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Habitat Relations of *Corydalis aquae-gelidae*, a Rare Riparian Plant

Abstract

The relationships between the environment and the abundance of *Corydalis aquae-gelidae*, an herbaceous perennial and a USFWS species of concern, were explored. Information concerning habitat relations was pursued to determine possible conservation measures. *Corydalis* grows in headwater streams, up to 1300 m elevation, and down to 585 m on the fifth order Clackamas River, Mt. Hood National Forest, Oregon. Occupied streams had smaller seasonal flow fluctuations than streams where the species was absent, and had summer air and substrate temperatures averaging 17.7 C and 10.6 C, respectively. *Corydalis* abundance in plots was related to the distance to the summer water level, substrate texture and organic matter content, and plant community composition. Optimal conditions were identified: coarse, moss-covered, mineral substrates within 15 cm of the summer water level. Fine (<2 mm) or organic substrate material reduced *Corydalis* abundance. On the Oak Grove Fork, about 75% of the plants grew between the average winter high and summer low water level, an estimated vertical distance of 25 cm. The results were useful for management, and underscored the need to maintain stable hydrological conditions, avoid sedimentation, and protect riparian areas.

Introduction

Maintaining plant diversity has become a major objective of land management in the Pacific Northwest (USDA-FS, USDI-BLM 1994). Central to this effort is maintaining or enhancing the populations of rare species. One major cause of rarity is that a species may require a habitat that is itself rare (Rabinowitz 1981). Thus, management of habitat should be required to maintain species diversity, and information about habitat requirements of rare species may be necessary for effective management.

Corydalis aquae-gelidae Peck and Wilson (Fumariaceae, cold-water corydalis) has a limited range on the west slopes of the Cascade Range, both north and south of the Columbia River. It is considered a species of concern by the US Fish and Wildlife Service, and is a candidate for listing under the Oregon Endangered Species Act (Oregon Natural Heritage Program 1995). As an uncommon old-growth associated species, it is protected under the Northwest Forest Plan (USDA-FS, USDI-BLM 1994). *Corydalis aquae-gelidae* is restricted to streamside habitats, but details of its habitat requirements are not well known. Streamside plants may be particularly sensitive to impacts from management, because they are affected both by changes in the stream, as well as those in adjacent riparian and hillslope lands. Because upstream roads and clear-cuts can increase peak flows (Jones and Grant 1996), distant, downstream populations could be affected. *C. aquae-gelidae* population size and plant development were previously studied (Goldenberg 1992, Goldenberg and Zobel 1997). In this study, the environmental factors in natural populations within much of the species' range are described, including hydrologic regime, temperature, substrate, and associated vegetation. Based on these habitat characteristics, recommendations for management of the species were developed.

Study species

Corydalis aquae-gelidae is a large perennial herb. Its annual stems arise from large, fleshy taproots and grow to over one meter tall. The species does not spread rhizomatously, unlike the sympatric *C. scouleri*. *C. aquae-gelidae* has high habitat specificity, and is narrowly endemic (Goldenberg 1992). It grows within the *Tsuga heterophylla* and *Abies amabilis* forest zones of Franklin and Dyrness (1973), in Clackamas and Multnomah Counties, Oregon, and Clark and Skamania Counties, Washington (USDA Forest Service 1983, Oregon Natural Heritage Program 1990). An outlying population grows west of Mount St. Helens, in Cowlitz County, Washington. The lowest elevation site is at 460 m, near Tanner Creek in the Columbia River Gorge, while the upper elevational limit is at 1300 m, near Squaw

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Mountain. Within the Mt. Hood National Forest, the total number of reproductive adult *C. aquae-gelidae* plants was estimated at 8,400 (Goldenberg 1992). The total number of reproductive adults throughout the range of the species is 10,000 to 15,000. Its streamside habitat has been subject to disturbance by logging, fish habitat manipulation, and water diversion for hydropower (Goldenberg 1992). Detailed habitat data are needed to facilitate conservation of this species.

Methods

Data were collected 29 June to 8 September 1990, and 9 July to 10 September 1991. Study sites included known populations in the southwestern portion of the Mount Hood National Forest, Oregon (44° 55' to 45° 15' N latitude and 121° 50' to 122° 15' W longitude); this area supports most plants of the species (USDA Forest Service 1983, Oregon Natural Heritage Program 1990). Plots were located on and near two larger river reaches, the upper Clackamas River near Big Bottom, and the Oak Grove Fork of the Clackamas River; these plots occurred at 600 to 1006 m elevation. Plots were also located on small streams and springs to the northwest of these rivers, near Soosap Peak and near Squaw Mountain. These headwater populations occurred at 840-1250 m. Most of the sites were bordered by late-successional forest, except for eight plots from two sites in the Soosap Peak area, which had been clearcut in 1971.

In 1990, each of 75 1-m^2 plots was centered on an adult plant randomly selected from each 200 encountered during a population census. During 1991, for each of 25 plots centered around a selected adult, two additional plots were sampled, one upstream and one downstream. These additional plots were located at a random distance between 5 and 15 meters from the sample plant, and between 2 meters into and 3 meters away from the stream edge. Eleven of the additional plots included *Corydalis*. The 39 plots without *Corydalis* were used to compare nearby microsites that lacked the species. There were 150 plots in total.

To determine the abundance of *Corydalis aquae-gelidae,* we recorded percent cover, numbers of individuals in each of four growth stages, and average height and leaf numbers of the largest three adults. The four growth stages were seedlings (first year plants with cotyledons, almost never with a true, compound leaf), juveniles (plants with one or more true, compound leaves, but no cotyledons or above-ground stems), non-reproductive adults (plants with one or more above-ground stems), and reproductive adults. These growth stages corresponded to obvious morphological breaks among different sizes of plants.

For each 1-m^2 plot, we recorded air, substrate and water temperature; horizontal distance to water; vertical distance to water; water cover percent; surface cover percent of moss, mineral and organic material; surface cover percent of stones (>250 mm), cobbles (76 to 250 mm), gravel (2 to 76 mm), and fines (<2 mm, sand, silt, clay, and highly decomposed organic material); substrate type, including gravel and coarse sand (GS), gravel and sand dominant, with additional soil, mud or organic material (GX), and soil or mud dominant (LX); canopy cover percent; canopy species (shrubs and trees over 1 m above the plot); and understory species (species with cover below 1 m). Taxonomic nomenclature followed Hitchcock and Cronquist (1973). Air temperature was recorded in the sample plant's canopy, while substrate and water temperature was recorded at about 10 cm depth; these data were recorded at the time the plots were sampled. In forty plots occupied by *Corydalis aquae-gelidae*, a soil sample of about 1 L was sifted through a 2 mm sieve. Gravel, coarse (>2mm) organic material, and fine material were measured volumetrically.

Statistical Analyses

The seven variables indicating *Corydalis aquae-gelidae* abundance were transformed (natural logarithm or square root) to approximate bivariate normality on all pairwise comparisons (scatterplots were used to assess the relationship), and standardized as (X_i - mean)/standard deviation. Principal components analysis (using Statgraphics, STSC 1991) was used to combine abundance variables into two indices of abundance: a reproduction index (combining seedling and juvenile numbers) and a biomass index (combining cover, adult numbers multiplied by average leaf number, and adult numbers times average height). A constant was added to the indices to increase their minima to zero, corresponding to zero for the original variables. The dry mass of *Corydalis* plants was correlated with both their height and leaf numbers (r^2=0.96, 0.98, respectively, Goldenberg 1992); hence height and leaf numbers multiplied by the adult density correlated with the biomass in the plot. In addition, leaf number was correlated with pedicel numbers (r^2=0.87), and therefore with seed production.

Plant community ordination scores were calculated for each 1-m^2 plot, separately for canopy and understory species (exclusive of *Corydalis aquae-gelidae*) using PC-Ord (McCune 1991). Because of the wide variety of sites sampled and the small plots, the species by sample data matrices were largely zeroes (94% for the understory, 89% for the canopy). Therefore, the data matrices were transformed using the sociological favorability index (Beals 1984), which uses binary data. Bray-Curtis ordination (using city-block distance and variance-regression endpoint selection, Beals 1984) then extracted 48% of the understory variation on the first three axes. Ordination on the canopy species extracted 77% of the variation on the first three axes. A non-metric multidimensional scaling ordination analysis (NMS, Kruskal 1964) was run on the Bray-Curtis ordination scores. For the understory, both Bray-Curtis and NMS results are reported here. The results from NMS were used for the canopy species.

A smoothing procedure was used to relate environmental variables to *Corydalis aquae-gelidae* abundance indices. Reproduction and biomass index scores were ordered based on the scores for each of the environmental variables. The resulting ordered series (of reproduction or biomass index) were put through a smoothing procedure. Running averages were calculated using values from varying "windows" within the range of dependent variable data, with the average y value calculated where the x value is within +/- a chosen percent of the x range. For example, if the independent (x axis) variable ranged from 1 to 100, and a 10% window was chosen, all y values corresponding to x values between 40 and 60 were used to calculate the average y value at x = 50. Different windows were used to find an appropriate smoothed line, i.e., a line that removes excess scatter without becoming excessively flat. A visual basic algorithm was written in Excel (Microsoft 1993) to calculate the averages. This procedure produced a better fit to the data than a standard running average. This variation on the classic moving average is similar to LOWESS smoothing (Cleveland 1981), in that an average of y values is calculated based on the associated x values.

Spearman's rank correlation was used to test for statistical significance. Coefficients were calculated separately above and below optima, which were located by inspection of graphs generated using the smoothing procedure.

Time dependency was tested graphically and by linear regression; sample date or time of day was not correlated with the other variables, except as mentioned below.

The above statistical methods, smoothing and rank correlation, were chosen over parametric regression techniques because of the variability and complexity of the relationships. Also, regression could not be applied without violating the assumptions. The non-parametric methods chosen have few assumptions or limitations. Some measure of subjectivity is inherent in smoothing procedures, however, as the level of smoothing is chosen by the researcher. The rank correlations are limited to monotonic relationships, hence the separate analyses on different sides of the graphically chosen optima.

Results

Corydalis aquae-gelidae Abundance Indices

The two indices calculated to represent the biomass and reproductive success of *Corydalis aquae-gelidae* accounted for most of the variance in the input variables: the reproduction index (first PCA axis), 86%, and the biomass index, 96%. The two indices were correlated (r^2=0.48, $P<0.0001$) but graphing showed that reproduction was not necessarily high where adult biomass was high. The average values of the original variables that corresponded to given index values were calculated (Table 1). There was a gap in the values for the biomass index, due to few samples with small adults.

Geomorphology

Corydalis aquae-gelidae grew in a narrow band (in the active channel of Gregory et al. 1991) along streams of many sizes. Occupied headwater streams (smaller than first order) were mainly at high elevations in the Squaw Mountain and Soosap Peak areas. The largest stream was the fifth order channel of the upper Clackamas River, with *Corydalis* occurring down to 585 m elevation. Where *Corydalis* was present, adult abundance

TABLE 1. Correspondence of original *Corydalis aquae-gelidae* abundance variables with abundance indices. The equations defining these indices were:

1) Reproduction index = 0.71 ln(seedlings, no./m^2 + 1) + 0.71 ln(juveniles, no./m^2 + 1)

2) Biomass index = 0.57 (cover %)$^{1/2}$ + 0.58 ln(height, cm * adults, no./m^2 + 1) + 0.58 ln(no. of leaves * adults, no./m^2 + 1)

Index	Variable	Value of the index					
		0	1	2	3	4	5
Reproduction	Seedling numbers	0	1.6	5.5	15.6	41	*
	Juvenile numbers	0	1.9	7.5	23.8	71	*
Biomass	Adult numbers	0	0	1	2	4	13
	Leaf numbers	0	0	2	7	40	330
	Height (cm)	0	5	20	46	82	128
	Cover%	0	4	15	34	60	94

* The reproduction index does not exceed 4.

(the biomass index) varied significantly among stream orders (ANOVA, P=0.03), but the reproduction index did not. The largest, densest plants (high biomass index) grew along the largest streams. *Corydalis* abundance indices did not vary significantly with sample plot elevation.

River Flow Fluctuations

Streams occupied by *Corydalis aquae-gelidae* exhibited little bare gravel and rock above the summer water level, less than many streams without the species. Streams supporting the species apparently had less seasonal flow fluctuation. Gaging station data from the southwest Mount Hood National Forest supported this hypothesis. The coefficient of variability for annual and growing season stream flow fluctuation (standard deviation/mean of mean monthly flows) was lower for occupied stream reaches (0.24 to 0.35) than for unoccupied streams (0.40 to 0.73, P=0.01, n=8, one-tailed rank sum tests). The average annual stream flow (i.e., stream size) did not differ significantly between reaches occupied by *Corydalis* and other reaches, nor did the difference between high and low flow in cubic meters per second.

The relationship of *Corydalis aquae-gelidae* to seasonal river levels was explored. River flow data (Bingham Engineering 1985) for the Oak Grove Fork below Stone Creek were transformed into river surface levels using the relationship for the gaging station. This relationship varies downstream, depending on the bed shape. These distances were relativized to the mean July water level. Data points for each month in Figure 1 include the mean of monthly means for 25 years, and 25-year maximum and minimum monthly means. The growing season is generally late May through early September. This reach of the Oak Grove Fork is downstream from a dam, which regulates the stream flow.

During July, 1990, on the Oak Grove Fork, the lowest plant was rooted at 14 cm below the water surface, the median was 7 cm above (n=97), 95% of the plants were within a vertical range of 25 cm, and the highest plant was at 95 cm above the water surface. Measured plant locations were used to estimate the number of *Corydalis* plants that would be submerged (at least partially) under the river levels in Figure 1, yielding Figure 2, which shows that about 75% of the plants occupy the zone between average summer low and winter high water level.

Microsite Temperature Patterns

Corydalis aquae-gelidae grew in a cool environment. During field sampling, water temperature averaged 9.7°C (SD 2.0, range 5.2 to 14.1), substrate temperature averaged 10.6°C (SD 2.3, range 5.4 to 18.9), and air temperature averaged 17.7°C (SD 3.8, range 8.9 to 29.8). Because the substrate was often submerged, many plots had a similar water and substrate temperature. A regression model was built for temporal changes in air temperature:

$$\text{Air temp. } (^{\circ}\text{C}) = -20.8 - 0.025(\text{date}) + 5.4(\text{time}) - 0.18(\text{time}^2)$$
$$R^2=0.15 \quad P<0.0001 \quad n=150$$

Date was calculated as days since June 21. Time is in hours; minutes were transformed to decimals

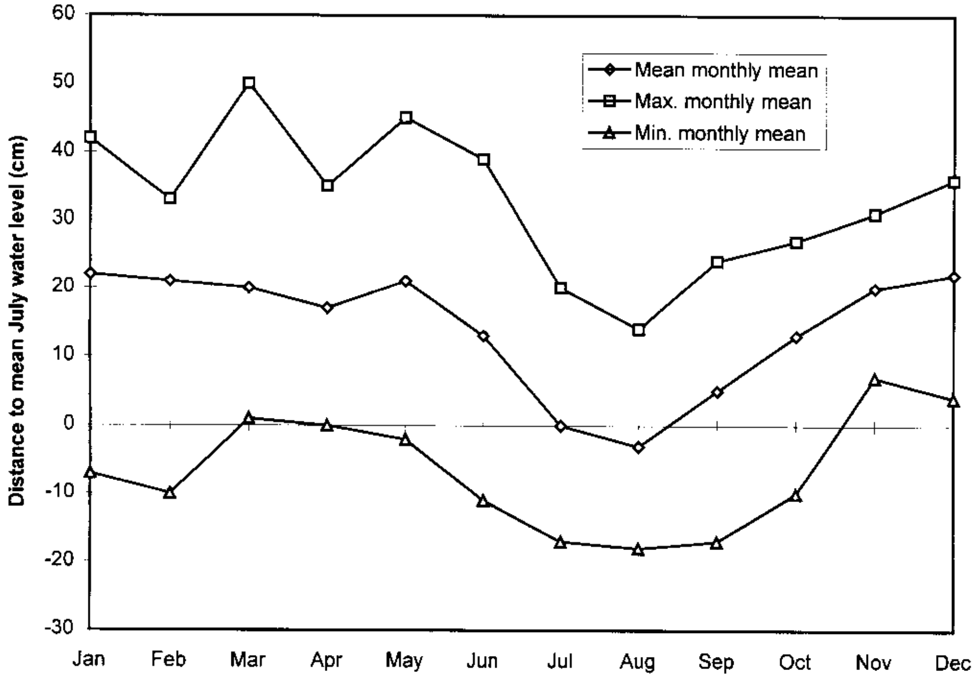

Figure 1. Average river level on the Oak Grove Fork as vertical distance to mean July water level. For 25 years on record.

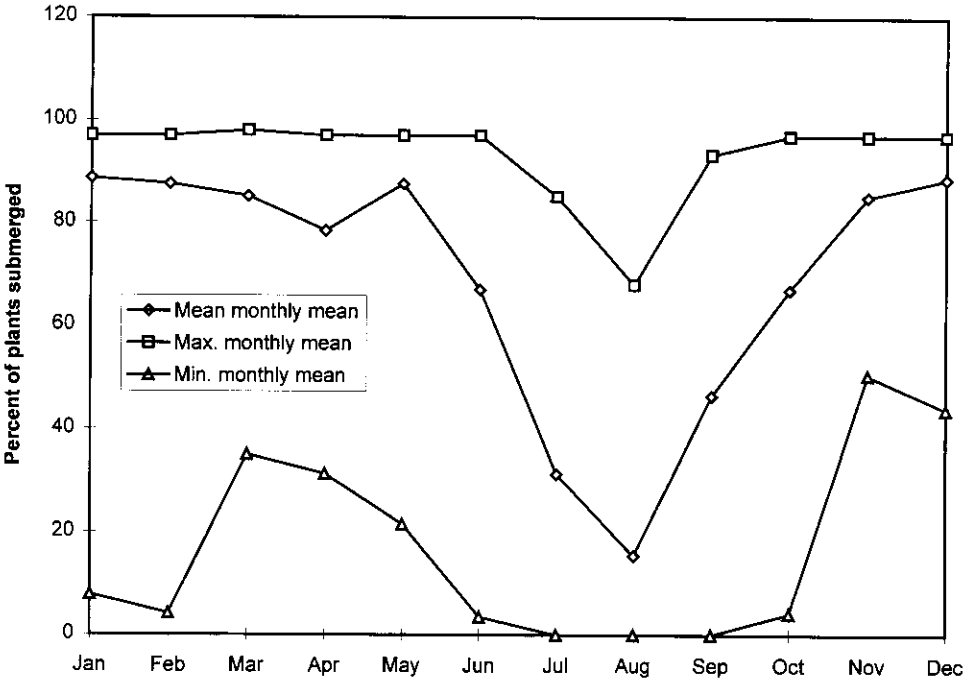

Figure 2. Average percent of adult *Corydalis* plants at least partially submerged.

of hours. The predicted July average maximum air temperature was 19.1 °C, cooler than July maxima for weather stations in these forest zones, which are 21 to 27 °C.

Substrate Analyses

Three types of substrates occurred in the sample plots. Gravel and sand (GS) substrates were stream sediments. Substrates containing gravel, sand and other materials (GX type substrates) represented mostly streambed deposits with additional siltation or organic matter deposition. Various loams or mud substrates (LX types) represented forest soils with litter layers, or deposits within the stream bed, often in marsh or swamp areas. Substrate components differed among the substrate types (Table 2).

Community Composition Ordinations

The positions of sample plots on axes produced by the understory and canopy community ordinations were correlated with environmental variables, especially elevation (Spearman rank correlation, r_s, .51 to .53), stream order (r_s .57 to .66), proximity to water (r_s .21 to .29), and substrate composition (r_s .01 to .36). The Bray-Curtis method gave results similar to the NMS ordination method. High values on the first understory axis indicated species of the wettest habitats (e.g., *Glyceria elata, Veronica americana, Oenanthe sarmentosa, Stachys cooleyae*, and *Petasites frigidus*), particularly on the larger, low elevation streams. Low understory axis values indicated species of either wet habitats with fine substrates or moist forest habitats (e.g., *Blechnum spicant, Trautvetteria caroliniensis, Cornus canadensis*, and *Tiarella trifoliata*); these latter species were often of higher elevations. The most frequent understory species were *Epilobium glandulosum* and *Mimulus guttatus*, which indicated intermediate axis values. Other species that had intermediate understory axis values include *Circaea alpina, Galium triflorum, Mitella ovalis, Montia sibirica*, and *Tolmiea menziesii*. For the canopy axis, high values indicated dense *Tsuga heterophylla* and high elevation canopy species (e.g., *Abies amabilis, Alnus sinuata*); low values indicated less dense canopies found on the larger rivers (e.g., *Thuja plicata, Alnus rubra*).

Response to Microsite Variables

The abundance indices differed significantly among the substrate types (Table 3). 34 of 64 correlations between the environmental variables and *Corydalis aquae-gelidae* abundance indices were statistically significant at alpha =0.05 (Table 4, 5). *Corydalis aquae-gelidae* abundance was related

TABLE 3. Median values of the reproduction and biomass indices for the three types of substrates (described in Table 2).

A. For all Plots. Significantly different among the substrate types (P=0.0002, reproduction index, P<0.0001, biomass index, Kruskal-Wallis test).

Type	n	Median Reproduction Index	Median Biomass Index
GS	73	1.64	3.53
GX	40	1.04	3.11
LX	36	0.0	0.0

B. For plots within the optimal range of water levels. Significantly different among the substrate types (P=0.006, reproduction index, P=0.0001, biomass index, Kruskal-Wallis test).

Type	n	Median Reproduction Index	Median Biomass Index
GS	54	2.06	3.63
GX	34	1.11	3.23
LX	16	0.29	0.09

TABLE 2. Substrate components (%) by substrate type. Components were measured volumetrically in 40 samples, within plots with *Corydalis aquae-gelidae*. GS substrates consisted of only gravel and sand. GX substrates are mostly gravel and sand, with other materials prevalent. LX substrates are mostly soil or mud, with other materials additionally. Fines are all materials less than 2 mm, including sand, silt, clay and organic matter. Standard deviations in parentheses.

Type	n	Gravel	Sand	All fines	Organic (>2mm)
GS	17	75 (12)	25 (12)	NA	NA
GX	17	57 (12)	NA	32 (17)	11 (10)
LX	6	19 (21)	NA	72 (19)	8 (7)

TABLE 4. The abundance of *Corydalis aquae-gelidae* correlated to environmental variables: results for the reproduction index. r and P values refer to Spearman rank correlations. Bray-Curtis (BC) and NMS are alternative ordination methods. Variables with significant correlations (alpha=0.05) are reported. Optima were determined by inspection of scatterplots. Generally, abundance increases to the optima (positive r), and decreases after the optima (negative r).

Variable	Optimum	<Optimum			>Optimum		
		n	r	P	n	r	P
Vertical Distance (cm)	7	86	0.45	<0.0001	66	-0.48	0.0001
Water Cover (%)	20	95	0.33	0.001	64	-0.49	0.0001
Moss Cover (%)	50	100	0.39	0.0001	65	-0.17	0.16
Mineral Cover (%)	40	90	0.32	0.003	70	-0.45	0.0002
Organic Cover (%)	20	96	0.04	0.71	66	-0.47	0.0002
Cobble Cover (%)	75	145	0.26	0.002	10	-0.26	0.43
Gravel Cover (%)	40	100	0.38	0.0001	58	0.03	0.80
Fines Cover (%)	45	100	0.04	0.72	54	-0.55	0.0001
NMS Understory Axis	0	68	0.48	0.0001	79	-0.28	0.015
BC Understory Axis	0.5	86	0.33	0.0025	62	-0.30	0.02
Canopy Cover (%)	60	39	0.33	0.04	113	-0.04	0.64
Associated Species Cover (%)	40	41	0.34	0.03	113	-0.21	0.03

TABLE 5. The abundance of *Corydalis aquae-gelidae* correlated to environmental variables: results for the biomass index. r and P values refer to Spearman rank correlations. Bray-Curtis (BC) and NMS are alternative ordination methods. Variables with significant correlations (alpha=0.05) are reported. Optima were determined by inspection of scatterplots. Generally, abundance increases to the optima (positive r), and decreases after the optima (negative r).

Variable	Optimum	<Optimum			>Optimum		
		n	r	P	n	r	P
Vertical Distance (cm)	15	107	0.23	0.02	45	-0.68	<0.0001
Horizontal Distance (cm)	40	109	0.04	0.70	44	-0.45	0.003
Water Cover (%)	30	108	0.33	0.0007	48	-0.26	0.07
Moss Cover (%)	80	136	0.36	<0.0001	26	-0.31	0.13
Mineral Cover (%)	45	96	0.43	<0.0001	60	-0.31	0.02
Organic Cover (%)	15	84	-0.03	0.81	68	-0.45	0.0003
Cobble Cover (%)	60	129	0.32	0.0003	25	-0.17	0.40
Gravel Cover (%)	35	92	0.50	<0.0001	62	-0.02	0.89
Fines Cover (%)	45	100	0.05	0.64	54	-0.55	0.0001
NMS Canopy Axis	-0.4	50	0.08	0.57	97	-0.20	0.048
NMS Understory Axis	0.5	114	0.44	<0.0001	33	-0.48	0.006
BC Understory Axis	0.55	105	0.41	<0.0001	44	-0.19	0.22
Associated Species Cover (%)	10	18	0.18	0.46	136	-0.18	0.04

to the distance to water, to the quality and texture of the substrate, and to the presence of other plants (Tables 3, 4, Figures 3-7). Several variables represented each of these four environmental factors; only the effects of the most significant variables are illustrated. Abundance peaked near the edge of the summer water levels (Figures 3, 4). *Corydalis* abundance was reduced in organic and fine-textured substrates (Figures 5, 6); substrate types became increasingly unfavorable from types GS to GX to LX (Table 3). The effect of water level varied among substrate types (Figure 6). Abundance varied with understory composition (Figure 7) and with the density of associated plants, and was weakly correlated with canopy cover (Table 4, 5).

Although substrate cover and substrate type were correlated with the water position variables,

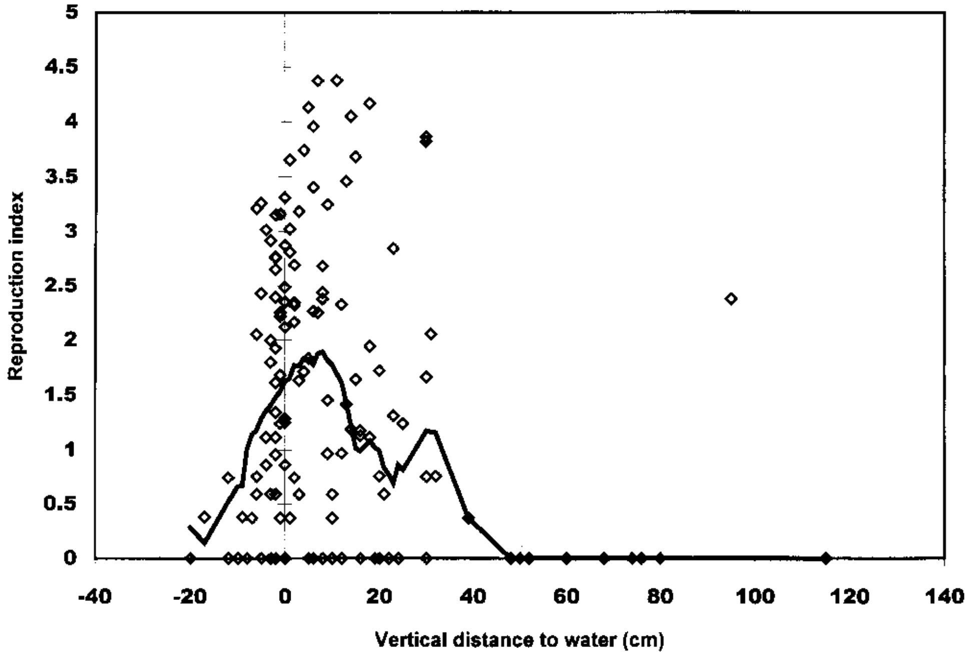

Figure 3. Relation of the vertical distance from water to the reproduction index. Many points represent more than one sample. The line is from the smoothing procedure described in the text.

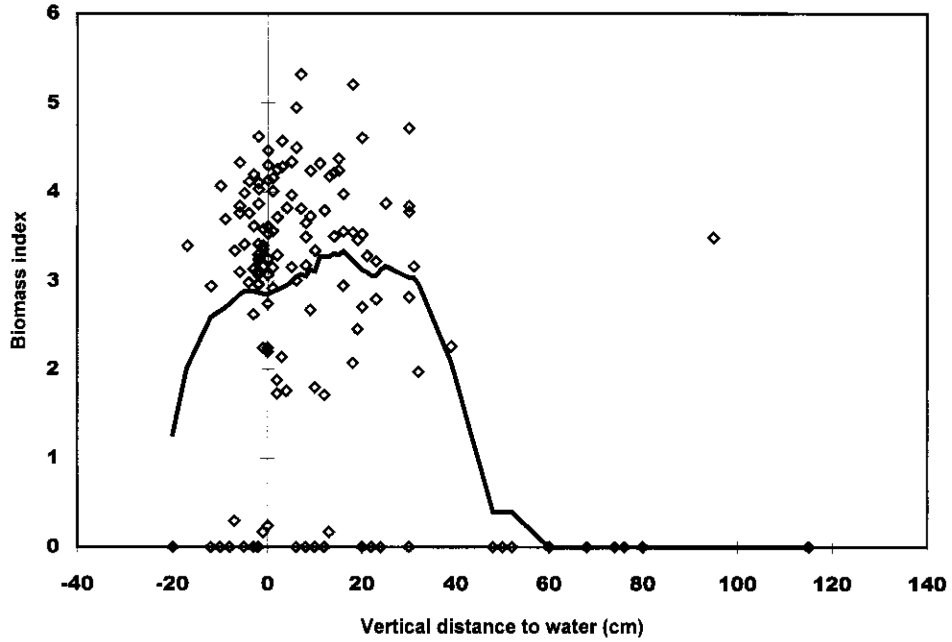

Figure 4. Relation of the vertical distance from water to the biomass index. Many points represent more than one sample. The line is from the smoothing procedure described in the text.

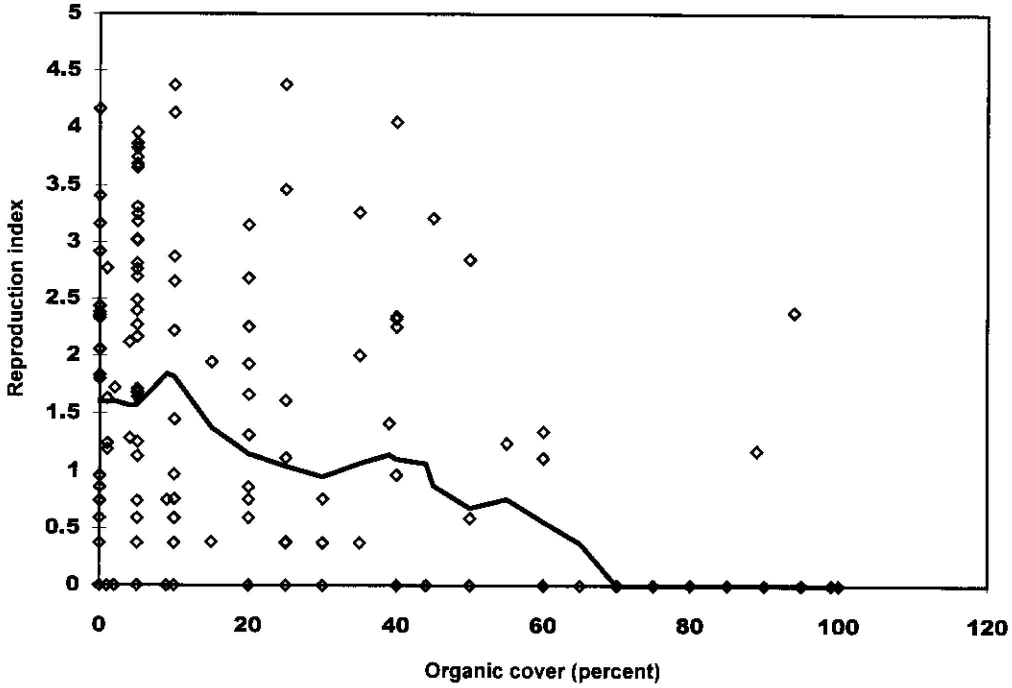

Figure 5. Relation of the cover of organic material on the plot surface to the reproduction index. Many points represent more than one sample. The line is from the smoothing procedure described in the text.

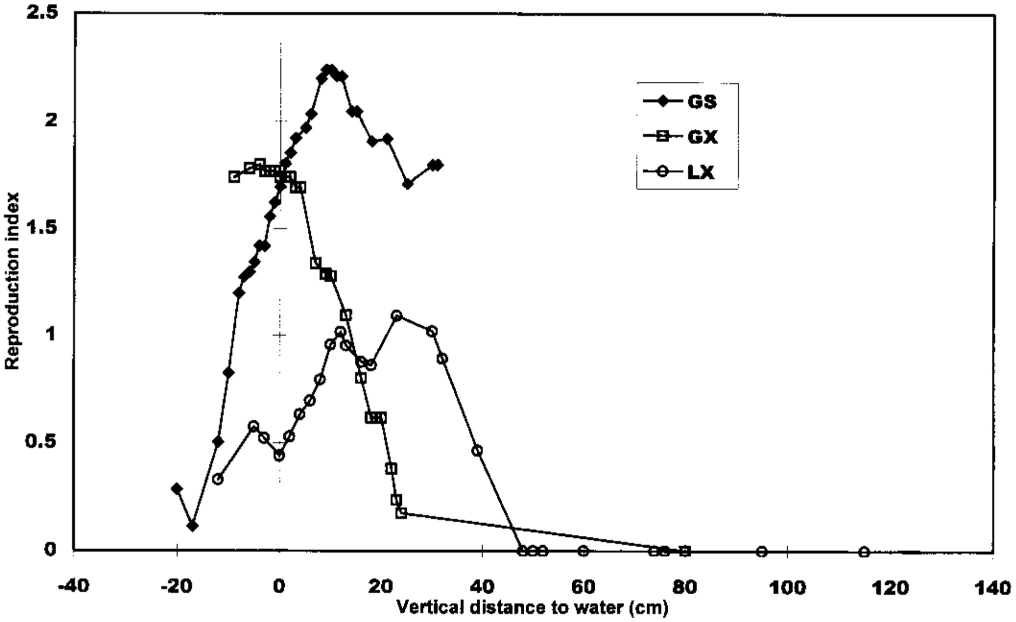

Figure 6. Relation of the vertical distance from water to the reproduction index, separating samples by substrate type. The types are GS, gravel and coarse sand, GX, gravel and sand dominant, with other materials, LX, soil or mud dominant. Associated data points are the same as the points in figure 3. The lines are from the smoothing procedure described in the text.

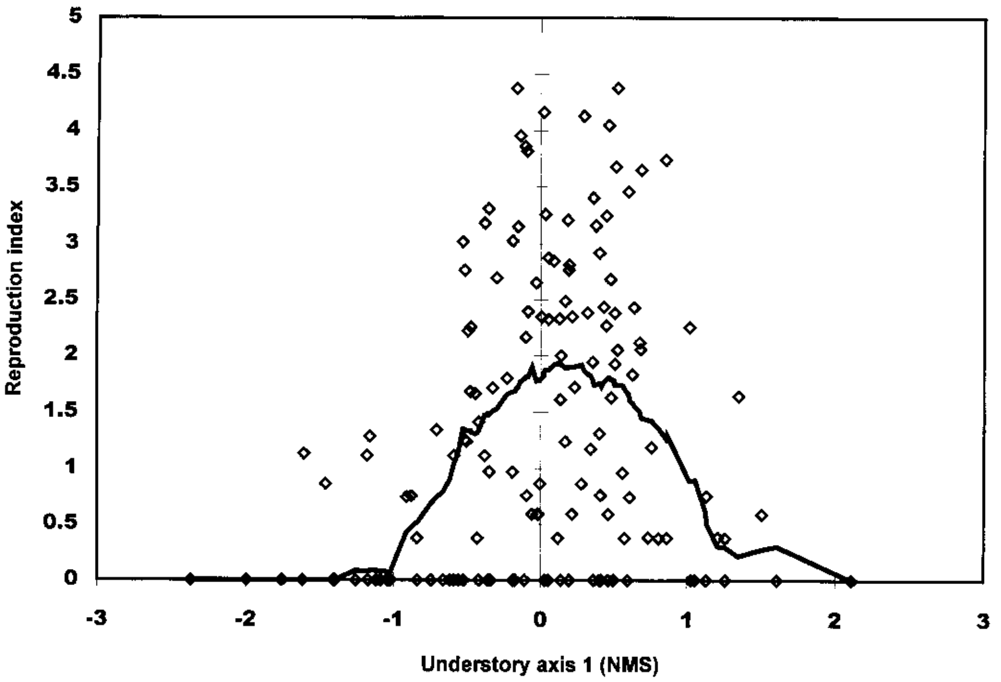

Figure 7. Relation of the first NMS understory community ordination axis to the reproduction index. Many points represent more than one sample. The line is from the smoothing procedure described in the text.

they also had an independent effect on *Corydalis aquae-gelidae*. Spearman rank correlations between the substrate cover variables, water position variables, and the abundance indices were calculated, using only the samples that were between -5 and 20 cm vertical distance to the water, the optimal range (Table 6). Within this range, the substrate cover variables were no longer significantly correlated with the water position variables, yet most remained correlated with the *Corydalis* abundance indices. The substrate types were also significantly different within this vertical range (Table 3).

Discussion

The Habitat of *Corydalis aquae-gelidae*

Corydalis aquae-gelidae grew in stream reaches with small seasonal flow fluctuations. Large

TABLE 6. Response of *Corydalis aquae-gelidae* to environmental variables where water position was optimal. Spearman rank correlations were calculated, using the 104 samples between -5 and 20 cm vertical distance to water. All correlations between the environmental variables and the vertical distance to water were not statistically significant (P > 0.05); no r values are given.

	Reproduction index		Biomass index		Vertical Distance
	r	P	r	P	P
Moss cover (%)	0.28	0.005	0.21	0.04	0.60
Mineral cover (%)	0.03	0.77	0.07	0.49	0.97
Organic cover (%)	-0.28	0.005	-0.29	0.004	0.54
Cobble cover (%)	0.21	0.04	0.30	0.003	0.19
Gravel cover (%)	0.11	0.28	0.12	0.21	0.66
Fines cover (%)	-0.26	0.008	-0.29	0.003	0.56

changes in flow would submerge plants in winter, and subject plants to drought in summer. In addition, high winter stream flows may physically disturb the substrate, burying or uprooting plants. *Corydalis* grew in late-successional riparian forest, mostly in areas not recently subjected to catastrophic floods. Elevational limits may have been more affected by hydrology than temperature; elevational limits coincided with the disappearance of stable stream flow regimes.

Maximum abundance occurred from 5 cm below to 20 cm above the summer water level (Figure 3), and within 40 cm horizontal distance to the nearest water surface (Table 4, 5). Optimal water cover was 10 to 30 % (Table 4, 5). The upper limit of *Corydalis* distribution along stream banks might be explained by drought, substrate differences, or a lack of the mild disturbance which could reduce competition. *Corydalis aquae-gelidae* seedlings had small root systems, with few fine roots, and died when they germinated in dry habitats (personal observation). Other plant species were denser away from the stream, which could increase soil dryness and competition. In addition, lack of cover by stream flow in the winter could allow the substrate to freeze; in cultivation, dormant plants were killed by winter substrate freezing, while plants kept indoors survived (personal observation).

Corydalis aquae-gelidae was rarely found in water deeper than 20 cm. Seedlings were only 2-4 centimeters tall, and rarely if ever survived growing completely submerged. The few adults found in swift water deeper than 20 cm grew horizontally, underwater, and appeared stunted. Substrate instability was also a problem in deeper water (personal observations).

Moss cover in *Corydalis* habitat was optimal at 50 to 80% (Table 4, 5). Low moss cover was associated with a high degree of scouring and low canopy cover. Habitats with higher moss cover were generally preferable for establishment, evidently because they were moist, only mildly disturbed, and without much litter buildup or vigorous existing herbaceous cover.

Substrates rich in organic matter, silt or clay were poor habitat for *Corydalis aquae-gelidae*. The physical properties of these substrates may account for this correlation. The bulk flow of water (as long as the substrate is fairly wet), air, and solutes decreases with smaller particle size (Hillel 1982). Coarse mineral substrates would allow faster water flow when near saturation, and faster air flow when drier. Organic matter in the less optimal soils would decrease their O2 concentration further, due to increased decomposition rates. Anaerobic processes, both chemical and biochemical, can produce substances toxic to plants, e.g., ethylene, organic acids, and ferrous sulfide (Hillel 1982), and low pH can lead to metal toxicity. Substrates rich in clays and fine organic matter have a higher capacity to hold toxic substances; greater water flow through coarser substrates would leach out these substances.

Corydalis aquae-gelidae abundance was related to plant community composition (Figure 7). Although the ordination axes provided no information for mechanistic explanations, community composition was a good indicator of habitat favorability for *Corydalis*. Species that had a response curve to the first understory axis similar to the response curve of *Corydalis aquae-gelidae* (Figure 7) include: *Epilobium glandulosum*, *Mimulus guttatus*, *Circaea alpina*, *Galium triflorum*, *Mitella ovalis*, *Montia sibirica*, and *Tolmiea menziesii*. These species were associated with favorable conditions for *Corydalis aquae-gelidae*, although they also grow in other conditions.

The relationships of *Corydalis aquae-gelidae* abundance to environment varied from a monotonic, nearly linear slope (Figure 5) to a complex curve (Figures 3, 7) reminiscent of the classic bell curve of niche theory (Austin et al. 1990). Aspects of this complexity included the large amount of variability, the lack of normally distributed residuals, and the interactions of the type evident in Figure 6, where the effect of water level varied depending on substrate type. The statistical methods were chosen because of the complexity of the relationships.

Management Implications

The relationships described here can be used to predict where *Corydalis aquae-gelidae* might be found during additional surveys, where it would be successful if it were to be introduced or naturally dispersed, and what effects natural or human induced environmental changes could have on its abundance. To allow persistence and regeneration of *Corydalis aquae-gelidae*, land managers should maintain canopy cover, and prevent sedimentation or other additions of fine or organic materials to streams. Percent canopy cover had a significant effect in this study, and *Corydalis aquae-gelidae* abundance is significantly reduced in clearcuts compared to other sites; plants with no protection in clearcuts experience severe solarization, i.e., yellowed and browned leaflets (Goldenberg 1992). Clearcuts along small streams often resulted in deposition of soil and logging slash in *Corydalis* habitat (personal observations). *Corydalis* may also be damaged by stream flow reductions, increased seasonal flow fluctuations, and catastrophic floods. Hydropower projects can modify stream flow and upstream timber harvest may destabilize hydrologic conditions and contribute to sedimentation. Upstream road building and clear cuts can increase peak discharges by up to 100% (Jones and Grant 1996). Coordination of stream and forest land management activities is critical to maintain optimal habitat conditions for *Corydalis aquae-gelidae.*

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