\text{sand})$	Responses differ by % shade and % sand
Shade, Sand, Cover	$\beta_0 + \beta_1(\text{shade}) + \beta_3(\text{sand}) + \beta_4(\text{cover})$	Responses differ by % shade, % sand, and % cover
Drainage	$\beta_0 + \beta_6(\text{basin})$	Responses differ by stream basin
Gravel	$\beta_0 + \beta_2(\text{gravel})$	Responses differ by % gravel

10% of the population. One population, however, had and estimate of nearly 30% of its individuals flowering.

Model selection and inference.—Table 2 provides a description of the candidate models used in model selection. Model selection results for plant density included two plausible models based on AIC$_c$, with the most parsimonious models including shade alone and gravel alone being best (Table 3). Parameter estimates for the best fitting model showed that an increase in plant number is expected with increasing levels of shade. Although 2.5 times less likely to be the best model of those provided, the model including the amount of gravel alone has a negative relationship with population density. The cover of other species, amount of sand

TABLE 3.—Candidate model selection for predictors of *Hydrophyllum brownei* population density based upon Akaike's Information Criterion adjusted for small sample size (AIC$_c$). Models are ordered from most to least likely based on Δ_i values

Model	−2 (log-likelihood)	Estimable parameter (K)	Δ_i	Akaike weight (w_i)	Evidence ratio (w_1/w_i)
Shade	5377.0	3	0	0.6254	1
Gravel	5378.9	3	1.9	0.2419	2.59
Shade, Sand	5377.8	4	3.1	0.1327	4.71
Basin	5397.7	4	23	<0.0001	>100
Cover	5409.2	3	32.2	<0.0001	>100
Shade*Cover	5409.9	3	32.9	<0.0001	>100
Shade, Cover	5409.5	4	34.8	<0.0001	>100
Shade, Sand, Cover	5410.1	5	37.8	<0.0001	>100
Global	5433.2	9	71.4	<0.0001	>100

Minimum AIC$_c$ = 5385.4

and basin in which the populations were growing were not important in modeling plant density.

Population stage structure.—Leaf number and root swelling number were strongly correlated ($n = 525$, $r = 0.542$, $P < 0.0001$). Therefore, leaf number distribution was used as the proxy for plant stage, since a greater sample size for leaf number was obtained. Additional evidence for using leaf number to indicate stage comes from the fact that of 56 plants about to flower, flowering or in fruit, only one had two leaves. All 55 others had three or more leaves. These data indicate that while individuals with one leaf may be the most abundant, they are not yet old enough or at a large enough stage to sexually reproduce. Individuals ranged from having one leaf to more than ten (a single individual produced 24 leaves), but since the number of individuals with more than five leaves was low, stages were defined as plants with one leaf, two, three, four and five or more leaves, resulting in five stage classes. Two stage class patterns emerged: (1) "dynamic," in which increasing stage class resulted in rapidly decreasing abundance and (2) "normal," a more even patterned stage class (terminology used from Oostermeijer *et al.,* 1994; Hegland *et al.*, 2001; Aguraiuja *et al.*, 2004) (Fig. 2). Eight populations displayed the dynamic stage class pattern, and six had a normal pattern. The chi-square analysis showed significant differences among sites ($P < 0.0001$, $dF = 52$).

Vegetative reproduction.—The vegetative reproduction experiment provided some unexpected results (Table 4). *Hydrophyllum brownei* was able to reproduce vegetatively from any portion of its root material, indicating that the species is a prolific asexual reproducer. Only one experimental pot out of 30 had no *H. brownei* growth. Intact rootstocks produced the highest proportion of individuals; only five rootstocks were planted in 2003, but 11 shoots were observed in 2004. All other treatments showed fewer individuals than the number planted. Still, the important finding is that all portions of the roots have the potential to grow into plants even when separated from the main rootstock.

DISCUSSION

Hydrophyllum brownei's tuber-like root swellings are unique among North American *Hydrophyllum* species. The roots were found to be remarkably effective in vegetative reproduction, with more than half of the experimental units resulting in individuals. Any portion of root material has the potential to produce a viable individual when separated from a parent plant. A benefit of such prolific vegetative reproduction can be illustrated by the observation of rooting by feral hogs (*Sus scrofa*) through a *H. brownei* population along the Cossatot River in 2001 (S. Walker, pers. comm.). After Walker's observation, the site was visited in April 2003 and a high density of non-sexually reproducing (dynamic stage) individuals was found growing in the area of greatest disturbance. Cossatot River State Park and Natural Area was known as a *H. brownei* location before the hog manipulation of the soil, but the population may have increased in number of individuals and decreased in stage of individuals with the disruption and separation of many roots. One hundred and forty-eight individuals were counted in only 2.5 m^2 at the site, 64% of which had only one or two leaves, indicating a dense dynamic stage population. This life history trait of abundant vegetative reproduction influences population density and stage structure after a disturbance. As an adaptation to rocky and gravelly substrates, the root swellings will produce new plants if separated from the main rootstock by shifting gravel (Kral and Bates, 1991). They also may be an adaptation to other site disturbances, such as large scale soil manipulations caused by animals or flash floods.

Modeling changes in plant density resulted in a best fitting candidate model. In terms of conservation of the species, population density is an important factor. With this

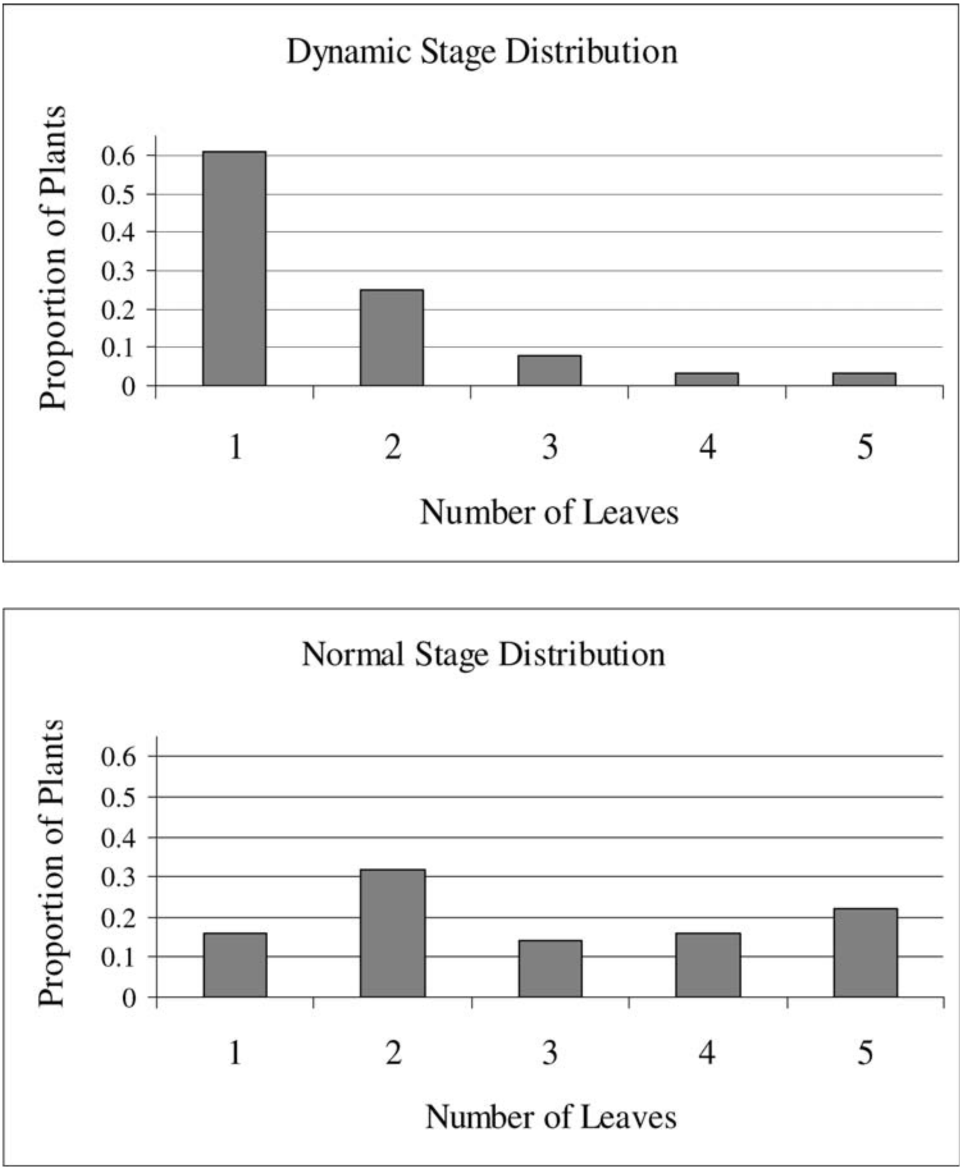

FIG. 2.—Representation of stage structure for two example populations measured. Eight populations exhibited dynamic stage distribution and six populations exhibited normal stage distribution. Stage is represented by the number of leaves: 1, 2, 3, 4 and 5+

understanding, a model incorporating shade would be most useful in making management recommendations, given the results from this study. Simply, the shadiest sites are best for *Hydrophyllum brownei* population density, and if sites are to be managed to maximize *H. brownei* populations, increased shade should be a priority. It is important to recognize that all

TABLE 4.—Summary of number of plants generated from each root treatment in the vegetative reproduction experiment

Description of treatment	Single root axis with root swellings	Root axis stripped of swellings	≥2 swellings joined by roots (no root axis)	"New" root swellings	"Old" root swellings
Number of roots planted per pot	1	6	4 in 2 pots, 5 in 1	15	20
Number of pots	5	3	3	10	9
Total no. of observed new plants	11	16	4	92	67
Range of no. of living individuals per pot	1–4	5–6	0–2	4–13	4–10

the sites investigated were shady, but that even small increases in shade values correlate with increased densities. Based on previous research (Beckmann, 1979; Kral and Bates, 1991; FTN Associates, pers. comm.) it is understandable that shade amounts would be influential in determining densities of a shade-requiring species.

The strong correlation between number of root swellings and number of leaves provides evidence that leaf number is a good indicator of plant stage. In addition, most *Hydrophyllum brownei* plants appear to require a minimum of three leaves to produce flowers. Therefore, flower production may be the result of an individual reaching a critical stage (Morgan, 1971). Instead of an absolute age, the stage acts as a relative measure indicating that a plant with one leaf is less equipped for sexual reproduction than a plant with six. Plants of a young age will likely be in an early stage, but older plants may be in a range of stages (Boucher, 1997). Whereas a young *H. brownei* individual will have only few leaves, an older individual may have few or many leaves depending on external factors such as rootstock division. However, if root swelling number and number of leaves are an indication of stored starch and nutrient reserves required for sexual reproduction, actual age may be entirely irrelevant when studying *H. brownei* reproductive dynamics.

An important finding of this research was that population variability observed in 2002 (in terms of individual leaf number and proportion of flowering individuals) was caused by different population stage structures. Two basic patterns emerged: the "normal," even-stage structure and the "dynamic" stage structure, weighted toward few leafed individuals (Oostermeijer *et al.*, 1994; Hegland *et al.*, 2001). No populations had only late stage, "regressive" individuals, indicating that no populations were in a state of senescence. However, populations with such high numbers of young recruits may be telling of the prolific reproduction of individuals in this species. Differences observed in stage class may be an indication of disturbance to populations. Populations with "dynamic" stage classes may have been disturbed more recently than those with a "normal" stage distribution. However, "dynamic" populations could also mean that the populations were more recently established (Aguraiuja *et al.*, 2004). With only 56 of 1181 individuals (4.7%) flowering, *Hydrophyllum brownei* plants seem to rely heavily on vegetative reproduction to recruit new individuals. Still, important population parameters of survivorship and fecundity remain unknown. Like *Fritillaria camtschatcensis*, studied by Yonezawa *et al.* (2000), *H. brownei* has a similarly complex life history, which requires further understanding for conservation and careful management of the species.

An important note to future investigators of *Hydrophyllum brownei* is that studies conducted on *H. brownei* must consider a very important aspect of the species' phenology: non-flowering individuals only have visible shoots from mid-March through the first week in May, and even then they may begin senescing as early as late April. On the other hand, flowering individuals, which produce shoots as early as those not flowering, only flower from late April through mid-May. Population studies, therefore, in which both non-reproductive and reproductive individuals are important may not be able to be investigated at the same time, and the study window is short for both.

This research provides important observational information about a newly described and very little known Ouachita Mountain endemic species. However, the study has created opportunity for future investigation in almost every aspect of *Hydrophyllum brownei*'s biology. New sites were discovered as a result of previous research (Marsico, 2003), but the distinction between site and population is left unexplored. In addition, care must be taken when interpreting number of populations and population sizes when considered from the population genetics standpoint. It is now known that the species has great potential for vegetative reproduction and individual or population persistence. Two questions come out of such knowledge: why, if the individuals of the species are so good at reproducing, is the species so limited in extent and distribution (*i.e.,* not all shady riparian habitats in the Ouachita Mountains support *H. brownei* populations), and what is the ratio of sexual to vegetative reproduction in terms of the next generation? If vegetative reproduction is the main source of new individuals, genetic variability may be excessively low in *H. brownei.* Having an understanding of the genetic diversity within *H. brownei* could help answer the question, "What is the most serious risk to the persistence of populations or the species?"

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