

## Allocation, Growth and Estimated Population Structure of *Corydalis aquae-gelidae*, a Rare Riparian Plant

### Abstract

The pattern of biomass allocation to roots, shoots and reproductive parts, the growth rate, and the population structure, in terms of both stages of development and age, were determined for *Corydalis aquae-gelidae*. The species had a relatively high allocation to belowground structures (adult belowground/aboveground ratio of about 2), largely in the form of starch storage tissue. The allocation to reproduction was relatively low (8%). The growth rate was slow, with an estimated 7 years (6-9 years, with 95% confidence) required for reproductive maturity. This herbaceous perennial appeared to be a stress-tolerator, whose populations would not rebound quickly after disturbance. The population age structure, estimated from a growth model and size measurement of 25 plants in successive years, implied successful reproduction. The methods developed here provided management-related information, including estimates of growth rates, population structure and current reproductive success, as well as probable response to disturbance and the species' successional status. These methods required only two years of data, and could be used for other herbaceous perennials.

### Introduction

Conservation of rare plants requires understanding of their biology and population status: are they reproducing effectively, and how might they respond to disturbance or manipulations intended to aid their persistence? Population status can be determined using long-term studies that monitor population changes (Owen and Rosentreter 1992, Law 1983), following changes in plant numbers, or the survival and reproduction of individuals. Alternatively, population status can be estimated from current population age structure (Crisp and Lange 1976); for example, age structures can be used to help ascertain if adequate reproduction has been occurring. For many herbaceous species, however, estimating the age of individuals is tedious or impossible. Estimates of the age of individuals can be made, however, if plant sizes are known and if growth rates for a given plant size can be measured.

The concept of plant adaptive strategy allows one to use combinations of characteristics of a species to predict how it will respond to environmental change or disturbance. Hypotheses about plant strategy include those of *r*,*K* selection (MacArthur and Wilson 1967, Pianka 1970), and the competitive, stress-tolerant, and ruderal strategies of Grime (1979). Plant species with differ-

ent strategies vary in their rates of growth, and in their allocation of resources to different functions, e.g., to reproduction or storage. For example, stress-tolerators are slow growing plants of relatively unproductive environments, which allocate relatively more resources to storage and long-term survival.

We used measurements of allocation, plant size, and growth rate to estimate the strategy and population status of a rare plant, *Corydalis aquae-gelidae* Peck & Wilson, Fumariaceae (cold-water corydalis), that cannot be aged directly and for which there is little biological information. Information about this species' growth rates and allocation patterns indicated a stress-tolerant plant that may not respond well to disturbance, while the estimated population age structure indicated a stable, successful population.

### Study Area

This study was conducted in the southwest portion of the Mount Hood National Forest, Oregon (45° N latitude and 122° W longitude), with sampling at Rhododendron Creek and nearby on the upper Clackamas River. Vegetation is representative of the *Tsuga heterophylla* zone of Franklin and Dymess (1973), with streamside forests dominated by *Tsuga*, *Thuja plicata* and *Alnus rubra*. Growth measurements were recorded for plants in a 7x2 m plot on a gravel bar between the main stem and a side channel of Rhododendron Creek.

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The plot was in typical conditions for *Corydalis aquae-gelidae* (Goldenberg 1992): moist, coarse mineral substrates in or next to the stream, with few herbaceous competitors and fairly dense tree canopy cover.

### Study Species

*Corydalis aquae-gelidae* is locally endemic in northwestern Oregon and southwestern Washington. It is an herbaceous perennial without vegetative reproduction. The shoots arise from large, fleshy taproots and grow to over one meter tall. The species grows in or within 2 m of flowing water, along spring-fed streams with relatively little variation in flow rate (Goldenberg 1992). It is a US Fish and Wildlife Service species of concern, and a candidate for listing under the Oregon Endangered Species Act (Oregon Natural Heritage Program 1995). Its habitat has been disturbed by logging, fish habitat improvement, and hydropower development. Information useful for evaluating its population persistence and reaction to streamflow reduction and streambank manipulation is needed to aid in its conservation.

### Methods

On September 5, 1990, near the end of the growing season, 25 plants were marked by placing a numbered tag at a recorded distance and direction from their base. The plants were classified into four growth stages: reproductive adults, non-reproductive adults (smaller plants with a stem but no flowers), juveniles (very small, stemless plants), and seedlings (first-year plants with cotyledons but usually no true leaves). The sample included five reproductive adults, one non-reproductive adult, nine juveniles, and ten seedlings. The number of leaves, the total length of the leaf blades, plant height, and the number of fruiting pedicels were recorded for each plant. All fruits were dehiscent (only pedicels remained), but the plants had not begun senescence.

On September 10, 1991, these plants were remeasured. The shoots were harvested and separated into stems, leaves (including petioles), and raceme axes (pedicels and peduncles), and oven-dried. In addition, three reproductive adults (two including roots), six juveniles with roots and five seedlings with roots were collected from a nearby side channel of the Clackamas River, separated into parts, and oven-dried. Fine roots were collected to the extent possible.

During July, 1991, thirty flowers were collected from five plants outside the study plot at Rhododendron Creek. The flowers were dried and weighed after the pistils were removed. Nine fruits and twenty-five seeds were also collected during August. The number of seeds per fruit was recorded for 122 fruits at Rhododendron Creek and the Clackamas River.

Dry mass of reproductive structures was used to estimate the dry mass lost from each pedicel on the plants collected in September, 1991. For each reproductive adult, total flower mass was estimated as the number of pedicels multiplied by mean sampled flower mass, and likewise for total fruit and total seed mass. Leaves produced early in the season do not senesce in mid-season, but rather at the end of the season along with the entire plant, therefore sampling in September only had to account for reproductive structures lost at an earlier date. An allometric regression of root mass on total estimated shoot mass was used to estimate root mass for plants whose roots were not sampled.

### Statistical Analyses

A series of regressions was made relating the proportional mass of each plant part to the total estimated mass, using Statgraphics (STSC 1991). These regressions provided a model of how biomass allocation varies with total mass. Scatter diagrams and residual analyses were used to determine appropriate transformations and the order of the regression equations.

A linear relationship between root mass and shoot mass was calculated (equation 4, table 1). The allometric constant is the slope of this regression line (Hunt 1990). The root mass estimated from equation 4 for the largest reproductive adult whose roots were sampled was far from the observed value (20.53 g, vs. 15.91 g observed); therefore, a quadratic model was fitted (equation 5, table 1). Equation 5 gave a much more realistic estimate (e.g. 16.36 vs. 15.91 g observed) for the reproductive plants, had a higher adjusted  $r^2$ , and was used to estimate root masses where roots were not sampled. The linear model is presented, however, as this is often used as the standard relationship (Hunt 1990).

For those regressions that showed no statistically significant relation between total biomass and allocation to a particular plant part ( $P > 0.05$ ),

TABLE 1. Regression models relating root and shoot mass. All masses are in grams.

4.	$\ln(\text{root mass}) = 1.00 + 0.972 \ln(\text{shoot mass})$ n=12 P<0.0001 r <sup>2</sup> =0.993 adjusted r <sup>2</sup> =.993
5.	$\ln(\text{root mass}) = 1.09 + 0.868 \ln(\text{shoot mass}) - 0.0226 (\ln(\text{shoot mass}))^2$ n=12 P<0.0001 r <sup>2</sup> =0.996 adjusted r <sup>2</sup> =.995

the methods in Neter et al. (1989) and the suggestions of Peterman (1990) were used to determine the detectable effect size (DES) in the slope of the regression equation. The DES is a function of the chosen alpha (the significance level), beta (statistical power) and the degrees of freedom. The DES was calculated using a desired alpha of P=0.05 and power of 95%, and six degrees of freedom. The DES represents the smallest population mean slope that could be detected (found to be statistically significant), given the sample size and analysis method.

#### Relationships Between Age, Stage and Size

To estimate the size at first reproduction, 130 adult plants from 111 population survey plots from throughout the southwestern Mt. Hood National Forest (from Goldenberg 1992) were used to calculate the proportion of plants flowering at different sizes, measured by the number of leaves. Leaf number was converted to mass using an allometric equation derived from the destructive samples. An equation was determined relating leaf mass to proportion flowering. This equation was used to estimate the weight of plants where 10%, 50% and 90% of plants were flowering. Plant age was estimated from plant mass, using the growth model, as the year at which plants were predicted to first equal or exceed the given mass.

#### Growth Model

To construct a growth model, the total mass of each plant in the sample plot was estimated using the plant's total leaf blade lengths for both year one and year two and regression equations 13 and 5 (see results), except where actual shoot masses were sampled.

Mean relative growth rate (*RGR*) was calculated for each of the 25 sample plants using the equation (Hunt 1990, p. 26):

$$RGR = (\ln M_2 - \ln M_1) / (t_2 - t_1) \quad (1)$$

where  $M_i$  is dry mass at the time  $t_i$ . This equation was used to give a mean growth rate for the

year. To determine *RGR* as a function of plant mass, *RGR* was regressed against the natural logarithm of year one mass to yield the regression equation:

$$RGR_{M_t} = a + b \ln M_t \quad (2)$$

We used the iterative exponential growth model:

$$M_{t+1} = M_t \exp(RGR_{M_t}) \quad (3)$$

where  $RGR_{M_t} = a + b \ln M_t$ . The observed mean seedling mass was used for  $M_1$ . If *RGR* decreases with increasing plant mass, the model yields a sigmoidal curve; growth is exponential, but as  $M_t$  approaches  $\exp(-a/b)$ ,  $RGR_{M_t}$  approaches 0, and  $M_{t+1}$  approaches  $M_t$ . Equation 3 may be derived from equation 1, with  $t_2 - t_1 = 1$ . Equation 3 is also similar to the general model for exponential growth (Hunt 1990, p. 84),  $M = M_0 \exp(rt)$ , with  $r = RGR$  and  $t = 1$ .

#### Population Age Structure

The population structure of 2615 plants in the population survey plots (Goldenberg 1992) was calculated as the percentage of plants in each of the four growth stages: reproductive adults, non-reproductive adults, juveniles, and seedlings. A hypothetical age structure was generated with these percentages, and the age range for each stage estimated from the growth model. An exponential decay function was fitted algebraically to the resulting histogram.

## Results

#### Allocation

The regression equations in table 2 were used to build a model of *Corydalis aquae-gelidae* allocation patterns. The regressions for the reproductive parts were not significant (table 2, equations 9-12), which implies the possibility of constant reproductive allocation. Because the regression slope detectable effect sizes (DES) were large for equations 9-12, a conclusion of no biologically significant change in reproductive allocation with increasing total mass was not war-

TABLE 2. Regression models describing allocation to plant structures as a function of total mass. Equations 7 to 12 applied only to adults. "Racemes" included only peduncles and pedicels, the supporting structures. All masses are in grams.

6.	root mass/total mass = 0.777 - 0.0175 ln (total mass) - 0.00504 (ln (total mass)) <sup>2</sup> n=37 P<0.0001 r <sup>2</sup> =0.91
7.	stem mass/total mass = 0.125 - 0.0642 ln (total mass) + 0.0130 (ln (total mass)) <sup>2</sup> n=8 P=0.0002 r <sup>2</sup> =0.97
8.	leaf mass/total mass = 0.0708 + 0.0378 ln (total mass) n=8 P=0.0038 r <sup>2</sup> =0.78
9.	raceme mass/total mass = -0.000681 + 0.0021 ln (total mass) n=8 P=0.14 r <sup>2</sup> =0.32
10.	flower mass/total mass = 0.0176 - 0.000697 ln (total mass) n=8 P=0.66 r <sup>2</sup> =0.04
11.	fruit mass/total mass = 0.0215 - 0.000854 ln (total mass) n=8 P=0.66 r <sup>2</sup> =0.04
12.	seeds mass/total mass = 0.0510 - 0.00203 ln (total mass) n=8 P=0.66 r <sup>2</sup> =0.04

ranted, however. Therefore, the equations are presented as hypotheses which require more data for evaluation. All of the regression equations were used in the allocation model (table 3), so that the total allocation proportions always added to about one, regardless of total mass. The largest plant sampled completely had 23.9 g total mass.

Allocation to roots was large but declined as plants increased in size (table 3). Allocation to roots peaked in juveniles at 0.2 grams total dry mass, which was about the third growing season, according to the growth model. The thickened roots functioned as storage tissue; they had a starch

TABLE 3. Proportional allocation of dry matter estimated for *Corydalis aquae-gelidae* of varying total masses. Calculated using equations 6 through 12. Growth stages include seedlings (0.009 g), juveniles (0.2 g) and two sizes of reproductive adults (10 and 25 g).

Total mass (g)	0.009	0.2	10	25
Roots	0.73	0.79	0.71	0.67
Shoots	0.27	0.21	0.29	0.33
Root/Shoot ratio	2.70	3.76	2.45	2.03
Stems			0.046	0.053
Leaves			0.158	0.192
Raceme axes			0.007	0.006
Flowers			0.016	0.015
Fruits			0.020	0.019
Seeds			0.046	0.044
Reproductive total			0.089	0.084

grain concentration comparable to that of potatoes. Fibrous root mass was small compared to that of the thickened storage roots. As total plant mass increased, the mass of the leaves and stems increased at the expense of roots; stems increased at a greater rate than leaves. Larger plants apparently required relatively more supporting structure.

#### Growth Model

Relative growth rate (RGR) peaked in juveniles, rather than seedlings, and then declined as plant mass increased (figure 1). Outliers with low or negative RGR were removed, due to their poor growth; the intention of this model was to illustrate the growth of healthy plants in favorable microsites. The iterative model given in the methods (equation 3) yielded a time course of dry mass gain (figure 2). Values for the confidence limits for the slope and intercept terms in the regression (figure 1), as well as the mean values, were used in the model to show the possible variation in the growth rates. The mean regression model did not reach an asymptote with any realistic size; this reflects the fact that some of the largest plants sampled grew substantially. Larger plants must be sampled in order to estimate a maximum size for the species.

Figure 3 shows the relationship between the actual and predicted masses for the plants in year two. Because the actual year two masses were used to determine the model parameters, this plot can not be used as model validation. The plot does support the validity of the general form of the growth model, however.

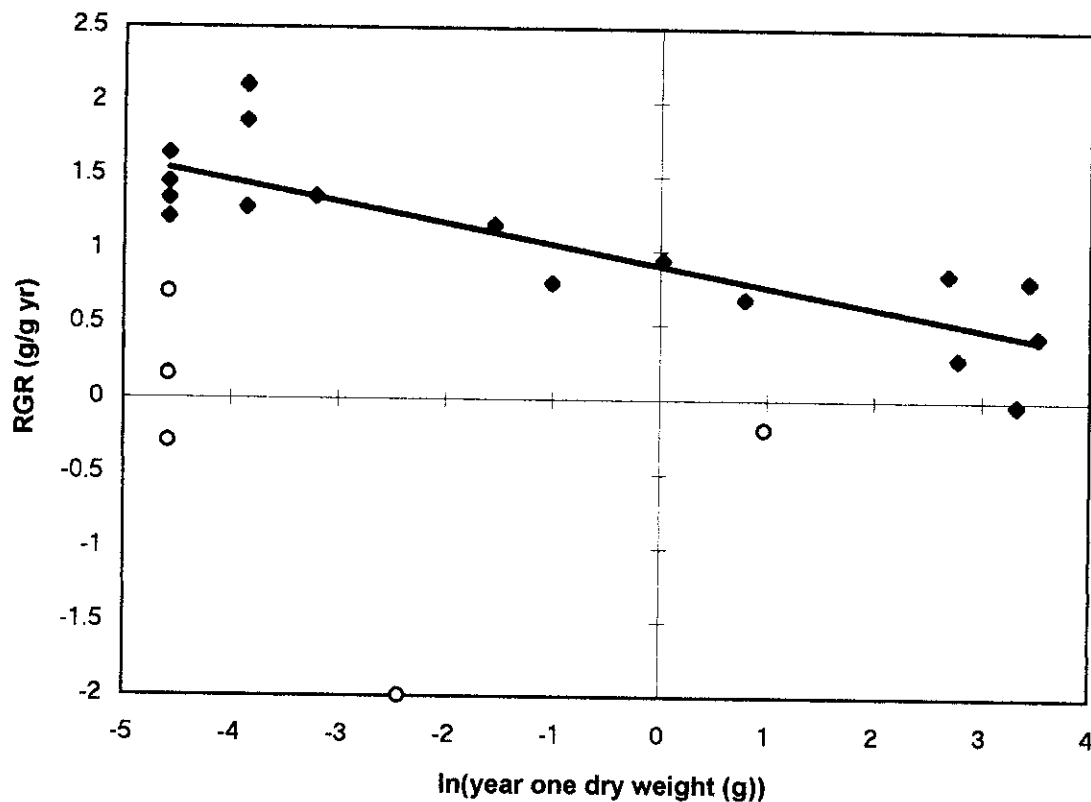


Figure 1. Relationship of the relative growth rate (RGR) to the total dry plant mass in the first sampling year. The outliers specified by circles were removed from the regression due to their poor growth.  $RGR = 0.9011 - 0.1408 \ln(\text{year one mass, g})$ ,  $n=18$ ,  $r^2=0.71$ ,  $P=0.0001$ . The 95% confidence interval for the intercept and slope were 0.7374 to 1.065 and -0.1882 to -0.0934 respectively. Some points represent greater than one sample. First year seedlings are represented by the first column of data points.

#### Relationships Between Age, Stage and Size

The mass of plants at growth stage transitions was estimated. Seedlings are, by definition, only first year plants. The size of seedlings at the end of their first growing season averaged 0.009 g ( $n=5$ , range 0.0045 to 0.0150). One plant in the plot changed from juvenile to non-reproductive adult between the sampled years, with estimated total mass in year two being 2.64 grams, which was used as the size of first stem production.

Total mass at which 10%, 50% and 90% of the plants were flowering was calculated as 4.2, 4.8 and 6.4 grams, respectively, using equation 15 (table 4). The non-linear regression in equation 15 was run using data points for leaf numbers of 4 to 14 with leaf number being converted to mass using equation 14. No plants were flowering at 4 leaves, while all plants were flowering

at 10 leaves and above. Estimates for ages of different sized plants were calculated (table 5). Using the growth model, it is estimated that the first stem would develop in the sixth year, and reproduction would begin about the seventh year.

#### Population Age Structure

Population survey plots ( $n=111$ ) contained 2615 *Corydalis aquae-gelidae* plants, with 38% seed-

TABLE 4. Regression models used in the growth analysis. All masses are in grams.

13.	$\ln(\text{shoot mass}) = -6.30 + 1.47 \ln(\text{total blade lengths, cm})$ $n=21$ $P<0.0001$ $r^2=0.98$
14.	$\ln(\text{total mass}) = -0.287 + 1.23 \ln(\text{leaf no.})$ $n=11$ $P<0.0001$ $r^2=0.94$
15.	$\text{proportion flowering} = 1 - 64.56 \exp(-1.014 \text{ total mass})$ $n=11$ $P<0.0001$ $r^2=0.93$

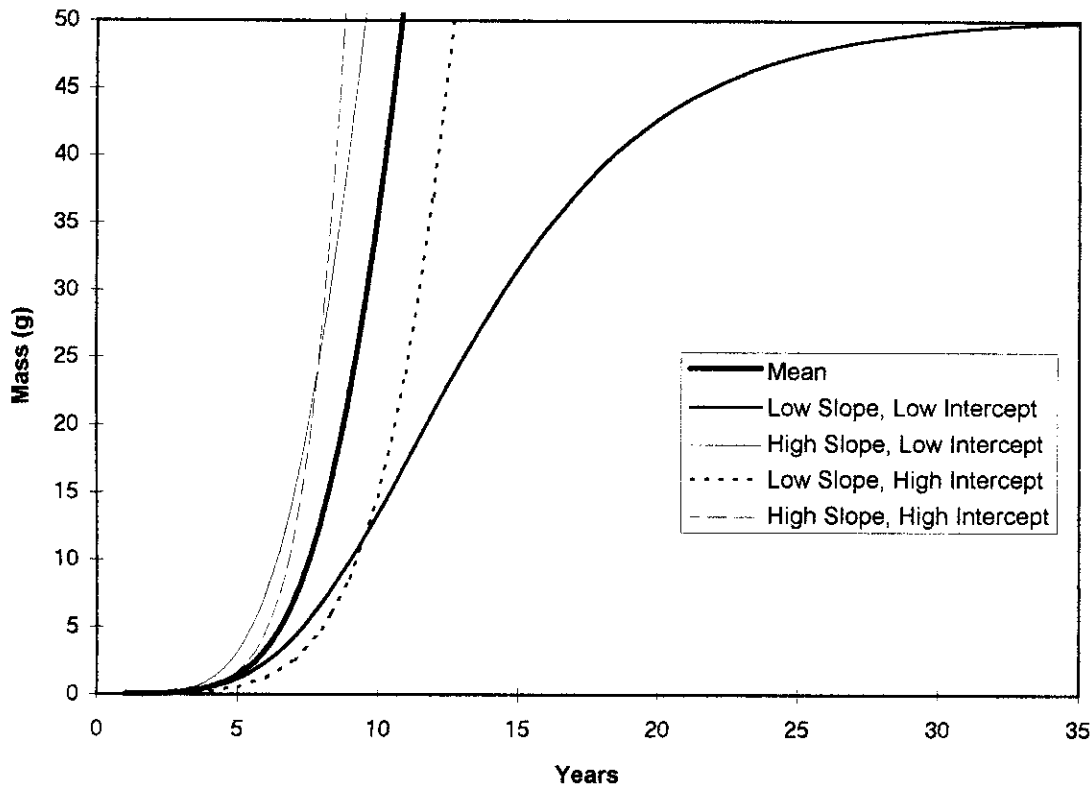


Figure 2. Increase in total plant dry mass with age, as calculated from a growth model. Reproduction began between 4 and 7 grams. The largest plant used to develop the growth model was 70 g; the largest plant weighed (root mass estimated) was 217 g. The 5 lines represent models using the mean regression coefficients and 95% confidence interval coefficients for the slope and intercept, as parameters for the relative growth rate regression equation (equation 3).

TABLE 5. Estimated ages in years at which plants reach specified masses. Estimates were calculated using the mean regression values and 95% confidence interval limits for the slope and intercept in the iterative growth model. The combination of slope and intercept confidence limits giving the widest confidence interval are displayed.

Growth stage	Mass (g)	Years		
		Mean	Lowest estimate	Highest estimate
First stem	3.15	6	5	8
10% reproductive	4.2	7	6	8
50% reproductive	4.8	7	6	9
90% reproductive	6.4	7	6	9
Largest plant in the plot	70	12	10	a
Largest weighed plant <sup>b</sup>	217	17	12	a

a = asymptotic near 50 grams for the slowest-growing model.  
 b = root mass estimated using equation 5.

lings, 49% juveniles, 3% non-reproductive adults and 10% reproductive adults. There were no significant differences in these percentages among four geographic subareas (Goldenberg 1992). The duration of each stage was estimated from the growth model, with a hypothesized maximum age of 25 years (this maximum age is entirely hypothetical, but appears reasonable, as the age of the largest plant was estimated at 17 years (table 5)). The durations include one year for seedlings, four years for juveniles, one year for non-reproductive adults, and 19 years for adults. A density histogram depicting the age structure was formed by dividing the percentages given above by the duration in each stage, and an exponential curve was fitted to the histogram to approximate a survivorship curve (figure 4). The age structure, with its large number of seedlings, suggests successful reproduction and population maintenance. Fecundity and mortality appeared to be consistent, because of the

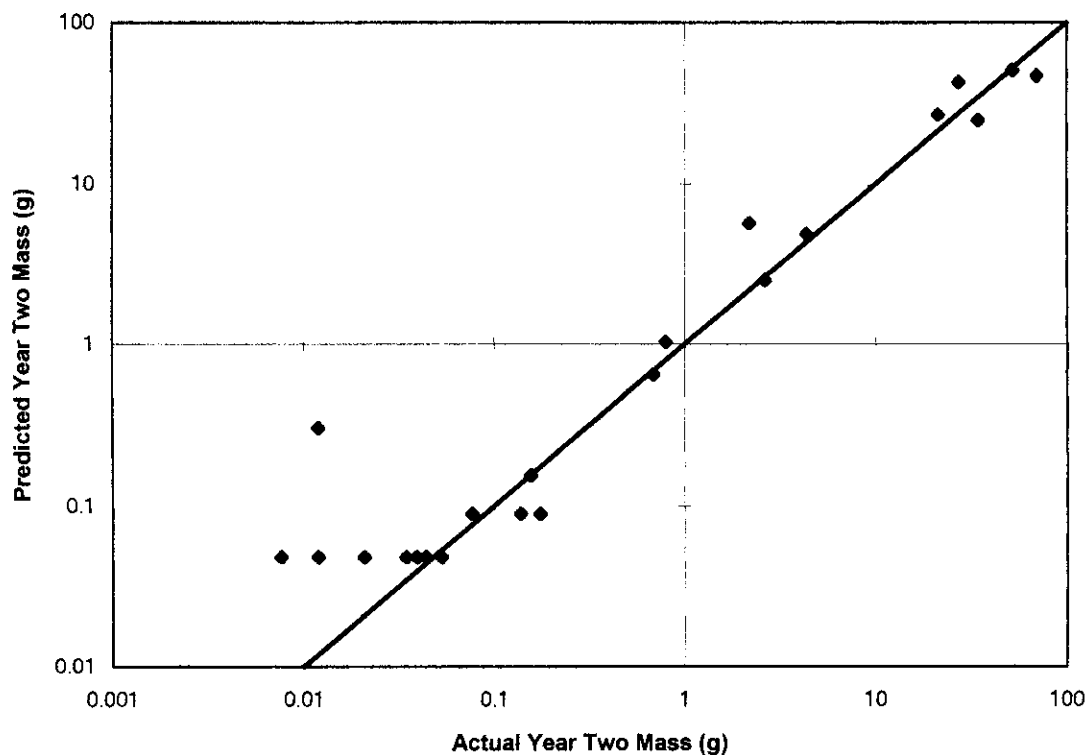


Figure 3. Relationship between actual year two masses and predicted year two masses based on year one masses and the growth model equations. A logarithmic scale was used to show the patterns at smaller sizes. The line represents equality of actual and predicted values.

descending curve of the age structure (the data fits an exponential decay curve), and because of the lack of differences among the geographic areas.

## Discussion

### Growth and Age Structure Methods

Information valuable for rare plant management, rates of growth and development and a population age structure, was obtained with only two seasons of data collection. In contrast, other methods of obtaining this information, e.g., by constructing life tables, would require the collection of many years of data on a much larger number of plants. The methods developed here should be useful to resource managers with a limited budget, who need relatively quick results.

The extrapolation of the data presented here to *Corydalis aquae-gelidae* throughout its range must be viewed as tentative. Additional sampling would be necessary to give results that could be validly applicable to the plant throughout its range.

A larger sample size, with randomly selected samples taken from throughout the area of interest, would be necessary to capture possible regional variation in growth and allocation patterns. With a rare plant, destructive sampling must of course be minimized, and calculating relative growth rate as a function of plant size (e.g., total length of leaves) rather than weight, removes the necessity to harvest the plants. Retaining data from some plant populations for independent model validation would additionally help to test the broad applicability of the results.

An estimation of population age structure which uses these methods requires certain plant behaviors. Consistent fecundity and mortality may be a requirement. If good seedling production only occurs in certain years, for example, interpretation of a single year's data may be difficult. This problem can be identified if a large number of growth stages or size classes were used to produce the age structure; inconsistent mortality and fecundity would produce a number of peaks and

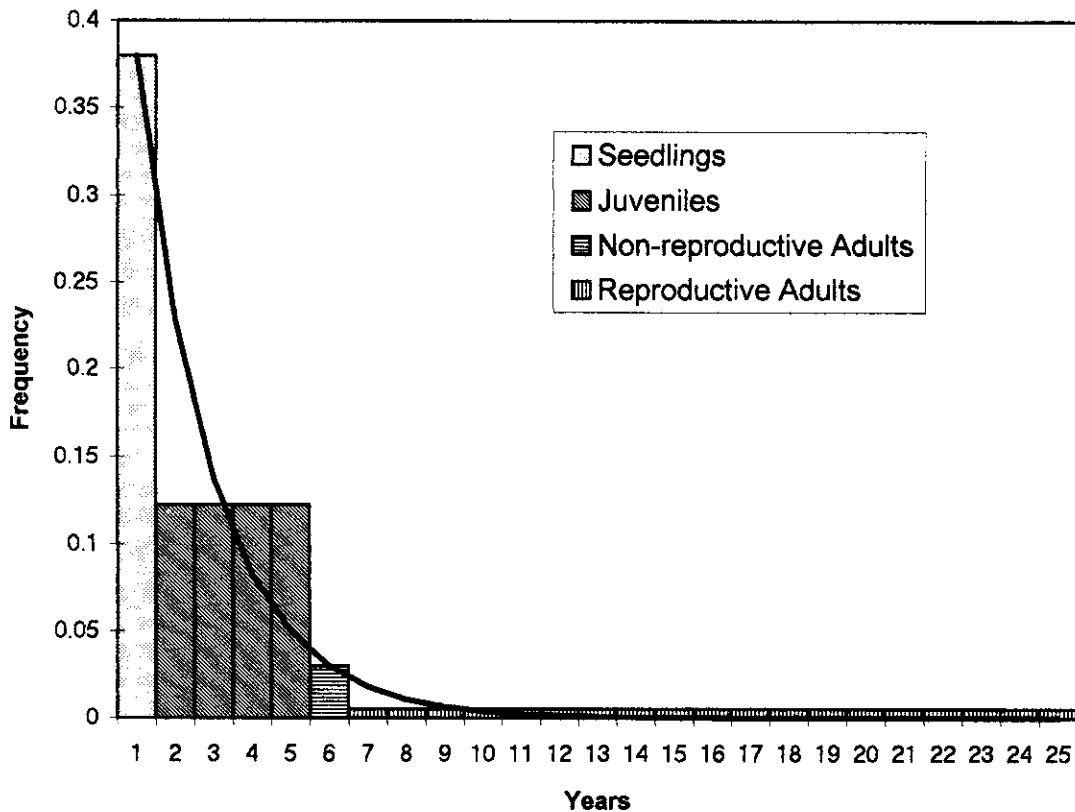


Figure 4. Hypothesized age structure for *Corydalis aquae-gelidae* on the Mt. Hood National Forest. From a sample of 2615 plants throughout the Mt. Hood National Forest. The curve was produced by the exponential decay function: frequency =  $0.6314 \exp(-0.5078 \text{ year})$ , which was fitted to the histogram data.

valleys in the age structure. *Corydalis aquae-gelidae* appeared to fit this requirement of consistency; all plants with 14 or more leaves flowered, many seedlings were observed during both study years, and the age structure showed a monotonic decline.

#### Plant Strategies

Grime (1979) predicts that plants of relatively resource-poor environments will be intrinsically slow-growing, with high allocation to storage, rather than reproductive or resource-gathering organs. *Corydalis aquae-gelidae* had the relatively high root/shoot ratio (about 2.4-3.8, table 3) and low reproductive allocation of a stress-tolerator (about 8%). Apparently, most of the photosynthate produced by seedlings their first year is stored as starch in the tuberous root; seedlings rarely produced any true leaves their first

year. These allocation patterns would lead to a high root/shoot ratio. Many other plants have relatively less biomass allocation to belowground structures. For example, eight perennial Compositae and Umbelliferae species had a mean belowground/aboveground biomass ratio of 0.74 (range 0.22 to 2.89, Lovett-Doust 1980, Abrahamson and Caswell 1982); rhizomes were included with roots. Harper (1977) suggests that herbaceous perennials allocate 5 to 25% to reproduction.

*Corydalis aquae-gelidae* also had the comparatively slow growth and long non-reproductive period of a stress-tolerator. Shade-tolerant temperate forest herbs cited by Bierzychudek (1982) require one to ten years for first reproduction; *Corydalis*, at 7 years (or between 6 and 9 years) according to the growth model, was at the high end of this range. *Corydalis* was generally found

in cold, wet, shaded conditions, with a coarse, mineral substrate, i.e., relatively unproductive habitats. Catastrophic disturbances during floods are relatively infrequent in *Corydalis aquae-gelidae* habitat (Goldenberg 1992).

#### Management Implications

The results imply that *Corydalis aquae-gelidae* populations would not rebound vigorously after disturbance, due to its slow growth and a long pre-reproductive period. Disturbance due to land management would, instead, favor more ruderal or competitive species. Ruderal species are fast-growing species with high reproductive allocation, while competitive species are fast-growing, but with allocation to continued vegetative growth (Grime 1979). Preservation of the habitat should be adequate for preserving the species, however. Human intervention seems unnecessary, as the

populations appear to be reproducing successfully, as based on the estimated age structure.

*Corydalis aquae-gelidae* is generally considered to be associated with late-successional or old-growth forest (USDA-FS, USDI-BLM 1994), and this work confirms that view. Grime (1979) considers that stress-tolerant plants are typical of late-successional forest understories. These plants must tolerate deep shade and a lack of free nutrients. Disturbance due to fire or timber harvest would increase available sunlight and nutrients, and should favor other species.

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