Howellia aquatilis (Water Howellia) Ponds of the Swan Valley: Conceptual Hydrologic Models and Ecological Implications

Montana Natural Heritage Program
and Conservation Biology Research

by: Mark Shapley
419 Adams St.
Helena, MT 59601
mshapley@Desktop.org

Correspondence to:
Dept. of Geology and Geophysics
108 Pillsbury Hall
University of Minnesota
Minneapolis, MINN 55455

and

Peter Lesica
Conservation Biology Research
929 Locust
Missoula, MT 59802

To: U.S. Fish and Wildlife Service
P.O. Box 25486, Denver Federal Center
Denver, CO 80225

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Introduction

Howellia aquatilis Gray (water howellia) comprises a monotypic genus in the Family Campanulaceae (McVaugh, 1943). It is known historically from northern California, western Oregon, western and eastern Washington, northern Idaho and northwestern Montana (Shelly and Moseley, 1988); however, many of these populations are thought to be extirpated. *Howellia aquatilis* is considered threatened or endangered throughout its range in the Pacific Northwest (Lesica and Shelly, 1991) and is listed as a Threatened species under the Federal Endangered Species Act.

Howellia aquatilis occurs in ephemeral ponds or the margins of shallow permanent ponds. The apparent physical habitat limitations of *H. aquatilis* in Montana (Lesica, 1990) dictate a need for developing ecological models grounded in the hydrology of the supporting wetlands. A necessary first step toward this goal is the formulation of conceptual models to guide investigations of the heretofore unexamined hydrologic behavior of *H. aquatilis* ponds. The goals of this report are to survey the pertinent hydologic and ecologic literature and the available data, to propose conceptual models of *H. aquatilis* response to hydrologic variables, and to offer a preliminary framework for investigations to test the hypothesized relationships. While we examine hypothetical responses to forest management practices as part of this analysis, a thorough evaluation of such responses awaits testing of the conceptual models presented.

A summary of the ecology and life history of *H. aquatilis* precedes a review of the hydrologic and geologic data availability and setting of the Montana occurrences. The presentation of model scenarios follows. Conceptual models focus on wetland water budgets, basin geometry, and nutrient supply as characteristics with a high likelihood of affecting *H. aquatilis* success in a particular wetland. The evaluation of conceptual models will serve as the first step in understanding hydrologic controls on *H. aquatilis* success, and will identify additional data which must be collected in order to make reliable management recommendations.

Ecology and Life History of *Howellia aquatilis*

Howellia aquatilis is an annual aquatic macrophyte native to the Pacific Northwest United States (Shelly and Moseley, 1989). It has flaccid, usually branched stems 10-100 cm long and alternate, linear, entire-margined leaves, 1-5 cm long. Single flowers occur in the axils of upper leaves. Lower flowers produce seeds under water without opening, while upper flowers have tiny white

corollas and float on the surface of the water. The inferior ovary matures into a 1-to 4-seeded, sausage shaped fruit 5-13 mm long.

In Montana nearly all *H. aquatilis* colonies occur in shallow glacially formed ponds on the floor of the Swan Valley. It germinates in October and remains as a small seedling beneath the winter snowpack. Growth begins in spring beneath as much as 2 m of water. Flower and seed production occur as long as water is present. Once the ponds have dried *H. aquatilis* plants quickly die and decompose.

Nutrients, temperature and water regime strongly influence the composition of aquatic macrophyte communities (Barko et al. 1982, Chambers 1987, Chambers and Kalf 1987, Gosselink and Turner 1978, Keddy and Reznicek 1982, Spence and Chrystal 1970, van der Valk and Davis 1978, Walker and Coupland 1968), and the occurrence of *H. aquatilis* is controlled by these same factors.

Water regime. *Howellia aquatilis* can complete its life cycle only in ponds in which all or at least a portion is inundated in spring and early summer but dry in late summer and fall. *Howellia aquatilis* requires pond drawdown by August/September, but ponds must be flooded from April through July. All else being equal, *H. aquatilis* plants that remain flooded longer grow larger and produce more seeds; however, complete drydown of germination sites is needed for germination of following year's cohort (Lesica 1990, 1992).

Changes in hydrologic regime may have indirect effects on the abundance of *H. aquatilis* by affecting the composition of associated macrophyte communities. Higher and/or more stable water levels may cause a shift in dominant species composition from *Carex vesicaria/Equisetum fluviatile/Sium suave* toward taller, rhizomatous emergents. *Carex atherodes*, a species that occupies hydrologically similar sites to *C. vesicaria*, does not tolerate deep water (Millar 1973, Squires and van der Valk 1992). On the other hand, *Typha spp.* achieve greater abundances in lakes with less fluctuation of water levels (van der Brink et al. 1995) and are adapted to prolonged submergence (Squires and van der Valk 1992). Most mature reed swamps are monocultures that resist invasion by submerged species (Sculthorpe 1967, p. 427). Furthermore, *P. arundinacea* monocultures produce deep, continuous, thatch-like litter that decomposes slowly compared to the patchy, quickly decomposing litter produced by the native marsh vegetation. This dense litter layer may inhibit the growth of seedlings (Bergelson, 1990), thereby excluding *H. aquatilis*. *Howellia aquatilis* is rare or absent with tall, dense emergent vegetation, such as *Typha latifolia* or *Phalaris arundinacea* (Shelly and Moseley 1988, Lesica 1996).

Depth of water also affects algal assemblages (Jones and Mayer 1983), probably due to light attenuation (Kairesalo 1983). Changes in epiphytic algae

and phytoplankton may reduce the amount of light reaching *H. aquatilis* leaves (Spence 1982), causing reduced abundance or extinction. The composition and succession of epiphytic algal communities on *H. aquatilis* is not known.

Nutrients. *Howellia aquatilis* requires organic surface horizons to grow to maturity, and occurs only in pond water with low ionic concentrations (Lesica 1990, 1992). Increased nitrogen or phosphorus may increase the density of epiphytic or planktonic algae, reducing the amount of light reaching leaves, thereby causing a loss of reproductive output. Usually either phosphorus (P) or nitrogen (N) limit the density of algae in aquatic systems, and P is limiting in most lakes (Lund 1965). N:P ratios below 5:1 indicate N limitation, while ratios above 10:1 indicate P is limiting (Chiandani and Vighi 1974, Watson et al. 1990). Rooted aquatic macrophytes obtain the majority of their nutrients from the substrate, while epiphytic algae obtain most nutrients from the water. Nutrient enrichment (especially by P) of the water can cause an increase in the density of epiphytic algae and phytoplankton (Lalonde and Downing 1991, Moss 1969, Phillips et al. 1978, Roos 1983), lowering the light reaching macrophyte leaves, and resulting in a decrease in the density of the macrophytes (Moss 1976, Moss and Eminson 1979; Phillips et al. 1978; Sand-Jensen 1977; Spence 1976, 1982; Vadineanu et al. 1992). The nutrient status and N:P ratio of *H. aquatilis* pond waters is not generally known; the molar inorganic N:P of occurrence P025 was near 55 when sampled.

Water chemistry and nutrient status partly determine which aquatic macrophytes will dominate (Pip 1988). Increased nutrients may favor rhizomatous emergent species such as *Phalaris arundinacea* or *Typha latifolia*, resulting in shading and possible reduction in reproduction or extinction of *H. aquatilis*. Furthermore, increased nutrients generally increase the productivity of reed swamps (Bayley et al. 1985, Neeley and Davis 1985). *Typha latifolia* increases in abundance with increased nutrients, especially N (Neill 1990), and *Phalaris arundinacea* grows best with high P and NH4-N (Haslam 1978).

Temperature. Water temperature of ponds supporting *H. aquatilis* populations was generally low in May (10-13 ^{o}C) but quite warm by August (17-21 ^{o}C); however, water temperature was not correlated with *H. aquatilis* abundance in 1989 (Lesica 1990). Warmer water temperature could result in increased macrophyte biomass, possibly resulting in shading of *H. aquatilis* plants by community dominants. Although temperature by itself does not have a strong effect on the geographic distribution of aquatic macrophytes (Pip 1989), macrophyte biomass increases with increasing temperature (up to 28 ^{o}C) (Barko et al. 1982). Warmer water temperature may also result in increased density of epiphytic algae on *H. aquatilis* (Dale and Swartzman 1984), causing a reduction in reproduction.

Climate

Small, seasonally transient wetlands such as those occupied by *Howellia aquatilis* are likely to be sensitive to climatic variability. The plant has specific habitat requirements reflected in intra - annual, annual and interannual pond water budgets. Although the details of climatic influence on the species are not yet known, it is clear that precipitation and evapotranspiration rates must play a role in the habitat and reproductive success of *H. aquatilis*.

Climatic data are collected at several sites within and surrounding the Montana range of *H. aquatilis*. Long-term records of temperature, precipitation, and snowfall exist for active stations at Lindbergh Lake, Swan Lake, Seeley Lake and Big Fork (NCS). No evaporation data are collected in the Swan Valley; a Class A pan maintained at the Hungry Horse Dam NCS climatic station is the nearest regularly maintained evaporation monitoring site. Limited pond evaporation estimates have been developed for wetlands in the Mission valley (Phillips, 1985); climatic and vegetation contrasts discourage the drawing of inferences between the Mission and Swan valleys, however.

Distributed estimates of mean annual and mean monthly climatic conditions are available from the MAPS Climatic Atlas of Montana (Caprio et al, 1994). These estimates are developed from concurrent climatic station data sets (from the years 1941 to 1970) contoured across Montana and averaged over 3 minute X 3 minute cells within the MAPS database. Estimates of mean precipitation, temperature, potential evaporation and various other climatic and geographic characteristics can be retrieved from MAPS for any point within Montana. Although conveniently regionalized, these estimates do not attempt to estimate interannual variability for these characteristics.

Figure 1 shows the seasonal distribution of precipitation at the Lindbergh Lake and Swan Lake climatic stations, plotted with the Penman estimates of potential evaporation generated by the MAPS Atlas for these sites. Annual average precipitation at the Lindbergh Lake station is 26.86 inches over a 34-year period of record, and the potential (Penman) annual evaporation is 31 inches. Average annual precipitation for the Swan Lake station is 29.45 inches over the period of record, with an average potential evaporation (Penman) of 30.3 inches. The Hungry Horse evaporation pan, located in a grossly similar climatic setting, recorded an average evaporation rate of 29.14 inches for a partial season of measurement over a different period of record. Close to 50% of the annual average precipitation at each site is recorded during the months of November through March (Running et al, 1989; NCS data); most of this seasonal total is probably stored in the winter snowpack and released as spring snowmelt.

Running et al (1989) developed a regional evapotranspiration model that

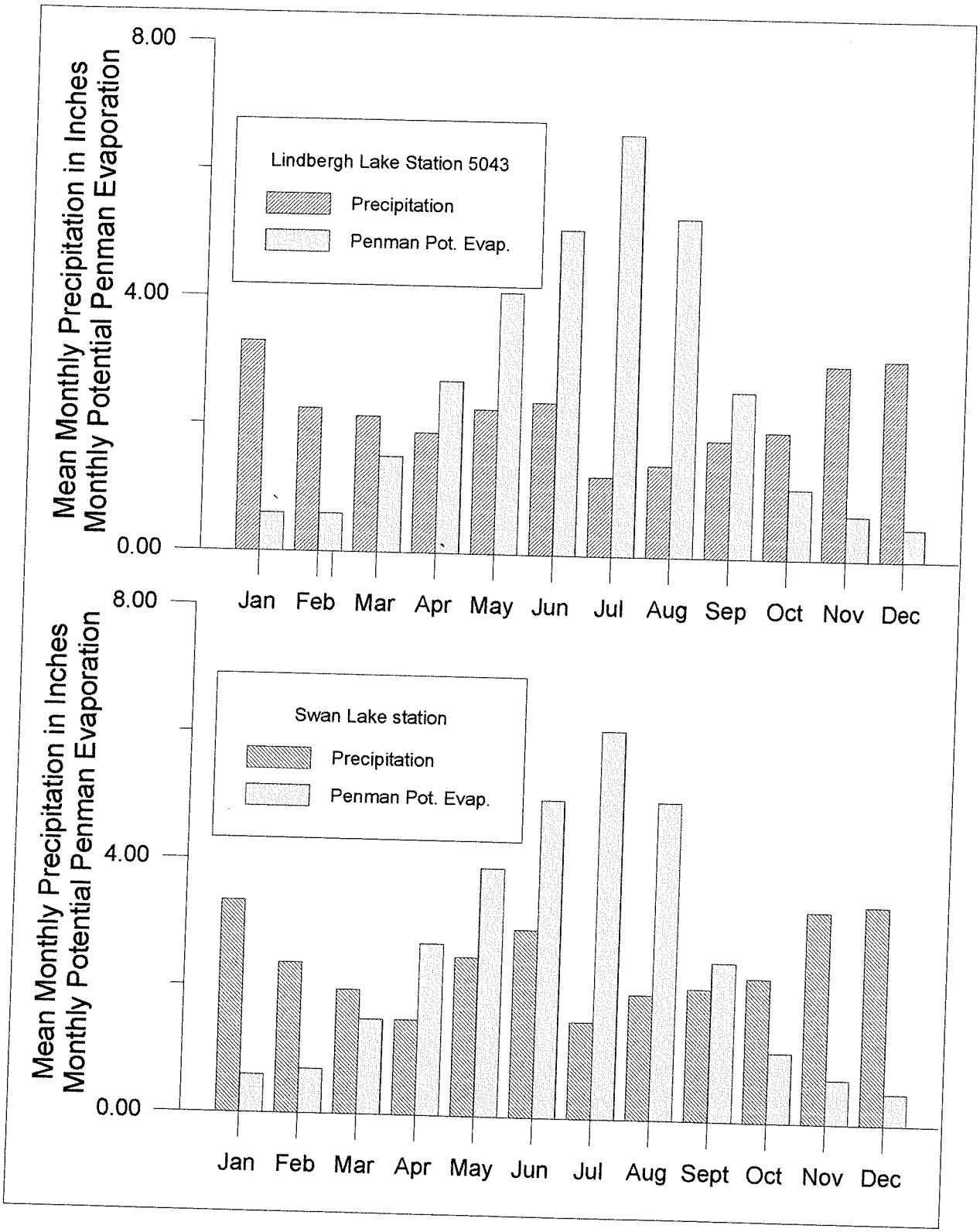

Figure 1. Monthly precipitation and potential evaporation in the Swan Valley.

imagery for the development of leaf area index (LAI) values for 1.1 km cells across the model domain. Other input variables such as soil water holding capacity and insolation were developed for each model cell on the basis of local soils, climatic and topographic information. The model calculates estimates of annual and daily evapotranspiration and photosynthesis rates for each cell. The authors compared the modeled rates to calculated watershed evapotranspiration for two gauged basins within the Swan Valley, finding good agreement between the modeled and runoff-based values.

Through the leaf area index (LAI) model, Running et al calculated annual evaporation of >55 cm (> 21.65 inches) for most model cells in the central Swan Valley incorporating *H. aquatilis* occurrences. The runoff-based estimate of annual evapotranspiration from the upper Swan Valley, used as a check of model output, is 55 cm. Running et al cite other studies (Knight et al, 1985; Running and Nemani, 1985) indicating that most or all of the summertime precipitation is lost to evapotranspiration, and that most recharge to subsoil systems below rooting depth occurs during snowmelt season.

Precipitation and potential evaporation are distributed similarly at the Lindbergh Lake and Swan Lake climatic stations, with wintertime precipitation maxima, secondary peaks in the late spring/early summer, and substantial precipitation deficits with respect to potential evaporation (and in comparison to the Hungry Horse evaporation pan) during the late spring and summer months.

Figure 2 shows the magnitude of the variability shown by precipitation patterns at the Lindbergh Lake station. Standard deviations around the monthly averages are a large percentage of the average values, and the historical lows recorded for the months of July, August and September approach zero. Historical annual totals over a 35-year period of record range from 17.23 to 36.33 inches. Since yearly evaporation and evapotranspiration probably bear an inverse relationship to yearly precipitation, the range in the seasonal water deficit for *H. aquatilis* ponds is probably proportionately wider than the range in precipitation.

While these data provide a general picture of the climatic setting of Montana's *H. aquatilis* habitat, developing quantitative pond water budgets will require more detailed estimates of evapotranspiration losses from the ponds.

Geology and Soils

Ubiquitous glacial deposits of late Wisconsin age (Ostenaa et al, 1990; Witkind and Weber, 1982) underlie the Swan Valley lowlands, except where alluvium, lacustrine and paludal deposits of Recent age have been deposited by modern streams and water bodies. Most *H. aquatilis* sites are underlain by till deposited by one of the two major diverging trunk glaciers occupying the Swan -

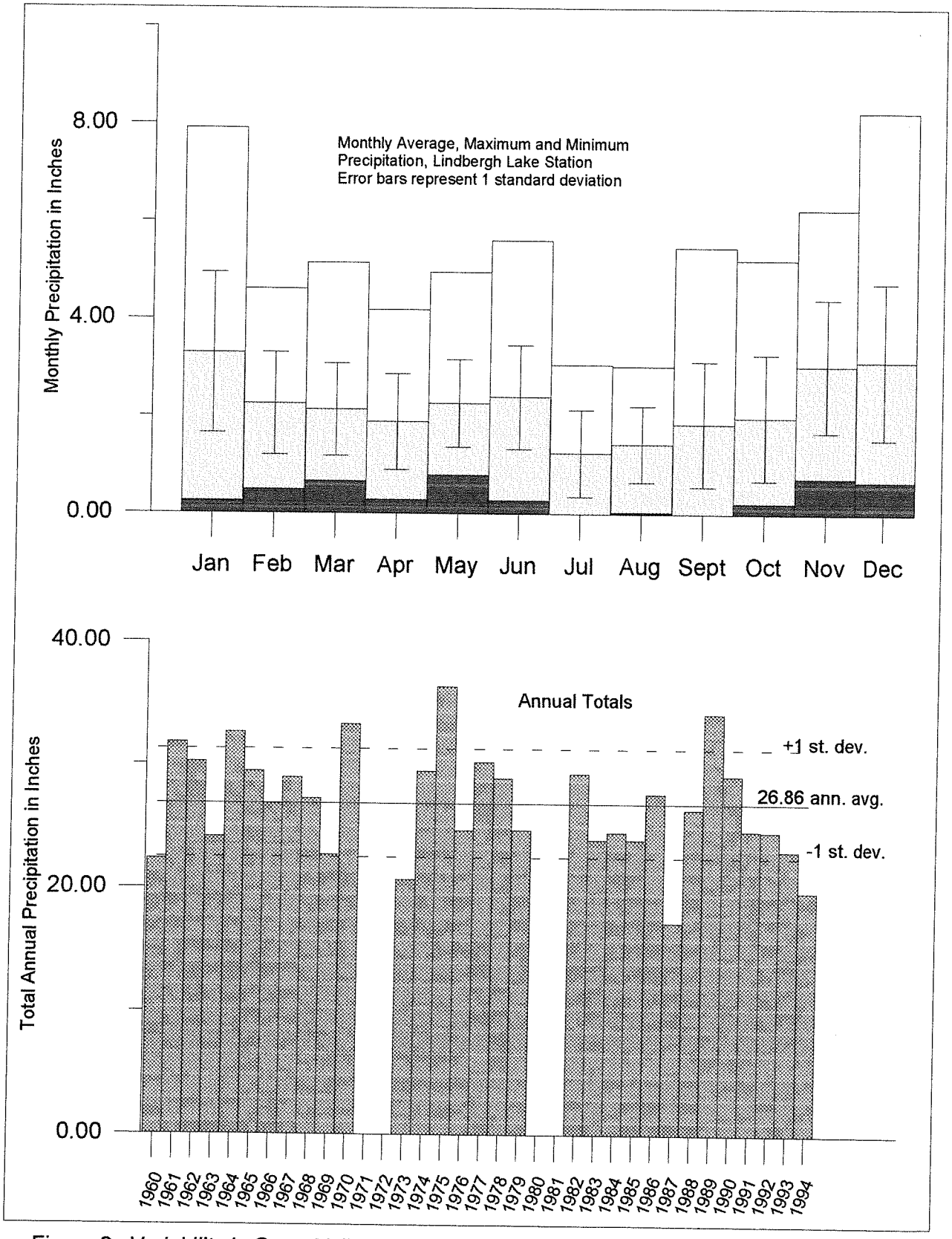

Figure 2. Variability in Swan Valley precipitation.

Clearwater Valley during the later Pleistocene, the Swan Valley and Clearwater Valley Glaciers (Witkind and Weber, 1982). About 60% of the *H. aquatilis* sites are underlain by "valley facies" till deposited by the northward-flowing Swan Valley Glacier. About 5% are underlain by valley-facies till of the south-flowing Clearwater Glacier, and about 25% by deposits of tributary glaciers, especially the Lindbergh Lake and Holland Lake tills. The remainder of the known sites are underlain by less widespread lithologies (e.g., the Holland Lake outwash fan), or cannot be clearly associated with depositional units at the available map scale.

Matrix textures of the Swan Valley and Clearwater Valley tills are described as sandy (Witkind and Weber, 1982), although sediments immediately underlying wetlands are clay-rich where examined (Shapley observations). Prominent fluting and drumlin development of the till sheet in many areas between the Clearwater divide and Big Fork indicate origins as a compressed lodgement till. Sediments of a set of sampled ponds are characterized by a thin (<30 centimeters) organic layer underlain by clay and silt-rich glacial sediments (see Appendix A). The abundant shallow and typically undrained depressions supporting *H. aquatilis* wetlands may in some cases reflect ice-block depressions formed in ablation till (kettles); others appear to occupy undrained topographic lows defined by drumlin development. Pond complexes with superficial similarities in the Mission Valley have been interpreted as pingo remnants (Phillips, 1994).

Most *H. aquatilis* sites are found within 3 soil/landform classification units of Martinson et al (1983). Soil/landform units 26C-7 and 26D-7 incorporate 82 of the identified *H. aquatilis* ponds. Another 8 sites occurring within map unit 26L-7, and the remainder are scattered among 5 or 6 other soil/landform classes. Martinson et al (1983) describe all three major land types as underlain by till and as having medium-textured surface layers influenced by loess deposits. Recognized inclusions within these dominant map units include areas of fine silty soils within topographic depressions, developed on local lacustrine deposits. Landtype 26L-7 is described as displaying comparatively finer-grained subsoil textures in it's dominant soil profiles, and also is described as displaying a more integrated drainage pattern than 26C-7 and 26D-7. Dominant slopes are described as 10-20 percent for all three major land types.

Anderson (1992) described the geology and hydrology of one *H. aquatilis* occurrence located in floodplain sediments of the Swan River. The Swan Oxbow is an atypical *H. aquatilis* site in terms of geologic and hydrogeologic setting, as few of the other known occurrences are associated with extensive alluvial deposits. Anderson described a complex sequence of till, glaciofluvial and glaciolacustrine sediments, and Holocene - aged alluvium composing a relatively permeable, unconfined aquifer underlying the Oxbow wetland complex. He found the Oxbow pond to be a groundwater - flowthrough system, with the

predominant source of recharge to the "Preserve Aquifer" being local infiltration of water from Lost Creek, a tributary of the Swan River. Water levels in the *H. aquatilis* wetlands are controlled by seasonally dynamic groundwater elevations in the underlying aquifer system. Anderson (1992) developed an approximate water budget for the Swan Oxbow wetland, based on measured and estimated aquifer characteristics, measured and estimated hydraulic gradients, and regional estimates of evapotranspiration. Anderson's numerical groundwater flow model provides additional interpretation of aquifer behavior and wetland water budgets at this site.

***Howellia aquatilis* Pond Size, Setting and Geomorphology**

Water body geometry, volume and drainage basin configuration are fundamental to understanding water budgets and the sensitivity of *H. aquatilis* to hydrologic disturbance in the large majority of occurrences which occupy small closed basins (Winter, 1977; Winter, 1983; LaBaugh et al, 1987; Cherkauer, and Zager, 1989). The rate of shoreline recession and the time-variant area of seasonally desiccated substrate available for seed germination are determined by the interaction of pond inflows, outflows and pond geometry. Topography exerts a strong but complex influence on groundwater flow paths, determining in part the groundwater inflow and outflow components of wetland and lake water budgets (Winter, 1983; Meyboom, 1967; Toth, 1963).

Most *H. aquatilis* ponds are small, shallow wetlands lacking obvious surface outflow. Surrounding local relief ranges from very subdued to moderately steep. Few data have been collected describing the variations in local geometry of *H. aquatilis* ponds, or of nearby wetlands lacking *H. aquatilis* populations. Some Montana Natural Heritage Program (MNHP) element occurrence records include qualitative observations of water depth at the time of site inventory. Lesica (1992) included general observations of seasonal drying in 23 *H. aquatilis* sites monitored during 1989. Annual pond stage observations (1988 through 1991) and water depth profiles (1992 and 1994-96) have been collected at 5 sites as part of the Flathead Forest's population monitoring program. No stage/volume relationships are known for H. *aquatilis* ponds in Montana.

The shape of pond basins will affect how changes in flooding regime controls *H. aquatilis* abundance. For small shallow ponds, faster drawdown may mean lower production in average years because plants will have less time to grow and produce seed; in dry years there may be insufficient water to allow reproduction. In large ponds, area of appropriate habitat may decline, but pond subpopulation will not go extinct. For steep-sided ponds, slower drawdown may mean a loss of some habitat in average years and all habitat in wet years. In

gently-sloping ponds there may be a shift in the position of appropriate habitat but pond subpopulation will not go extinct.

In shallow ponds, lower water levels may mean lower production on average years and no production in dry years. In deeper ponds there may be a shift in the position of appropriate habitat but pond subpopulation should not go extinct. For steep- sided ponds, higher water levels may mean a loss of some habitat in average years and all habitat in wet years. In gently-sloping ponds there may be a shift in the position of appropriate habitat but pond subpopulation should not go extinct.

Small changes in timing and amount of water input will affect small shallow ponds more than larger, deeper ponds. However, under optimum conditions, shallow ponds provide more appropriate habitat than steep-sided ponds. On the other hand, under changing conditions steep-sided ponds are more likely to provide refuges from local extinction.

Most *H. aquatilis* ponds are estimated to be no more than 5 acres in size. Little topographic information at the scale of the individual pond can be discerned from available 1:24,000 scale mapping. Topographic maps show 8 sites with channelized surface water inlets and 13 sites with channelized surface water outlets; the remainder lack mapped surface drainage. Field inspection indicated that some ponds lacking mapped surface drainage do have ephemeral inflowing and/or outflowing streams, however. The available topographic information is of insufficient resolution to show drainage basins for most *H. aquatilis* ponds. Careful instrumental surveys would be required to define many of the basin areas.

Inspection of 1:24000 scale topographic mapping of the *H. aquatilis* sites suggests some qualitative geomorphic distinctions not well distinguished by geologic or soils map units. The Condon Creek *H. aquatilis* occurrence cluster occupies ponds near the toe of the regional change in slope defining the contact between the 'valley' and 'foothill' till facies of Witkind and Weber (1982). The till surface is pitted and generally lacks drumlinoid features, and topographic gradients are dominated by the regional slope. The Cilly Creek occurrence cluster occurs within prominently drumlinoid terrain, with several sites adjacent to locally steep slopes and overall relief strongly influenced by local topographic features. The Lindbergh Lake cluster occurs across a pitted but well-defined sloping surface of till(?), extending downgradient from the outlet of Lindbergh Lake and incised by the Swan River. This area displays somewhat more integrated drainage than the Condon Creek and Cilly Creek clusters. Several *H. aquatilis* occurrences within the Lindbergh Lake cluster occupy ponds having mapped interconnecting streams, and the underlying surface has a stepped cross-section, with pond surfaces interrupting the general northeastward land slope.

Water chemistry of *Howellia aquatilis* sites

Only limited data describing the water chemistry of *H. aquatilis* ponds are available. Montana Natural Heritage Program files contain laboratory pH, specific conductivity and alkalinity measurements for water samples collected from 10 *H. aquatilis* sites in 1987. Reported pH values range from 6.8 to 7.7, specific conductance from 54 to 322 microsiemens/cm, and alkalinitity from 32 to 130 milligrams/liter as $CaCO_3$. Habitat characterizations by Lesica (1992) included seasonal field monitoring of temperature, dissolved oxygen, pH, and specific conductivity in 23 H. aquatilis ponds and in 10 similar wetlands lacking *H. aquatilis* populations. Generally aqueous geochemistry of the surveyed wetlands was dilute and circumneutral in character. pH ranged from about 6.1 to about 7.9, reflecting both seasonal and inter-site variability. Specific conductivity values for the 23 sites monitored were all below 300 microsiemens/cm, with 16 of the sites remaining near or below 100 microsiemens/cm during the period of monitoring. Dissolved oxygen concentrations ranged widely, with several of the monitored sites showing notably depressed values (< 5 mg/l) throughout the 1989 growing season. Ionic compositions were not determined as part of this study.

Statewide wetland water and sediment sampling conducted by the Montana Department of Environmental Quality (DEQ) in 1994 included one-time sampling of one *H. aquatilis* site (MNHP EO P025) and an adjacent pond not known to contain a *H. aquatilis* population. These sites, part of the Condon Creek pond cluster, are designated WET15 and WET16 in the DEQ data set. P025/WET15 is considered marginal *H. aquatilis* habitat, as it is among the *H. aquatilis* ponds with a narrow drydown zone and an extensive semipermanent water body (Lesica observations). Data from these two sites include field measurements of pH, specific conductivity and temperature, complete analyses of major inorganic ions and nutrients, and analyses of a selected suite of trace elements from the water column and from wetland sediments. Biological sampling (benthic invertebrates and diatoms) was also a part of the DEQ program. These are the only comprehensive water chemistry data available for closed-basin *H. aquatilis* sites in Montana.

These data showed the ponds containing MNHP element occurrence P025 and DEQ sampling site WET15 to have been mildly acidic (pH of 6.1) at the time of sampling, with dilute calcium-bicarbonate chemistry and specific conductivity of 75 and 53 microsiemens/cm respectively (Shapley, 1995). At the time of the DEQ sampling, total organic carbon, total phosphorous and ammonium concentrations in WET15, which has experienced logging to the pond shoreline, were about twice those in P025/WET16, which retains a buffer of forest. Orthophosphate concentrations were essentially identical in the two

of forest. Orthophosphate concentrations were essentially identical in the two ponds at the time of sampling. Water in these two ponds was undersaturated with respect to calcite at the time of sampling. The more concentrated *H. aquatilis* ponds monitored by Lesica (those with specific conductance in the range of 200 to 300 microsiemens/cm) may be calcite -saturated, however.

Anderson (1992) reported data from streams, groundwater in two different aquifer systems, and the Swan Oxbow itself. Total dissolved solids concentrations of 140 and 116 milligrams per liter (mg/l) for this groundwater-supported wetland indicate specific conductance values within the range reported by Lesica (1992) for more typical *H. aquatilis* habitat. Samples from spring discharges and wells supplied by the unconfined "Preserve Aquifer" show dissolved solids concentrations of 180 mg/l and less, indicating groundwater specific conductance within the range of *H. aquatilis* sites in the Swan Valley. The pH of pond water was essentially neutral when sampled, while groundwaters were found to be slightly alkaline. Groundwater sampled from shallow piezometers was found to be in near-equilibrium or slightly oversaturated with calcite. During the spring of 1991, Anderson found the dissolved solids concentration of the Oxbow was less than that of Lost Creek, interpreted to be the principal source of aquifer recharge contributing to the Oxbow. This was attributed to dilution of discharged groundwater by direct precipitation and snowmelt.

Pond Hydrology

Numerous studies have examined the hydrologic behavior of lakes and small surface water bodies such as the Swan Valley wetlands, using a variety of different hydrogeologic (Meyboom, 1967; Labaugh et al, 1987; Cherkauer and Zager, 1989), geochemical (Swanson et al, 1988), and isotopic (Hunt et al, 1996) techniques. The relative importance of different inflow and outflow mechanisms influences lake or pond hydroperiod, geochemistry, and ecological functions of naturally functioning systems (Swanson et al, 1987; Poiani et al, 1995). The sensitivity of lake/pond hydrology to different types of disturbance is therefore also dependent in part on the mechanisms by which water moves into and out of lakes and ponds.

Howellia aquatilis pond water budgets provide an expression of important relationships between pond inflows and outflows which, in combination with pond geometry and antecedent conditions, govern the availability of suitable *H. aquatilis* habitat from year to year. The most general expression of the water budget of a *H. aquatilis* pond with unknown groundwater relationships is governed by the principle of conservation of mass, and can be given as:

$$(I_{gb} + I_{ge} + I_s + P) - (ET + O_g + O_s + S_p + S_g) = 0$$

where I_s is surface water inflow, I_{gb} and I_{ge} are groundwater inflow from the local topographic basin and from any larger area contributing groundwater respectively, P is direct precipitation incident to the wetland surface, ET is evapotranspiration (including free-water evaporation), O_s and O_g are surface water and ground water outflow components respectively, and S_p and S_g are the changes in water stored in the pond and in the associated groundwater system.

In this form, the water budget equation is not time dependent. Time dependent forms may be written as the summation of individual water budget components over some period of interest, i.e., an annual budget may be expressed as the summation of monthly time budget components.

Groundwater inflow in this equation includes both shallow subsurface flow recharged within the immediate topographic basin (local flow) and any discharge from larger-scale flow systems. An important role for seasonal shallow groundwater flow from seasonally recharged flow systems is consistent both with published research on the mechanisms of runoff generation in forested landscapes, and with qualitative observations of shallow groundwater behavior within the soil/land types supporting *H. aquatilis* ponds (Dean Sirucek, personal communication). Seeps observed in roadcuts constructed in soil/land type 26D-7 indicate the development of shallow saturated flow conditions, possibly controlled by shallow stratigraphy. Studies in humid forested areas indicate that a large fraction of runoff generated by small basins has a significant subsurface residence time (Dincer et al, 1970; Sklash et al, 1976; Sklash and Farvolden, 1976; Buttle and Sami, 1992). Soils reportedly do not freeze in the Swan Valley during most years and overland flow is considered rare (Running et al, 1989). Even in boreal and arctic settings where seasonal soil freezing is intense, subsurface flow has been shown to be a major component of snowmelt runoff generation (Gibson et al, 1993; Obradovic and Sklash, 1986).

Surface drainage is known to influence pond water levels at some *H. aquatilis* sites (Shapley observations). A relatively small percentage of the known sites have mapped inflow or outflow channels, however, and the stabilizing effects of surface outflow on pond water levels are inconsistent with the habitat requirements of *H. aquatilis'* if sustained into the late summer and fall. We believe that streamflows and outlet elevations are influential in a relatively small minority of *H. aquatilis* sites in the Swan Valley.

Where the catchment is very small relative to the pond volume, direct incident precipitation might dominate a pond's input, with both surface water and groundwater inflow volumes relatively minor. A calculation using the ET estimates of Running et al (1989) and average precipitation from the Lindbergh Lake station indicates that available inflow (calculated as the difference between

ET and precipitation, and assuming that recharge does not enter larger flow systems) approximates or exceeds direct precipitation when catchment diameters exceed twice the pond diameter. Most ratios of catchment to pond diameter are believed to be higher than 2.

The importance of groundwater outflow is probably variable among *H. aquatilis* ponds. Observations of several *H. aquatilis* ponds suggest a clay-rich character to the underlying till. In a review of the hydraulic characteristics of glacial sediments, Fetter (1994) cites several studies showing hydraulic conductivities in the range of 10-8 to 10-7 cm/sec for unweathered basal tills with high clay and silt content. Hydraulic conductivities in this range imply seepage outflow rates which are low relative to potential evaporation rates in the Swan Valley. Groundwater outflow from lakes or ponds may also be precluded simply by potentiometric relationships, particularly at times of "focused recharge" around water body margins (Winter, 1983). However, in at least one site (P002) *H. aquatilis* reportedly grows in water 5-6 feet deep (MNHP records; Steve Shelly, personal communication), suggesting seasonal pond stage declines far in excess of what can be accounted for by evapotranspiration. One possible explanation for this observation is a comparatively high rate of groundwater seepage from this pond. It is also possible that pond desiccation may fracture the clay-rich substrate of *H. aquatilis* ponds, resulting in temporary increases in pond seepage potential.

Throughflow in a local groundwater flow system is believed to be the most important hydrologic control at Swan Oxbow Preserve, an atypical *H. aquatilis* site which has been the subject of hydrologic investigation (Anderson, 1992).

Many of the *H. aquatilis* occurrences are found in closely spaced clusters of ponds. The dynamics of groundwater flow between depressions in hummocky terrain are complicated; complex saturated and unsaturated gradients link such pond/groundwater systems (Winter, 1983; Swanson et al, 1988; Toth, 1963). Pond stage and water chemistry are determined in part by the position of a pond along groundwater flow paths (Labaugh et al, 1987; Donovan, 1993; Meyboom, 1967). Complex interpond groundwater flow probably occurs around at least some *H. aquatilis* ponds. Whether such pathways are important to the hydrologic behavior of *H. aquatilis* habitat depends on whether the water budgets of individual ponds are significantly influenced by inter-pond groundwater flow.

Pond Hydrology and Forest Management

The hydrologic effects of timber management are of obvious interest with respect to *H. aquatilis* habitat, since timber harvest is widespread in the Swan Valley. Numerous studies in other areas have investigated the effects of forest canopy removal on snowpack accumulation, with most showing significant

increases in snowpack as interception is reduced or eliminated (e.g., Woo and Heron, 1987; Seuna, 1988). Along with increased snowpack, lack of forest canopy tends to result in accelerated spring snowmelt, as the snowpack surface is exposed to more direct insolation (Woo and Heron, 1987). Runoff peaks generated by snowpack ablation may be advanced by 1 - 2 weeks in logged areas relative to adjacent areas with coniferous forest canopy (Cheng, 1989).

Studies in both rainfall dominated (Hicks et al, 1991) and snowpack dominated (Cheng,1989) environments have demonstrated significant increases in water yield (measured at the watershed scale) as a result of forest canopy removal. Other studies directly measuring soil moisture response show increases in moisture content, implying increased rates of recharge to shallow groundwater systems (Adams et al, 1991; Troendle and Nilles, 1987).

Persistence of the positive water balance perturbations resulting from forest removal varies. Long term paired-basin studies in rainfall dominated environments have shown runoff effects persisting for as long as 25 years after harvest (Hicks et al, 1991). Data from certain watersheds show a short period of post-logging water yield excess followed by a period of water yield deficiency relative to control basins, an effect ascribed to the rapid development of dense riparian hardwood vegetation in response to the removal of the shading forest canopy (Adams et al, 1991; Hicks et al, 1991).

Studies examining nutrient fluxes in soil and subsoil of forested environments often show increases in soluble nitrogen concentrations in response to forest removal (Stark, 1979; Troendle and Nilles, 1987). Some studies in forested peatlands (geochemically dissimilar to shallow Swan Valley groundwater) also suggest increased phosphorous fluxes in shallow groundwater systems following logging (Ahtiainen, 1988). Troendle and Nilles (1987) attempted to directly evaluate saturated groundwater chemistry response to logging. They found increases in nitrate and chloride concentrations relative to a control site, and increases in groundwater export of all other dissolved constituents examined as a result of enhanced groundwater flux. Where the persistence of enhanced subsurface nutrient concentrations have been analyzed, however, nutrient effects are short-term (Stark, 1979; Knight et al, 1985).

Finally, forest disturbance is inferred to have effects on microclimate which could affect both pond water budgets and the immediate physical environment of H. aquatilis. Removal of surrounding forest may increase solar energy input to the pond and increase average wind speeds at the pond surface, thereby increasing evaporation rates. The magnitude of these effects is related to the size of the pond (and consequently the diameter of the opening in the established forest canopy), the height of the canopy and the effectiveness of any forest buffer left surrounding the wetland. Generally, a small pond with higher

surrounding canopy will receive less direct insolation and lower wind speeds than a larger pond or one with lower surrounding canopy, and will therefore be more susceptible to perturbation if forest cover is removed.

The Models

We initially examined six possible hydrologic configurations for *H. aquatilis*-supporting wetlands, incorporating different elements of the generalized water budget, prior to selecting two which we consider most useful for inclusion in conceptual models of ecological response.
Our models assume equilibrium over a period of years, with no net change in storage within ponds or within the associated groundwater systems. This is a simplifying assumption serving as a starting point for consideration of the *H. aquatilis* pond system. Changes in the storage components do occur with changes in pond volume and water table elevation, when inflow and outflow components are unequal. The magnitude, variability and timing of intra-annual changes in the surface storage component of pond water balances are critical to the life cycle of *H. aquatilis*. Under the assumption of longer-term (years to decades) hydrologic equilibrium, interannual pond storage changes represent variability around some "average" annual trend. Under certain conditions, interannual variability reduces the reproductive success of *H. aquatilis* by 1) reducing suitable habitat, 2) by changing the spatial distribution of suitable habitat within or between ponds, or 3) by limiting the ability of *H. aquatilis* to take advantage of suitable habitat due to unfavorable antecedent hydrologic conditions. Increases, decreases and redistribution of suitable habitat in response to longer term hydrologic change are tied to the interaction between changes in the storage components and pond geometry.

Model 1 includes only surface water inflow from runoff and direct precipitation to the wetland surface. Subsurface inflow is treated as unimportant. Outflow is through evapotranspiration from the wetland and littoral vegetation, and by unsaturated seepage outflow through the pond bottom. In this model, the pond is a source of recharge to groundwater, possibly resulting in mounding of an underlying water table. The water balance equation for this model is

$$(I_s + P) - (ET + O_g + S_p + S_g) = 0$$

and, if long-term equilibrium conditions are assumed (no change in the storage factors), simplifies to

$$I_s + P = ET + O_g$$

We eliminated this model from detailed consideration after reviewing published studies generally showing subsurface flow to be an important hydrologic process in humid forested settings (see above).

Model 2 includes shallow groundwater inflow from local flow systems (recharged within the immediate topographic basin) and direct precipitation to the wetland surface. Groundwater flow may be controlled in part by permeability contrasts between the weathered soil horizons and underlying unweathered glacial deposits. Surface runoff from beyond the confines of the wetland is considered unimportant in this scenario. Outflow is through evapotranspiration from the wetland and from marginal vegetation, and through seasonally saturated or unsaturated seepage. In this scenario the pond may bear a seasonally variable relationship to groundwater, having a flow-through relationship during certain times of year, and being a locus only of groundwater discharge at other times. Gradient reversals in shallow groundwater systems connected to the wetland may occur and may be important in water budget and solute dynamics. The water balance equation in this model is

$$(I_{gb} + P) - (ET + O_g + S_p + S_g) = 0$$

and if long-term equilibrium is assumed, simplifies to

$$I_{gb} + P = ET + O_g .$$

Model 3 includes channelized surface water inflow and/or outflow as important water budget components, in addition to the shallow groundwater inflow and outflow and direct precipitation components considered important in models 2 and 3. In Model 4, outlet elevation may influence the hydrograph of the wetland; migration of the drydown zone in response to positive water budget changes is considered to be limited by the spill elevation of the basin. Wetlands may bear either recharge, discharge or flow-through relationships to groundwater. The water balance equation is

$$(I_{gb} + I_s + P) - (ET + O_g + O_s + S_p + S_g) = 0$$

and, under equilibrium assumptions,

$$I_{gb} + I_s + P = ET + O_g + O_s.$$

Some *H. aquatilis* ponds have at least seasonal surface water inflows and/or outflows; however, we believe these ponds comprise a small minority of *H. aquatilis* sites. Therefore the models considered in depth do not include surface water outflow. Nevertheless the influence of surface water drainage needs to be evaluated through field investigations on a site-by-site basis.

Model 4 includes shallow groundwater inflow and direct precipitation incident on wetland surfaces, as in models 2 and 3. Model 4 is influenced by fine-grained, low-permeability clay and silt deposited early in the post-glacial history of the pond. This material allows groundwater inflow and potentially outflow in marginal littoral areas, but limits the potential seepage outflow during lower pond stages. Actual recharge to the groundwater system (pond outflow) depends on the direction and magnitude of groundwater gradients; ponds may have seasonally variable recharge, flowthrough or discharge relationships to groundwater. Most pond outflow in this model is considered to be evapotranspiration from the wetland and surrounding vegetation. The water balance equation is

$$(I_{gb} + P) - (ET + S_p + S_g) = 0$$

and, where equilibrium is assumed,

$$I_{gb} + P = ET$$

This model represents the simplest configuration consistent with what is known about *H. aquatilis* ponds, and forms the basis of the "Local Model" developed below.

Model 5 includes groundwater inflow from flow systems extending beyond the immediate topographic basin containing the wetland ("intermediate" or "regional" systems in the sense of Toth, 1963). Local groundwater discharge and direct incident precipitation still constitute important inflows, but with an additional contribution from the larger flow systems. Outflows consist either of evapotranspiration plus groundwater outflow (in a flow-through case) or evapotranspiration alone (in the case of a groundwater discharge setting). The water balance equation is for this hydrologic configuration is

$$(I_{gb} + I_{ge} + P) - (ET + O_g + S_p + S_g) = 0$$

and under the equilibrium assumption

$$I_{gb} + I_{ge} + P = ET + O_g$$

with the groundwater inflow and outflow components involving both locally recharged and larger-scale flow systems. This model forms the basis of the "Extended Model" expanded below.

Some *H. aquatilis* occurrences (such as the Condon Creek cluster) occupy wetland sites where possible discharge from larger-scale groundwater systems might be anticipated strictly on topographic grounds. However, in the

case of the Condon Creek sites, the the presence of very dilute water undersaturated with calcite argues against the discharge of groundwater with long residence time.

Model 6 includes the same set of inflow and outflow components as in the previous model, but with a shallow groundwater flow system linking adjoining wetlands. In this model (a special case of Model 5), pond water and solute budgets may be dependent in part on the status of upgradient ponds and on transient gradients of the common groundwater flow system. For reasons of simplification, we did not give further consideration to interpond effects in this analysis. Such effects may be important at some sites, however, and should be considered in the formulation of study field designs.

Conceptual Models

For the purposes of this analysis, we selected two alternative hydrologic models as the basis for evaluating data needs, proposing important hydrologic controls on *H. aquatilis* success, and evaluating the possible responses of *H. aquatilis* populations to hydrologic perturbations. The Local and Extended models are likely to apply to most *H. aquatilis* sites and can serve as bases for field study design. We rejected from further consideration models which rely on significant overland flow and models which do not include shallow groundwater inflow as an important hydrologic input. We view these as inconsistent with published research on runoff mechanisms in similar settings. We also set aside for the present models which incorporate channelized surface water inflow, as stream inflows seem to be rare among *H. aquatilis* ponds. Channelized outflows are considered in the context of possible hydrologic changes in pond water budgets and water level stability.

The Local model is based on Hydrologic Model 4, assuming strictly local subsurface inflow recharged within the immediate topographic basin and volumetrically small groundwater outflow relative to evapotranspiration. The Extended model is based upon the components of models 5 and 6, allowing for both interpond groundwater flow and possible discharge from larger scale flow systems. By making simplifying assumptions, the Local Model can be subjected to a semi-quantitative evaluation which is useful as a sensitivity analysis. The Extended Model cannot support such evaluations without evaluating groundwater components.

Hydrologic components of the Local and Extended Models represent two possible points along a gradient of increasing influence of larger-scale groundwater flow systems. While part of a continuum of possible hydrologic configurations, the two conceptual models lead to different evaluations of

ecological sensitivities and may suggest qualitatively different management strategies for *H. aquatilis* habitat.

The Local Model

The Local Model (Figure 3) assumes that direct precipitation and shallow subsurface flow recharged seasonally within the immediate topographic basin are the dominant sources of pond inflow. Overland flow, channelized inflow and discharge from larger-scale groundwater systems are absent or unimportant. Outflow occurs dominantly through evaporation from the pond surface and transpiration by emergent and phreatophytic vegetation. Seepage outflow to local groundwater systems is limited by unfavorable pond-bottom hydraulic characteristics or by groundwater gradients, and is small compared with evapotranspiration. We assume very low solute loading from the shallow groundwater flow system to account for the low concentrations of dissolved solids in evaporative pond systems.

Since hydrologic inputs are from within the local basin, water balance and water quality effects occur only in response to perturbations within the basin. We ignore airborne transport of nutrients and regional effects on precipitation.

A first approximation of the relative importance of the direct precipitation and shallow subsurface runoff inflow components of ponds conforming to this model can be derived by making two additional assumptions: 1) No groundwater recharge within the local basin enters larger groundwater flow systems, and 2) Shallow groundwater recharge and direct precipitation inflow both occur as essentially instantaneous events during spring snowmelt. The first assumption is consistent with the local flow system framework adopted in this model. The second assumption is generally supported by studies of soil water budgets in forested montane settings that show recharge beyond the rooting zone to be a highly seasonal occurrence driven by snowmelt (Knight et el, 1985; Running et al, 1989). Direct precipitation to the wetland surface of course occurs at all times of the year. A review of the Swan Valley precipitation data suggests, however, that 70-75% of annual precipitation occurs either as snow or as spring and early summer rainfall at times when the seasonal wetlands supporting *H. aquatilis* are near maximum extent; only 25 - 30% of precipitation occurs as rainfall during the summer/fall period of pond drydown. It is therefore reasonable as a first approximation to consider direct incident precipitation to affect a constant wetland area, despite the characteristic seasonal transience of *H. aquatilis* ponds.

This line of reasoning leads to a simplistic but useful index of pond inflow for the Local Model. For the purposes of this indexing, total inflow can be expressed as

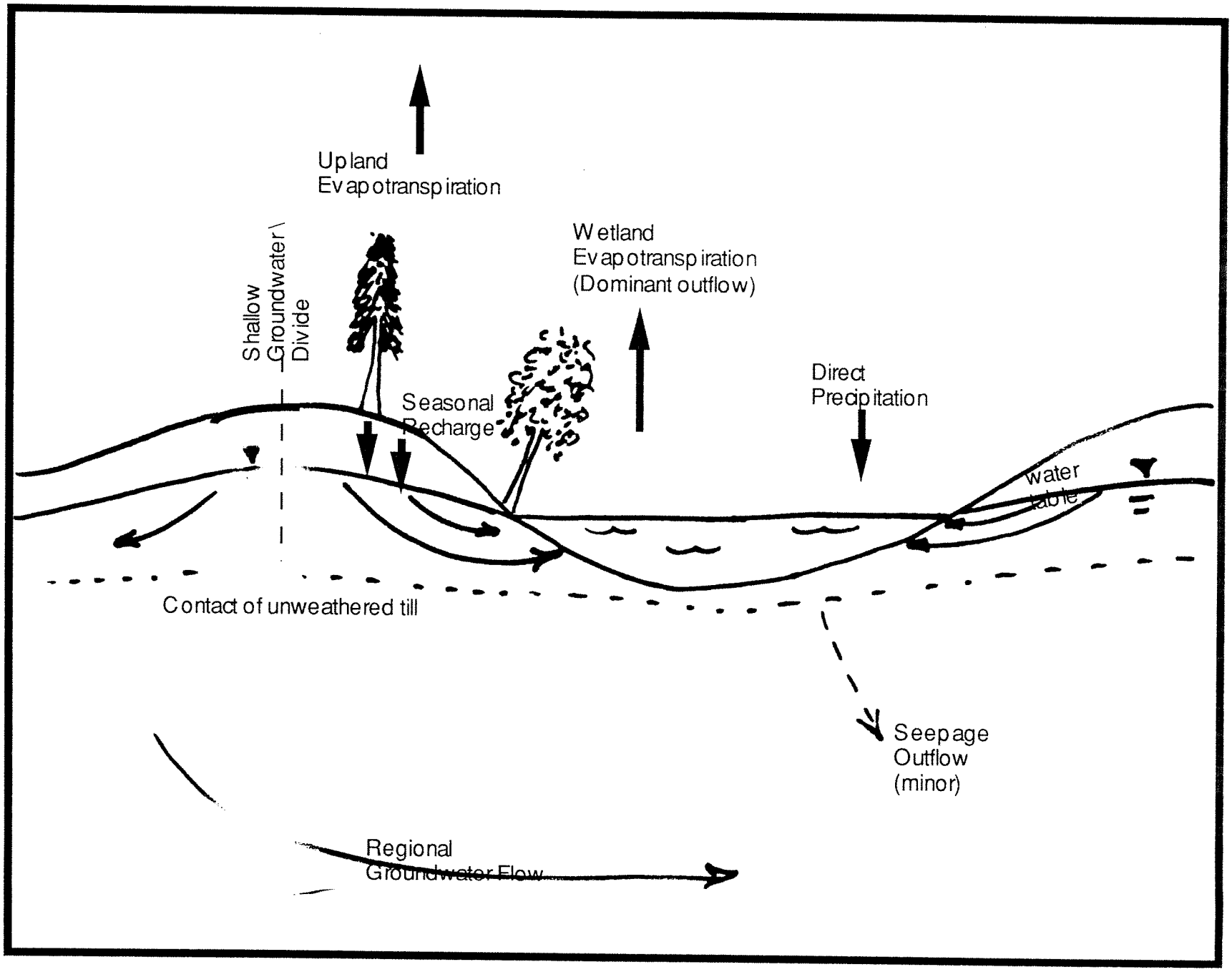

Figure 3. Hydrologic components of the Local Model.

$$I_t = (P * A_w) + [(P - INT - ET_u) * (A_b - A_w)]$$

where I_t is total inflow to the wetland, P is precipitation, INT is interception by the forest canopy, ET_u is the average evapotranspiration from upland portions of the basin, and Aw and Ab are the wetland and total basin areas, respectively. Where A_w/A_b is large, the component of inflow attributable to direct incident precipitation is comparatively large. Where A_w/A_b is small shallow groundwater is a proportionately greater contributor. Approximately equivalent contributions of direct precipitation and shallow groundwater inflow are expected where $(A_b - A_w)/A_w = P/(P-ET)$; in the Lindbergh Lake area, with estimated annual evapotranspiration of 23.6 inches (Running et al, 1989) and average annual precipitation of 26.9 inches (NCS data), equal contributions would occur where $(A_b - A_w)/A_w \simeq 8$.

The Local Model therefore implies that the water and solute budgets of ponds with low values of Aw/Ab are more susceptible to perturbations resulting from disturbances (land management activities, fire, interruptions of groundwater flow paths, etc.) in upland basin areas. Stage hydrographs for ponds with proportionately large upland basins might peak and decline later than those for geometrically similar ponds with proportionately small upland basins; dissolved solids loads, alkalinity and other geochemical characteristics might be expected to correlate negatively with A_w/A_b values as a reflection of proportionately larger contributions from shallow groundwater flow systems.

Pond drydown in the Local Model is driven predominantly by evaporation from the pond surface and transpiration from emergent and littoral vegetation. Assuming instantaneous annual inflow, the amount of habitat made available for *H. aquatilis* seed germination is a function of pond area, initial pond stage at the beginning of the drydown cycle, annual evapotranspirative outflow, and geometry of the pond. For a given starting pond stage and evapotranspiration rate, ponds with constant low-angle slopes within the seasonal range in stage will expose more area for potential seed germination than ponds with steeper slopes within the seasonal range in stage, assuming evaporation rates to be linear and the area of seasonally dessicated pond bottom to be a function of the sine of pond slope (Figure 4). Since seed production is probably enhanced by longer growing season submergence, the optimal *H. aquatilis* site may be a pond with a parabolic contour within the seasonal range of water level. During favorable conditions, such a pond geometry may provide relatively lengthy submergence and high seed production, a large area of potential germination success, and (in contrast with a flat-bottomed, "pan - shaped" basin) a remnant area of drydown available for germination during suboptimal years of positive water balance.

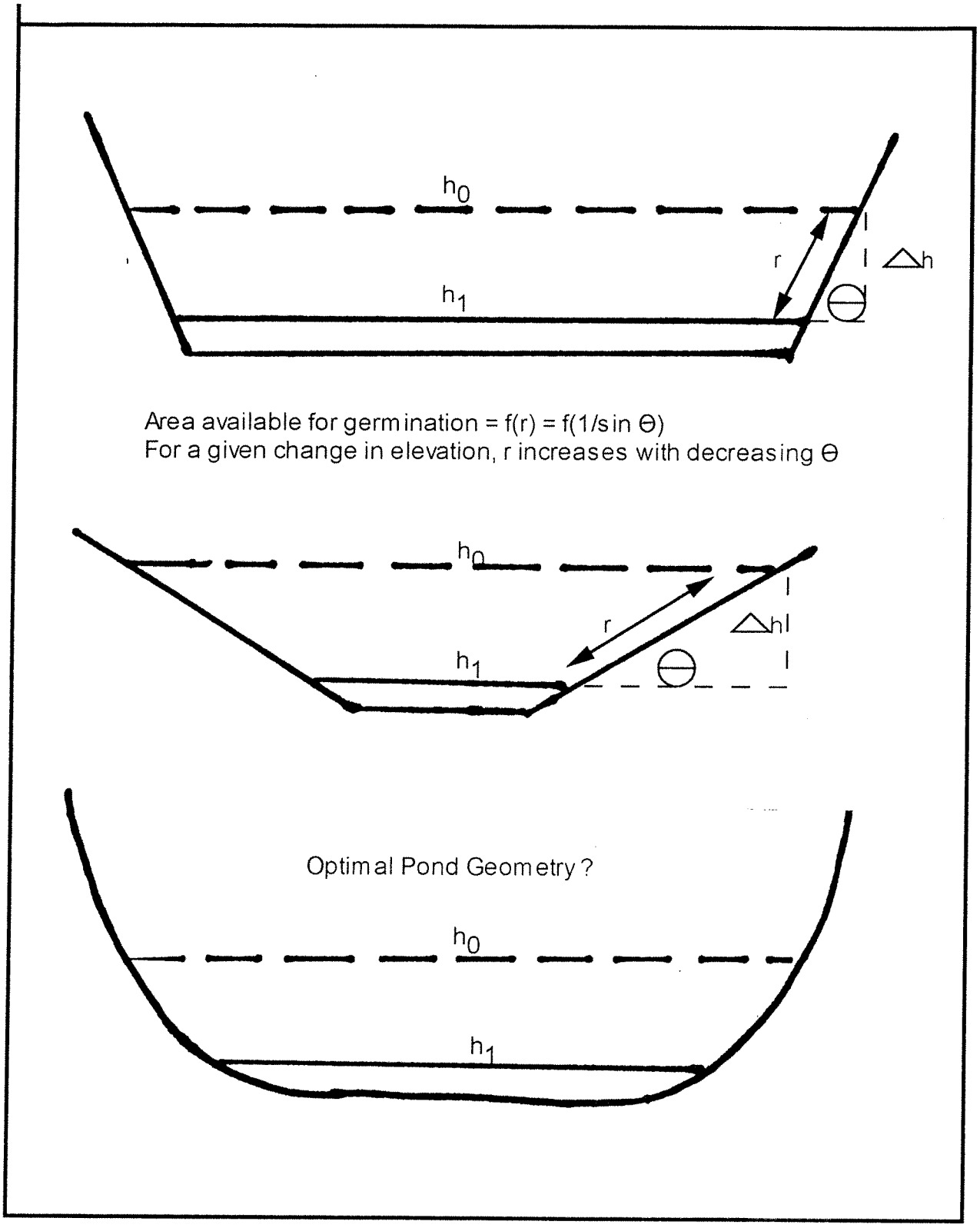

Figure 4. Hypothetical *H. aquatilis* pond geometries.

In the Local Model, the sensitivity of *H. aquatilis* to perturbations in water balance and in a pond's drydown cycle depend on these geometric relationships and on limiting factors of pond geomorphology such as surface water drainage. For conical pond cross-sections of different slope, water balance changes resulting in the same change in mean pond stage may result in greater lateral displacement of the zone suitable for *H. aquatilis* germination in low - angle ponds than in ponds with steeper cross-sections. Lateral offsets of germination habitat are unlikely to greatly reduce *H. aquatilis* densities, however, since seeds migrate readily within ponds by floating (Lesica observations). Positive water balance changes which lead to channelized pond outflow over an extended portion of the year will result in greater stability in pond water levels and a reduction in *H. aquatilis* habitat suitability in such a pond.

Positive water balance changes (e.g., increases in precipitation or decreases in evapotranspiration due to climatic or vegetation changes) will extend the average season of inundation in ephemeral ponds, resulting in more favorable conditions in sites presently unlikely to support plant growth and flowering. Seed production may increase in shallow ponds, and previously unsuitable shallow ponds may become candidates for *H. aquatilis* colonization. Conversely, deeper ponds with convex profiles may experience a reduction in available germination habitat. Ponds of any size may experience unfavorable narrowing of the drydown zone if surface outflow is established.

Negative water balance changes (e.g., decreases in precipitation or increases in evapotranspiration) lower average water levels in semi-permanent ponds, resulting in more favorable conditions in sites presently unlikely to provide large areas suitable for seed germination. Germination success may increase in deeper ponds with convex or flat-bottomed profiles. Ponds with narrow drydown zones controlled by surface water outlets may develop suitable hydrographs and become candidates for *H. aquatilis* colonization if pond levels drop below outlet elevations. Conversely, shallower ponds may become unsuitable for growth and seed production.

In the Local model, the effects of water balance changes affecting *H. aquatilis* habitat on a larger scale (i.e., pond clusters or the Swan valley as a whole) depend on the distribution of pond and catchment geometry across the affected landscape, and on the ability of *H. aquatilis* to populate newly favorable habitat. The frequency distribution of pond/catchment geometries may be either favorable or unfavorable for *H. aquatilis* colonization of new sites in response to hydrologic change reducing the suitability of occupied sites. In a landscape with a high frequency of ponds presently too dry on average for *H. aquatilis* success, positive water balance changes result in a net increase in suitable *H. aquatilis* sites. Negative water balance changes under this distribution result in a net decrease in suitable sites. If the landscape has a high frequency of ponds presently too wet on average for *H. aquatilis* success, positive water balance

changes result in a net decrease in suitable sites while negative water balance changes diminish suitable sites. There is currently no information regarding the frequency distribution of different pond/catchment geometries within the Swan Valley.

The Local Model implies certain sensitivities to timber harvest and precludes other effects, thereby suggesting productive directions for future investigations of *H. aquatilis* hydrology as affected by land management. In the Local Model, enhanced snowpack accumulation, accelerated snowpack ablation and reduced upland evapotranspiration should result in a larger and earlier pulse of local groundwater recharge and pond inflow in basins where forest canopy is reduced or eliminated. The significance of the effect depends in part on the ratio of basin to wetland areas. The hydrographs of ponds with relatively large catchments (and by inference large inflow of shallow groundwater relative to direct precipitation) will be affected more than those with small catchments relative to pond area and volume.

In the Local Model, logging or fire within the immediate topographic basin will result in a pulse of increased nutrient loading to the pond persisting for perhaps 3 - 5 years. Some constituents (especially nitrate) are likely to increase in concentration, while loading of other constituents is more likely to result from an enhanced volume of shallow groundwater inflow. The importance of the perturbation depends on the pre-disturbance nutrient status, the eventual fate and long-term availability of nutrients introduced into the pond environment, and the responses of both *H. aquatilis* and potentially competing vegetation to nutrient enhancement.

Removal of surrounding forest may increase solar energy input to the pond and increase average wind speeds at the pond surface, both of which would tend to result in increased evaporation rates and proportional increases in rates of pond drawdown under the Local Model. Increased light and water temperatures are also expected to result, with possible effects on the growth of *H. aquatilis* and potentially competing vegetation.

The Extended model

The Extended model (Figure 5) assumes that groundwater inflow from beyond the immediate topographic basin contributes significantly to the (hypothetical) *H. aquatilis* pond, and allows for effects of upgradient water bodies with flow-through or recharge positions relative to groundwater. Groundwater outflow may be significant relative to evaporative losses, and perturbations to the hydrologic regime may result from water or solute budget changes anywhere in the recharge area of flow systems contributing to the pond. The seasonality of inflow may be less marked, where the contribution of

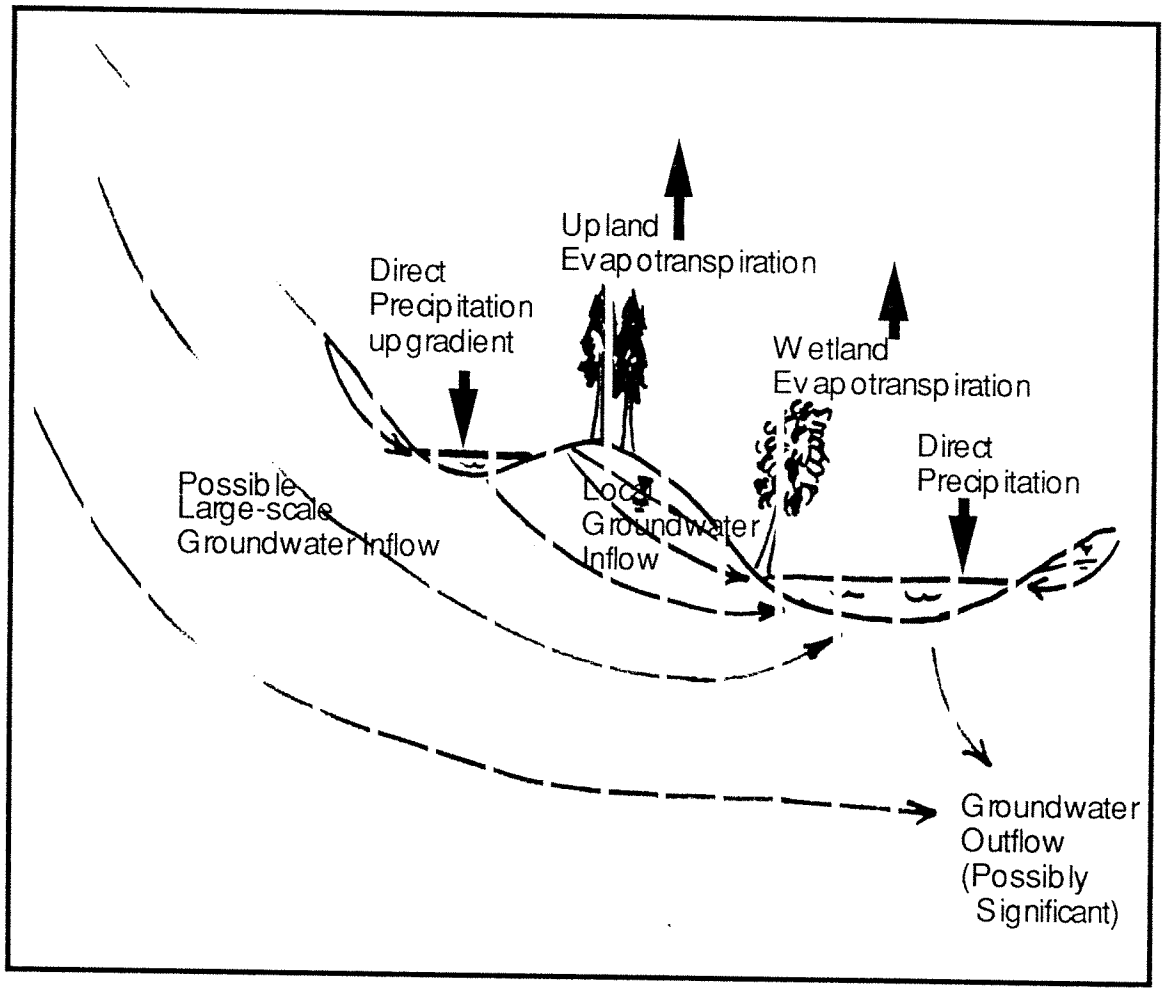

Figure 5. Possible hydrologic components of the Extended Model.

larger - scale flow systems is important. Direct precipitation and local groundwater inflow are also likely to remain important water budget components, depending on the rates of groundwater inflow from larger flow systems.

As with the Local Model, pond hydroperiod in the Extended Model may be sensitive to changes in areal recharge rates. In the Extended model, such effects may extend beyond the immediate topographic basin to larger areas contributing recharge to larger flow systems supporting pond inflows. Thus altered snowpack or evapotranspiration anywhere within the recharge area may alter water budgets and pond hydroperiod.

Model Comparisons

The Local and Extended models lead to different predictions for pond water budgets which can be used to test model applicability. The local model, for example, requires that net pond evapotranspiration during the drydown season be, in most years, sufficient to expose littoral areas for *H. aquatilis* germination. Qualitative observations of *H. aquatilis* pond depth (Montana Natural Heritage Program records) and climatic records suggest that this is generally the case. If the seasonal pond volume decrease exceeds that which can be accounted for through evapotranspiration, significant groundwater outflow must occur.

Similarly, the Local Model requires that the annual stage increase be accounted for by snowpack accumulating on the wetland, plus the fraction of upland precipitation which is not intercepted or transpired. If the local inflow sources cannot account for observed pond volumes, the Local model will be refuted and a contribution from larger-scale groundwater flow implied. Pond catchment areas are required to test this relationship.

The Local Model also requires that the geochemistry of *H. aquatilis* sites reflect some mixing of direct precipitation and locally recharged groundwater, without a component reflecting larger-scale groundwater flow systems. Chemical characteristics reflecting longer flow systems, such as elevated dissolved solids or evolved ionic ratios relative to very shallow groundwater, would lead to rejection of the Local model in favor of some variant of the Extended model.

In the Extended Model ponds may be less sensitive to water balance changes within the immediate basin than under the Local Model, due to the influence of larger scale hydrologic systems.

The Local and Extended Models also lead to different predictions for the sensitivity of *H. aquatilis* habitat to inter-annual hydrologic effects. In the Local

Model, pond hydroperiod is controlled mainly by water budget components with response periods of less than one year. Pond water levels are expected to track hydrologic perturbations closely in time; consecutive dry or wet years are years of consecutive negative or positive deviation from the average water balance of a pond. In contrast, the Extended Model allows for the possibility of groundwater inflow and outflow responding over longer periods to hydrologic perturbation. Pond hydroperiod may show a more complex response to climatic events because water budget components of different scale are in less close synchrony than in the Local Model. Antecedent groundwater conditions may buffer, offset or accentuate the effects of annual and inter-annual dry and wet periods.

Outline of Research Needs

A program of field data collection is needed to 1.) select the most appropriate model of *H. aquatilis* hydrology and 2.) parameterize model components to allow for quantitative predictions of *H. aquatilis* response to hydrologic perturbations. Meeting these objectives requires additional data describing geomorphology, geochemistry, water budgets, population dynamics and community structure.

Two principal challenges in resolving unanswered questions about *H. aquatilis* habitat are 1.) The complexity of shallow groundwater flow systems interacting with ponds, and 2.) The large number of sites supporting *H. aquatilis* populations. The water budget complexities of ponds have typically been examined through intensive hydrogeologic and climatic investigation. Surface and groundwater interactions are complex and biologically important; yet hydrogeologic investigation of all inventoried *H. aquatilis* sites is clearly out of the question due to logistics and cost. A strategy for better general characterization of all sites should be combined with a stratification approach which selects a small subset of ponds for intensive examination of water and solute balances.

I. Selecting the correct model

A. Sampling design

Within each *Howellia aquatilis* site cluster, a random subset of *H. aquatilis* ponds and unoccupied ponds should be selected for general characterization of geomorphic characteristics and water chemistry. The total number of sites, and their distribution among clusters, should be chosen to provide statistically robust results. The objective of sample stratification should be to ensure selection of ponds exhibiting a wide range of response to changes in hydrologic variables. In addition to location between clusters, land use and known geomorphic

characteristics (particularly wetland size, relief within the local basin and the presence or absence of surface drainage) should be employed as sample stratification criteria. Available *H. aquatilis* pond data indicate a range of solute concentrations suggesting variability in groundwater contribution to ponds. Therefore a comprehensive survey of specific conductance and pH of pond water should be considered to further define pond types useful for stratification.

B. Extensive site characterization

1. Determine drainage basin and wetland areas. Basin and wetland areas should be measured for all of the selected ponds, and staff gauges and permanent upland reference points established.

2. Pond profiling. Pond-bottom profiles should be surveyed to establish stage-volume relationships, so that simple stage monitoring can serve as a measure of the hydrologic state of *H. aquatilis* ponds.

3. Water chemistry analyses. Ionic water chemistry (major ions, nutrients and possibly selected trace elements) should be determined for early and late-season conditions in the selected subset of ponds. Chemical data are needed to interpret pond water budgets and to better define *H. aquatilis* habitat sensitivities.

4. Snow water measurements. Late-season snow water equivalent measurements and water level/volume data should be collected periodically over several spring and growing season cycles, and the data evaluated for consistency with the "Local Model" outlined above.

5. Potentiomanometer measurements (Winter et al, 1988) of local groundwater head relative to surface water elevations should be attempted in and around a few ponds. Low hydraulic conductivity substrate may thwart the use of this approach. If successful, however, early and late season characterization of relative groundwater elevations could be conducted relatively rapidly at a large number of pond sites, providing qualitative characterization of groundwater inflow/outflow regimes.

5. Establish evaporation records. Evaporation rates are a key component of models of *H. aquatilis* pond biohydrology, but are poorly constrained throughout the Swan Valley. Installation of evaporation pans at two locations in the northern and southern portions of the valley will provide data needed to correlate actual free water evaporation to the distributed estimates of MAPS (Caprio et al, 1994).

C. Intensive site characterization.

Concurrently with the extensive examination of geomorphic and geochemical characteristics described above, intensive examination of the groundwater interactions and water budgets of a small number of *H. aquatilis* ponds (2-3 sites) should be initiated. To the degree possible, these sites should be selected to reflect a range of basic geomorphic characteristics (relief and size) displayed by *H. aquatilis* ponds. The emphases of these investigations should include 1.) Testing the importance of seasonally recharged shallow groundwater flow in pond water budgets, 2.) Examining the role of the contact between the weathered soil profile and unweathered till in controlling pond inflow and outflow, and 3.) Estimating pond solute loading from shallow groundwater.

1. Piezometer installation. Hydrogeologic characterization will require the installation of piezometer nests sited to provide estimates of vertical and horizontal groundwater gradients, and hydraulic characteristics of weathered and unweathered till and of pond sediments. A minimum of three to five piezometer nests consisting of 3 piezometers per nest should be installed at each intensively studied pond. Where groundwater contribution from beyond the immediate catchment is inferred, additional piezometer installations will be required to define groundwater flow paths. Continuous records of piezometer water levels will be required, necessitating the installation of recording devices.

2. Time-series analysis of water chemistry. Biweekly sampling and analyses of groundwater and pond chemistry will improve understanding of water fluxes and solute sources and sinks.

3. Seepage meter measurements. Direct seepage meter measurements of water and solute fluxes across the pond boundaries may also prove effective in this setting. Seepage meter response typically shows high spatial variability within a water body; therefore 3 to 5 installations per pond may be necessary to produce meaningful direct measurements of pond boundary water flux. Two to three installations should be initially attempted in a selected pond to evaluate seepage meter effectiveness in the organic pond substrate. The required monitoring frequency will depend on seepage meter design and on rates of pond boundary flux. Installing and maintaining seepage meters will necessarily involve local disturbance of *H. aquatilis* habitat.

4. Hydrologic tracers. Possible approaches to clarifying Extended pond water balances include stable isotopic analysis of different components of the hydrologic system. Oxygen and hydrogen isotope analysis can, under some circumstances, serve as natural tracers and provide an effective means of estimating wetland water budgets (Hunt et al, 1996) without explicitly measuring

groundwater potentials or pond-boundary fluxes. This approach would require intensive sampling of precipitation, pond water and groundwater during and after pond - recharge events, and would also required on-site monitoring of precipitation rates.

II. Ecological model Paramaterization

A. Sampling design.

Sites should be drawn from the stratified sample identified for 1.B.1-5 above. The selected sites may constitute a subset of the ponds chosen for hydrologic characterization, but should include the full range of characteristics identified through section 1.B.

B. Intensive studies

1. Water level - *H. aquatilis* dynamics. Long-term studies to search for correlations between monthly water levels and *H. aquatilis* abundance will provide data necessary to predict how changes in hydrologic regime will affect population size. Time-series analysis of historic Swan Valley precipitation data may provide an estimate of the likely monitoring period needed to meet this objective.

2. Seed bank longevity. *In situ* as well as *ex situ*, long-term studies of the fate of seeds placed under permanent water and in soil under aerobic conditions will allow better predictions of multi-year effects of hydrologic change.

C. Extensive studies

1. Water chemistry. Knowledge of pond water nutrient levels throughout the hydrologic cycle (especially N and P dynamics) will increase understanding of how nutrient loading will affect algal and macrophyte competitors.

2. Algae floristics. Conducting a study to determine the principal epiphytic and free-living algae in *H. aquatilis* ponds throughout the growing season will allow better understanding of how nutrient loading will affect competitors.

3. Pond bottom profile/*H. aquatilis* abundance. Determining correlations between abundance of *H. aquatilis* (cover, density of seed) or area occupied and the shape of the pond (combine with I.B.2 above) will provide more quantitative understanding of relationship of pond shape, water budget and *H. aquatilis* population size.

Appendix A. Pond Sediment Observations

We conducted a field reconnaissance of pond sediments at eight ponds during low-water conditions (September 5, 1996). Four ephemeral ponds were dominated by *Carex vesicaria* and support abundant *Howellia aquatilis*. Two ponds had semipermanent water based on the presence of *Nuphar* sp.; one of these has a small population of *H. aquatilis* localized along pond margins, while the other lacks *H. aquatilis*. Two ponds contained abundant *Typha*; one of these supported a sparse *H. aquatilis* population, while the other apparently lacked *H. aquatilis*. We made sediment observations by hand-augering to depths of about 60 cm within and adjacent to the "drydown zones" of the ponds. We used observations and the inventory of Shelly (1988) to determine *H. aquatilis* abundance at these sites.

Organic deposits ranged from about 20 centimeters to about 35 centimeters in thickness. Wetlands with abundant *Howellia aquatilis* appeared to have shallower organic accumulations than ponds with sparse or no *H. aquatilis* populations, consistent with Lesica's (1992) findings. The nature of the organic profiles encountered differed between the wetlands examined; semi-permanent ponds are underlain in part by gelatinous gyttja - like sediment which may be derived from algal production, while wetlands with extensive drydown zones are underlain by thin peats with distinct acrotelm and catotelm components. *Typha* - dominated wetlands examined had coarser surficial peat than other sites, with abundant identifiable plant fragments.

In all of the ponds examined, organic deposits are underlain by clay - rich sediments of apparent low primary permeability. In several sites, these sediments appear to be till, based on the occurrence of abundant unrounded pebbles and small cobbles within the clay-rich matrix. In other sites, coring encountered little if any coarse material in the upper few centimeters of clay and silt, suggesting that these ponds may have accumulated lacustrine clay deposits after local deglaciation and prior to the establishment of stabilizing vegetative cover. We did not observe laminations in any of the pond-floor silt and clay; augering tended to disrupt the recovered samples, however, possibly obscuring sedimentary structures. In one pond, we encountered several centimeters of apparent tephra immediately overlying till. Volcanic ash was not readily apparent in the other sites examined.

The color and apparent weathering history of the clay - rich material we encountered beneath these wetlands varied considerably. Some appeared gray and uniformly reduced, while at other sites the clay was mottled orange or red in color and appeared to have experienced at least periodic oxidizing conditions. There was some tendency for the highly transient ponds with low angle drydown zones (i.e., high-quality *H. aquatilis* habitat) to appear more oxidized in the upper

There was some tendency for the highly transient ponds with low angle drydown zones (i.e., high-quality *H. aquatilis* habitat) to appear more oxidized in the upper few centimeters of the subsoil profile. Verifying such an interpretation requires sampling additional sites and performing mineralogical examinations of the subsoil materials, however. Apparent low permeability suggests that seepage inflow may be largely limited to very shallow subsoil flow paths. Likewise, seepage outflow may be a minor water budget component when water levels are within the typical zone of *H. aquatilis* abundance. Measurements of seepage and/or careful pond stage monitoring are needed to examine the role of groundwater outflow, however.

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