INFLUENCE OF ADJACENT UPLANDS AND GROUNDWATER ON THE HYDROLOGY AND INVERTEBRATE COMMUNITY COMPOSITION OF SEASONAL FOREST PONDS IN NORTH CENTRAL MINNESOTA

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Title

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Community Composition of Seasonal Forest Ponds in North Central Minnesota

By

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The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

MASTER OF SCIENCE

ABSTRACT

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Seasonal ponds are common throughout northern Minnesota's forested areas. Seasonal ponds typically flood due to snow-melt and high precipitation rates in early spring, then dry by mid-late summer. The dynamic hydroperiods of seasonal ponds create a unique fishless habitat hosting an abundance of many endemic aquatic species. Hydroperiod has long been considered a major controller of biological communities in seasonal ponds, but few data are available for testing hydrological linkages among seasonal ponds, their surrounding watersheds and their resident invertebrate communities. To identify hydrological pond function, I placed peizometers and monitoring wells in 8 sites in the Buena Vista State Forest in Beltrami County, MN, and 8 sites in the Paul Bunyan State Forest in Hubbard County, MN (16 sites total). Water levels were monitored weekly (2006-2009) from spring melt until ponds dried and water tables fell below readable depths. Invertebrate communities were also sampled weekly during 2008 and 2009. Results indicate that high but variable water exchange occurs between seasonal ponds and ground water. Hydrological patterns of seasonal ponds were related to several physical parameters including hydrological function, maximum depth, and canopy cover. Most relationships appear to be consistent between the 2 forest areas; however, some differences are notable, such as soil characteristics and influence of pond surface area on hydroperiod. Patterns in pond invertebrate communities were also related to hydrological function and hydroperiod, and these

patterns appear consistent between the 2 forest areas, suggesting that many invertebrates are generalist users of these areas.

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GENERAL INTRODUCTION

Seasonal ponds are a common type of wetland in regions that have experienced continental glaciation (Brooks 2005), including northern Minnesota (Hanson et al. 2009). Seasonal ponds are shallow depression wetlands underlain by bedrock or semi-impervious soil horizons (Brooks 2005). Seasonal ponds typically have small catchments and no permanent overland connection to other bodies of water (Brooks and Hayashi 2002; Brooks 2004, 2005; Tiner et al. 2002). Due to their hydrologic isolation, these aquatic systems are influenced directly by precipitation, evapotranspiration, and their connection to groundwater (Brooks and Hayashi 2002; Brooks 2005). Seasonal ponds are also generally small, < 1 meter in depth, and typically range from 0.1 to 0.25 ha in size, rarely approaching 1.0 ha (Palik et al. 2001, 2004; Brooks 2005). Due to their small size, seasonal ponds generally have a high perimeter-to-area ratio and thus are sensitive to disturbances in the adjacent uplands (Palik et al. 2001, 2004; Brooks 2005).

Seasonal ponds are typically inundated in early spring due to snowmelt and high precipitation rates, then become dry by mid to late summer (Brooks 2005; Mansell et al. 2000). Inundation during the growing season results in water-tolerant species dominating the plant community (Brooks 2005). The length of inundation, the number of consecutive days the pond basin contains standing water, is referred to as the hydroperiod (Mitch and Gosselink 2000). Seasonal ponds typically continue to fill throughout the early spring due to saturated soils, snowmelt and precipitation rates that typically exceed evapotranspiration rates. Once evapotranspiration exceeds precipitation, water levels in the ponds begin to decrease (Brooks 2004). Decreasing water levels generally occur during June, July and August when temperatures may be highest and adjacent forests have maximum leaf area (Brooks 2004, 2005). Evapotranspiration rates increase with increasing temperatures. In the fall, precipitation rates may increase and exceed evapotranspiration rates, which decline as leaf area decreases with falling temperatures (Brooks 2004); this can result in standing water accumulating once again in the pond basin.

Despite seasonal inundation, seasonal ponds support rich and diverse invertebrate communities with high seasonal variability, that are distinctly unique when compared to invertebrate communities of permanently flooded wetlands (Brooks 2000; Brooks, and Hayashi 2002; Batzer et al. 2004; Miller et al. 2008; Williams 2005). The uniqueness of aquatic invertebrate communities found in seasonal ponds increases their importance in maintaining a regions' biodiversity (Williams 2005). The environmental influence that sets invertebrate communities of seasonal ponds apart from permanently flooded wetlands is duration of flooding, or hydroperiod (Batzer et al. 2004; Brooks 2000; Collinson et al. 1995; Williams 2005). The duration of ponding in seasonal ponds is rather difficult to predict; therefore the invertebrates inhabiting these systems must develop adaptations (Batzer et al. 2004). Invertebrate adaptations can include, the ability to avoid desiccation by moving by flight from pond to pond, or having an accelerated life cycle which allows them to emerge, mature and reproduce before pond desiccation occurs (Batzer et al. 2004; Williams 1996, 2005). Other adaptations include the production of resting eggs, and the ability to enter dormancy as an immature. Maintaining densities of seasonal ponds across landscapes is also important given the very low dispersal rates specifically of non-flying aquatic invertebrate taxa, such as fairy shrimp (*Eubranchipus*), clam shrimp (Conchostraca), and Cladocerans, which are characteristic invertebrates of seasonal ponds.

The broad objective of my research was to contribute to better understanding of ecological relationships between riparian communities and characteristics of adjacent upland forests. The hope in this research is to contribute to and improve on current forest management practices. Understanding relationships between invertebrate communities in seasonal forest ponds, and the adjacent uplands will assist in making land management decisions which will help promote and maintain biodiversity, as well as healthy, sustainable forests, and to protect the integrity of unique areas such as seasonal forest ponds within forested landscapes.

This study was designed to identify relationships between environmental variables, in particular groundwater hydrology, and composition of the aquatic invertebrate community in seasonal forest ponds. The thesis is divided into two papers. The first paper focuses on environmental predictors of hydrology, specifically hydroperiod, potential relationships between seasonal forest ponds and groundwater. The second paper focuses on environmental influences, including groundwater influence on aquatic invertebrate community composition, and appears to be the first study of this relationship.

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PAPER 1. HYDROLOGICAL RELATIONSHIPS BETWEEN SEASONAL FOREST PONDS AND THE CHARACTERISTICS OF ADJACENT UPLANDS IN NORTH CENTRAL MINNESOTA

ABSTRACT

Seasonal ponds are common throughout northern Minnesota's forests. Seasonal ponds typically flood due to snow-melt and high precipitation rates associated with spring, and then dry by mid-late summer. The dynamic hydroperiod of seasonal ponds creates a unique fishless habitat that hosts an abundance of endemic species. Hydroperiod has long been thought to control biological communities in seasonal ponds, but few data are available for testing hydrological links between seasonal ponds, groundwater and the surrounding watersheds. To identify ponds' hydrological function, I placed peizometers and monitoring wells in 8 sites in the Buena Vista State Forest in Beltrami County, MN, and 8 sites in the Paul Bunyan State Forest in Hubbard County, MN (16 sites total). Water levels were monitored weekly from spring melt until ponds dried and water tables fell below readable depths. Precipitation data were collected weekly during 2008, and 2009. Water exchange between seasonal ponds and groundwater was high, but variable. Seven ponds were identified as recharge, 7 ponds as flow-through and 2 ponds identified as perched. Hydrological patterns in these seasonal ponds could be related to several physical parameters including hydrological function, maximum depth, and canopy cover. Most relationships appear to be consistent between the 2 forest areas; however, some differences are notable such as soil characteristics and the influence of pond surface area on hydroperiod.

LITERATURE REVIEW

Seasonal ponds are a common type of wetland in regions that have experienced continental glaciation (Brooks 2005), including northern Minnesota (Hanson et al. 2009). Seasonal ponds are shallow depression wetlands underlain by bedrock or semi-impervious soil horizons (Brooks 2005). Seasonal ponds typically have small catchments and no permanent overland connection to other bodies of water (Brooks and Hayashi 2002; Brooks 2004, 2005; Tiner et al. 2002). Due to their hydrologic isolation, these aquatic systems are influenced directly by precipitation, evapotranspiration, and their connection to groundwater (Brooks and Hayashi 2002; Brooks 2005). Seasonal ponds are also generally small, < 1 meter in depth, and typically range from 0.1 to 0.25 ha in size, rarely approaching 1.0 ha (Palik et al. 2001, 2004; Brooks 2005). Due to their small size, seasonal ponds generally have a high perimeter-to-area ratio and thus are sensitive to disturbances in the adjacent uplands (Palik et al. 2001, 2004; Brooks 2005).

Seasonal ponds are typically inundated in early spring due to snowmelt and high precipitation rates, then become dry by mid to late summer (Brooks 2005; Mansell et al. 2000). Water-tolerant species dominate the plant community in these basins (Brooks 2005). The length of inundation, the number of consecutive days the pond basin contains standing water, is referred to as the hydroperiod (Mitch and Gosselink 2000). Seasonal ponds typically continue to fill throughout the early spring due to saturated soils, snowmelt and precipitation rates that typically exceed evapotranspiration rates. Once evapotranspiration exceeds precipitation, water levels in the ponds begin to decrease (Brooks 2004). Brooks,

(2004) found a strong positive correlation between precipitation and change in pond water levels, and a weaker, yet still significant and consistently negative correlation, between pond water levels and evapotranspiration rates. Decreasing water levels generally occur during June, July and August when temperatures may be highest and adjacent forests have maximum leaf area (Brooks 2004, 2005). Evapotranspiration rates increase with increasing temperatures. In the fall, precipitation rates typically increase and exceed evapotranspiration rates, which decline as leaf area decreases with falling temperatures (Brooks 2004). During the winter months when air and soil temperatures are below freezing there is typically little or no evapotranspiration. A study by Brooks (2004) found that, on average, more than 2 cm of precipitation per week is needed during the growing season to equal the rate of evapotranspiration and maintain pond water levels. The influence of precipitation rates on pond water levels may also depend on the topography of the adjacent uplands. Brief periods of surface runoff into pond basins are a primary regulator on pond water-levels. Brooks (2004) reported differing pond responses to precipitation and evapotranspiration rates, suggesting it would be difficult to develop a general pond hydrologic model that could be applied to all seasonal ponds.

Topography can be a key factor controlling wetland formation through the influence of base-flow patterns (Sun et al. 2002). Watersheds that contain steep slopes generally have a higher influence on water levels in ponds, than watersheds containing relatively flat topography (Hanes and Stromberg 1998). Landscapes with "ground moraine land-type associations", which are glacially formed accumulations of unconsolidated soil and rock, typically have higher densities of wetlands, (Brooks 2005) such as in northern Minnesota. Soil permeability also effects wetland hydrology. Soils in North Central Minnesota were deposited as ground moraines and outwash by glaciers (USGS, Northern Prairie Wildlife Research Center 2006). Because of the influence of glacial processes on these soils, mineral soil textures range from clay to sand. These soils are typically well drained, however, numerous wetlands scattered throughout the landscape have very poorly drained soils, and more than 10% of the soils are peat (USGS, Northern Prairie Wildlife Research Center 2006).

Surface flow may affect wetland hydrology, although the influence is dependent on landscape position, topography, vegetative cover, soil permeability and saturation of soils adjacent to the wetland (Brooks 2005; Sun et al. 2002). Surface flow between seasonal ponds is generally rare except during brief periods of heavy precipitation or during spring snowmelt (Brooks 2004, 2005). During wet periods, wetlands are more likely to be affected by surface flow due to low infiltration rates caused by saturated soils adjacent to the wetland (Sun et al. 2002). Sun et al. (2002) reported that surface flow occurred only when the entire soil profile was saturated. Disturbances of upland vegetation such as removal can influence spring snowmelt or extreme precipitation events have on pond water levels by increasing the amount of runoff entering the system (Bent 2001). During dry periods surface flow may seep into the unsaturated soils to replenish storage in the vadose zone and never reach a seasonal pond. Soil type can also influence the permeability of the surrounding landscape. Specifically clay soils can have a strong influence on the permeability of the surrounding landscape and can increase surface flow due to its low hydraulic conductivity (Mitch and Gosselink 2007).

The relationship between groundwater and seasonal ponds is poorly understood. Mitch and Gosselink (2000) suggest that the hydrologic classification of a wetland, (e.g. recharge, discharge) is one of the most important characteristics of a wetland, however, the importance varies from wetland to wetland. The influence of surface-groundwater exchange on a wetland can vary depending on the relative position in the landscape and geologic conditions (Brooks 2005). Generally wetlands positioned high in the landscape are recharge wetlands and generally have shorter hydroperiods. Wetlands at a lower position in the landscape are discharge wetlands with longer hydroperiods (Brooks 2005; Winter 1989) and wetlands in between high and low points of the landscape typically have hydroperiods intermediate in length (Brooks 2005). In some instances, a wetland may be perched, meaning that the wetland has limited connection to groundwater due to impermeable soil horizons that contain high amounts of clay or even bedrock (Boelter and Verry 1977). Water levels in perched wetlands are solely a function of precipitation and surface runoff (Colburn 2004). Change in the pond water level therefore depends on the balance between precipitation and evapotranspiration (Brooks and Hayashi 2002). Wetlands that have limited connectivity to groundwater are typically more ephemeral when compared to wetlands that receive groundwater (Brooks and Hayashi 2002).

Wetlands are usually either discharge or recharge at any particular time depending on their connectivity to the regional water table (inflow of groundwater = discharge, flow to groundwater = recharge) however, some wetlands may fluctuate between periods of discharge and recharge depending on the time of year and wetness conditions (Phillips and Shedlock 1993; Winter 1989). Events such as a heavy rainfall or spring snowmelt may cause water table levels to rise and alter the hydrological state of a wetland, such as causing the wetland to shift from recharge to discharge (discharge, recharge or flow-through) (Phillips and Shedlock, 1993). As the water table rises, water discharges into the wetland (Mansell et al. 2000). When the water table drops below the water level in the wetland, water will seep out of the wetland recharging the groundwater. Phillips and Shedlock (1993) found that the water table did not always follow the topography of the land, as commonly assumed, but did show seasonal fluctuations for seasonal ponds on the Delaware coastal plain. During wet periods, particularly in the winter and spring, ephemeral groundwater mounds formed adjacent to seasonal ponds forming a hydraulic gradient towards the pond; when this occurs, groundwater discharges into the ponds (Phillips and Shedlock 1993; Hanes and Stromberg 1998). During dry periods especially in the summer the groundwater mounds disappear due to falling water table levels and increased evapotranspiration rates, causing the hydraulic gradient to shift towards the adjacent uplands. When this occurred, water flowed from the ponds to the adjacent upland (recharge). Water may also flow through a seasonal pond when water discharges along a portion of the pond and recharges through another portion (Mansell et al. 2000). Flow-through conditions may exist in relatively flat terrain especially where the water table is near the ground surface. These sites may be influenced by regional groundwater flow due to shallow water tables (Mansell et al. 2000).

Other processes, such as evapotranspiration, may influence and increase the complexity of wetland hydrology (Brooks 2005). Once temperatures begin to increase, evapotranspiration rates rise dramatically due to rapid vegetative growth which requires large volumes of water (Hanes and Stromberg 1998). Water recharges from seasonal ponds to the adjacent upland soils when evapotranspiration induces hydraulic gradients in adjacent upland soils (Brooks and Hayashi 2002; Brooks 2005; Hanes and Stromberg 1998; Hayashi et al. 1998; Phillips and Shedlock 1993). Shifting of hydraulic gradients, discharge/recharge, may be more pronounced in seasonal ponds due to their small size and typically high perimeter-to-area ratio. Miller (1971) studied wetlands in Saskatchewan Canada by comparing perimeter-to-area ratio to water loss, and found that an average of 60 percent of water loss from small ponds (0.10 acre or less in size) could be attributed to evapotranspiration by vegetation in the adjacent shoreline. A study by Lide et al. (1995) in the Thunder Bay area of South Carolina found that the fluctuation of shallow groundwater was dependent upon both precipitation and evapotranspiration. As a result of typically high perimeter-to-area ratios, disturbances in the adjacent uplands may have influences on pond hydrology, specifically hydroperiod (Batzer et al. 2000). Harvest of adjacent stands can lead to a reduction in evapotranspiration and elevated water tables (Kolka et al. 2000; Sun et al. 2000) resulting in an increase in soil moisture (Aust et al. 1997).

Precipitation interception or throughfall also decreases due to the removal of the tree canopy, which can lead to an increase in runoff (Batzer et al. 2000; Kolka et al. 2000). Hydroperiod may increase as a combined response to reductions in evapotranspiration that follow vegetation harvesting. Kolka et al. (2000) found that undisturbed sites had more dynamic hydrology when compared to disturbed (removal of vegetation) sites. Aust et al. (1997) studied tree harvesting techniques in the southeastern USA and found that hydrologic responses of harvested sites recovered to near pre-harvest conditions in as little as seven years. Hydrologic recovery to near a pre-harvest state in the northern USA may take longer due to the shorter growing seasons.

Hydroperiod has also been shown to have a positive correlation to the size of the pond basin (Brooks and Hayashi 2002; Brooks 2005). There are correlations that suggest large pond basins typically promote longer hydroperiods when compared to ponds with smaller basins. Large pond basins contain larger volumes of water and generally have smaller perimeter-to-area ratios resulting in a longer hydroperiod. These correlations are however not very strong. As pond size increases the perimeter-to-area ratio typically decreases resulting in a decrease in the amount of influence the adjacent uplands have on the wetland (Brooks 2005). Particularly, uplands surrounding small wetlands with high perimeter-to-area ratios can have an enhanced influence on the wetlands and likely lead to shorter hydroperiods (Brooks and Hayashi 2002).

Study Objectives

There have been few hydrologic studies of seasonal ponds. General relationships between precipitation, surface runoff, groundwater elevations, and hydroperiod are not fully understood (Colburn 2004; Mitch and Gosslink 2000). The lack of hydrological studies on seasonal ponds is due to the technical difficulty as well as it being costly and time consuming (Cole et al. 1997). Hydrology of wetlands was also not considered important until recently. Despite difficulties and costs, importance of understanding the relationship between seasonal ponds and groundwater remains. There are many factors affecting the hydrology of a wetland, including soil, precipitation patterns, groundwater, and the surrounding vegetation. The purpose of my study was to determine hydrological classification of seasonal forest ponds and assess potential hydrological effects of upland forest management on seasonal pond hydroperiod. In my study I have instrumented 16 ponds with monitoring wells and piezometers to identify their relationships to the groundwater, and to assess groundwater influence on length of hydroperiods.

MATERIALS AND METHODS

The study was conducted on 16 seasonal ponds, with eight sites located in the Buena Vista State Forest in Beltrami County, MN about 8 km or 5 miles north of Bemidji and eight sites in the Paul Bunyan State Forest which is located in Hubbard County, MN about 30 km or 18.5 miles south of Bemidji (Figure 1.1). The 16 seasonal ponds were selected from a larger study of 24 sites previously established by MNDNR in 1999 (Figure 1.2). These sits are surrounded by stands predominantly composed of aspen (Populus spp.) (Almendinger and Hanson 1998). Each site contains stands of aspen trees of relatively similar age. Sites were each assigned to one of 4 groups based on the age of adjacent aspen stand. Group 4 contained sites with adjacent stands ranging from clearcut to ≤ 9 years of age. Group 1 contained sites with adjacent stands of young growth ranging from 10 – 34 years of age, group 2 consisted of sites with adjacent stands of middle age growth ranging from 35 – 59 years of age and group 3 (control group) included old growth stands ≥ 60 years of age.

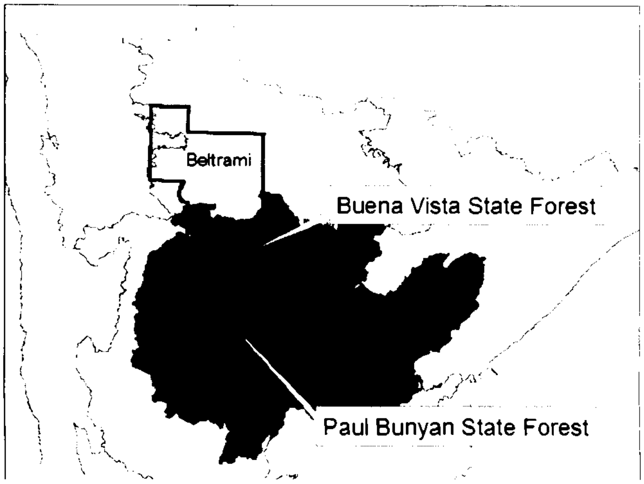

Figure 1.1. North Central area of Minnesota showing the locations of the Beuna Vista State Forest and Paul Bunyan State Forest. The blue area is the upper portion of the Mississippi River watershed (Minnesota Department of Natural Resources, layer wshd_lev08py3, 2007).

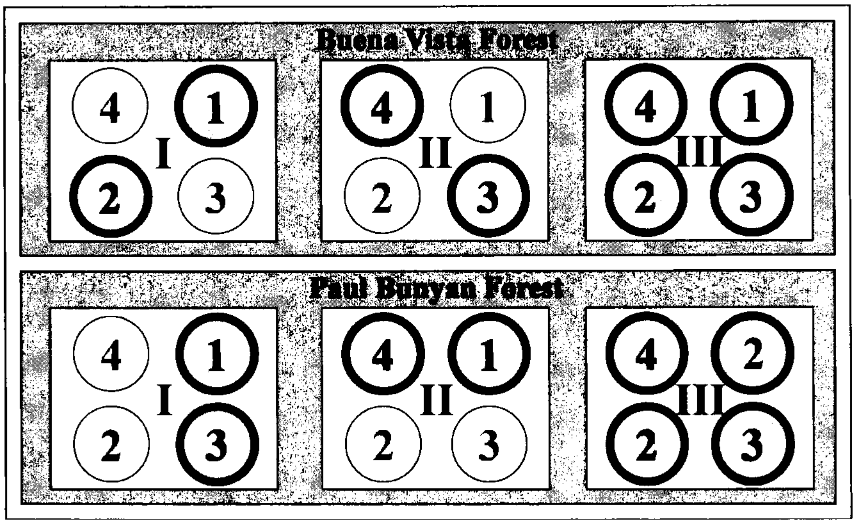

Figure 1.2. Sixteen sites (in bold, eight in each forest) selected from a larger study which included 24 sites. 1 = young growth (10-34 yrs.), 2 = middle age growth (35-59 yrs.), 3 = old growth (> 60 yrs.), 4 = clearcut < 9 years of age.

Hydrology

A staff gauge was installed in the deepest point of each seasonal pond (Figure 1.5) and constructed of 2.54 cm diameter PVC piping. The staff gauge was used to measure the standing water level within the seasonal pond basin. Piezometers (Figure 1.3) and monitoring wells (Figure 1.4) were installed following the methods of Sprecher (2000) in each of the 16 seasonal ponds. Monitoring of the upper most limit of the groundwater was measured through the use of the piezometers and monitoring wells. Five piezometer nests, each containing one shallow piezometer (60 cm), one deep piezometer (120 cm) and one monitoring well (120 cm), were deployed at each site. Four piezometer nests were installed at 4 locations along the delineated wetland boundary and a fifth piezometer nest was installed at the deepest point of the seasonal pond in close proximity to the staff gauge (Figure 1.5). The piezometers in the pond center were installed with extended PVC pipe extensions for the top openings to remain above the standing water level in the seasonal pond.

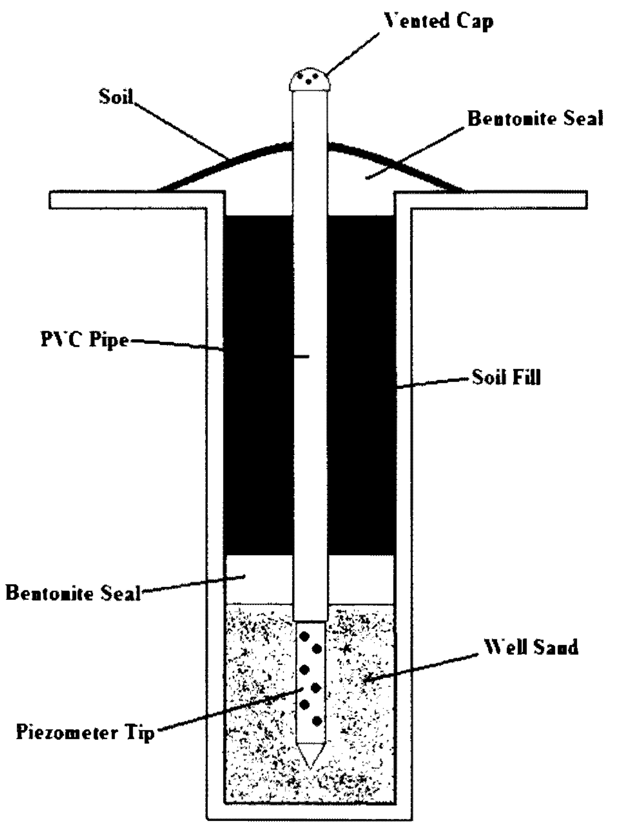

Figure 1.3. Piezometer installation in ground.

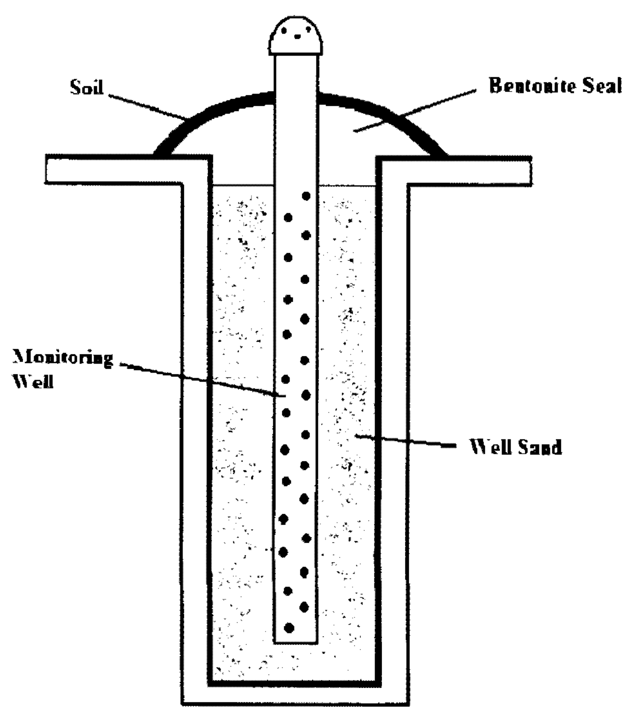

Figure 1.4. Monitoring well installation in ground.

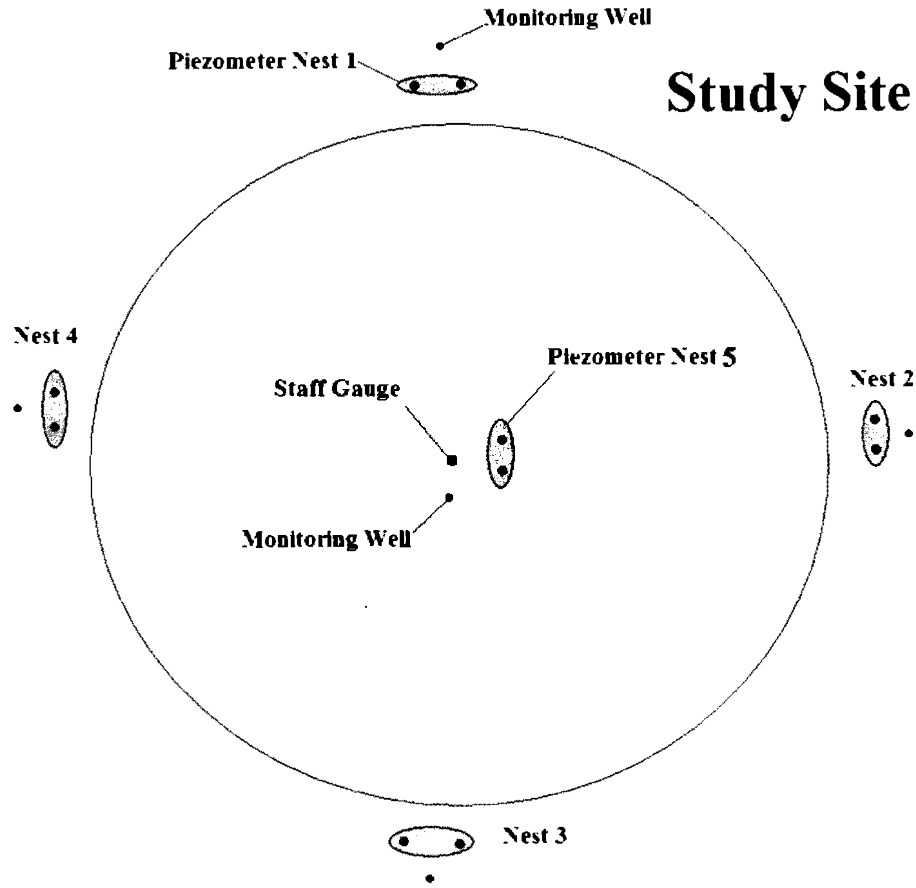

Figure 1.5. General layout of piezometer/monitoring well nests, and staff gage in each of the study sites within the Buena Vista State Forest, Beltrami County, MN, and the Paul Bunyan State Forest, Hubbard County, MN.

Piezometers were constructed using 2.54 cm diameter PVC piping glued to prefabricated piezometer tips (Forestry Suppliers). Monitoring wells were also constructed of 2.54 cm diameter PVC piping with perforations made using a hand drill along 120 cm of the lower portion of the PVC pipe. A perforated PVC cap was added, closing the lower end of each well. Fabric socks were constructed from synthetic mesh fabric, and placed over the perforated portion of each monitoring well to prevent sand from entering the well through the perforations. Holes for the wells and piezometers were dug using a hand auger with a diameter of 7.62 cm. After each hole was dug approximately 0.5 liters of silica sand was poured into the bottom of the hole. The well or piezometer was then placed in the hole to the appropriate depth, and sand was poured until the piezometer tip or the perforated length of the well was covered allowing free flow of groundwater (Figure 1.3 & 1.4). Bentonite was then added to form a top seal just above the perforated portion of the well or piezometer to prevent water seepage from above. Dredged soil was used to fill in around the remainder of pipe extension of the piezometer, and tamped firmly in place to limit air cavities. At piezometers, a second bentonite seal (Figure 1.3) was poured around the piping about 15.25 cm below the ground surface, until it formed a small mound just above the soils surface to further prevent any surface water seepage. The exposed top opening of each pipe was covered by a vented cap to prevent rain water or insects from effecting changing water levels within the pipes. Caps were vented to allow air movement due to changing water levels within the wells and piezometers.

Each piezometer and monitoring well was surveyed individually within each wetland permitting comparisons of water table elevation. The base (ground level) for each piezometer/monitoring well was surveyed, as was the location of the staff gauge to obtain its elevation in comparison to the deepest point of the pond. Groundwater depth readings were measured from the top of the pipe extension to the water level in the well or piezometer. The length of the pipe extension above ground was then subtracted to give the depth of water from the ground surface. The elevations of the piezometers and monitoring wells obtained through the surveys were then used to derive the elevations of the water levels in the piezometers and monitoring wells, in comparison to the deepest regions of each seasonal pond.

Water levels were read from a staff gauge located at the deepest point of each seasonal pond. Once the water level receded below ground level the center monitoring well was used to estimate the groundwater level immediately below the pond basin. Pond water level readings began soon after spring snowmelt, and were recorded weekly throughout the spring and summer. Starting in September pond water level readings were taken every other week until the ground froze or until water levels sunk below the readable depth of the center monitoring well. This data was used to assess the hydroperiod (consecutive days ponded) for each seasonal pond of each year. I defined the hydroperiod onset as the first date the pond was visited in which at least 20 percent of the pond basin contained standing water. The hydroperiod ended on the first date when less than 20 percent of the seasonal pond basin contained standing water, or when the standing water in the seasonal pond froze, usually occurring in late October or early November. Mean differences of hydroperiods were compared among the different stand-age treatments. Hydroperiods were also compared to approximate age of adjacent stands, as well as pond surface area, maximum depth, and percent canopy openness.

Pond Surface Area

Pond perimeters were plotted using a global positioning system with an external antenna to increase accuracy. The GPS data points were uploaded into the geographic information system software (ArcGIS 9.2, Environmental Systems

Research Institute Inc., 2007) to estimate the surface area of each pond in square meters.

Precipitation

Precipitation data were also collected weekly, concurrently with the pond water level readings. Precipitation volume was measured using a rain gauge positioned at about chest height in the center of three selected ponds in each forest, (a total of six rain gauges). Ponds were selected based on canopy openness. Gauges were installed in seasonal ponds with high canopy openness to eliminate effects of precipitation interception due to tree canopy. To compare 2006 and 2007, precipitation data was also used from the *Minnesota Climatology Working Group* (MCWG) (http://climate.umn.edu/wetland/wetland.asp). Data retrieved from the MCWG was compared to the field collected precipitation data to determine accuracy.

Canopy Cover

Percent canopy openness was assessed using a spherical densiometer. Two transects were randomly chosen in each pond and intersected at the center. Percent canopy openness readings were taken at five locations on each transect, with the third reading of each transect being at the center of the pond.

Groundwater

Groundwater level readings began soon after snow melt and shortly following ground thaw. Readings were recorded weekly throughout the spring, typically the beginning of May and into summer. In September groundwater level readings were recorded every other week until the ground froze typically in the beginning of November. Groundwater level readings were conducted using a pliable fabric measuring tape with a thimble attached to the end of it with the open side facing down. When the thimble contacted the water surface in the pipe, it would make a distinct popping noise allowing for easy and accurate water depth measurements.

Piezometers were used to measure the pressure head of the groundwater from the depth at which the lower perforated portions of the piezometers were located (Figure 1.3). Wells, which are perforated along the entire length below ground (Figure 1.4) were used to identify the actual level of the water table. The water levels in the piezometers were used in conjunction with the water levels in the monitoring wells to track and estimate the predominant function of each wetland (discharge, recharge, flow-through, perched). For example, when the water level in the piezometer indicates a positive head due to pressure differences (Figure 1.6. scenario B, water level is higher in piezometer than in monitoring well), it suggests there is an increase in hydraulic pressure at greater depths causing water to flow upwards (Sprecher 2000). The pressure then decreases as the water gets closer to the ground surface. If the water level in the piezometer indicates a negative head (Figure 1.6. scenario A, and C) which occurs when the water level in a piezometer is lower than the water level in the corresponding monitoring well, a negative hydraulic gradient has formed suggesting water is flowing into the ground ("recharge"). The downward movement of water causes a decrease in pressure with increasing depth causing water levels to be higher in the shallow piezometer and lower in the deep piezometer as seen in Figure 1.6, scenario A. For a wetland to be classified as a flow-through wetland the wetland must contain at least one piezometer nest that indicates groundwater discharge during the entire time or significant portion of the time the pond basin contains standing water, and at least one other piezometer nest indicating that pond water is recharging the groundwater. When this occurs the piezometer nests suggest that groundwater is discharging into the pond in one area of the pond basin, and pond water is then recharging the groundwater in another area of the pond basin. When there is little difference between the water levels in the monitoring well and two piezometers lateral groundwater flow is occurring.

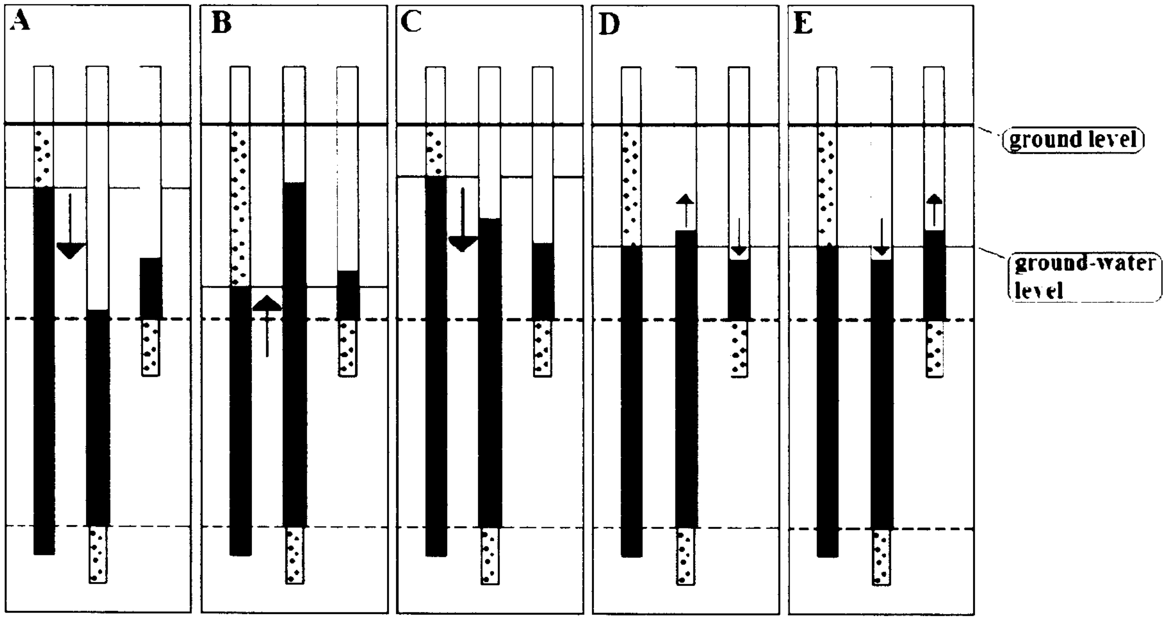

Figure 1.6. Piezometer and monitoring well scenarios encountered in the field. Scenario A: recharge, Scenario B: discharge, Scenario C: recharge, Scenario D & E: Transition between recharge and discharge.

A wetland may be perched or have limited connectivity to the groundwater due to an impermeable layer such as clay or bedrock. Impermeable layers can be located with soil assessments of the wetland. The water levels in the piezometers and wells may also suggest a perched wetland if subsurface levels behave independently of the standing water in the pond. For example, the peizometers and/or wells may become dry due to a falling water table and yet the pond still contains standing water in the basin. In some cases there can be different depths in the soils acting independently from one another such as in Figure 1.6, scenarios D and E. This is likely due to different soil horizons with different soil properties that the perforated portions of the piezometers intercept. In Figure 1.6 scenario D, the deep piezometer is showing discharge at that specific depth, while the shallow piezometer is showing recharge and just the opposite in Figure 1.6 scenario E. These differences can also result from impermeable layers located between the specific depths of the deep and shallow piezometer. Because different soil properties may be encountered at certain depths, soils were surveyed at all instrumented sites to allow interpretation of the hydrological data.

Soils

At each pond, soil profile descriptions were made and soil samples were collected, using a soil corer from locations in the deepest point of each pond and from one randomly chosen location in close proximity to one piezometer nest along the delineated wetland boundary. Soil profiles were described in the field and included identifying and measuring the depths of the soil horizons along with the matrix color, texture, structure, mottle colors, and mottle abundance of and within each horizon. Some addition data was collected for the upland soil locations and included the slope gradient and slope aspect. Soil core samples were collected and analyzed in the lab for particle size, pH, phosphorous, nitrogen, carbon, and exchangeable cations including $AlCl_3$, $CaCl_2$, CdCl, CuCl, $FeCl_3$, KCl, $MgCl_2$, $MnCl_2$, NaCl, $NiCl_2$, $PbCl_2$, SCl_2, and $ZnCl_2$.

Hydraulic Conductivity

Hydraulic conductivity of the soils was determined by using the pump and slug test (United States Environmental Protection Agency 1994) on each piezometer and well. This test must be conducted while there is still water in the well or piezometer in order to ensure that the soil is saturated, and to permit accurate hydraulic conductivity measurements. Water was pumped from the well or piezometer until dry and the amount of time from cessation of pumping until water returned to its original level within the well or piezometer was recorded. Using this technique allowed me to obtain the hydraulic conductivity of the soils immediately adjacent to the perforated portions of the well or piezometer.

Statistical Analysis

I began by fitting a linear mixed effects model to the hydroperiod data, with forest type, surface area, water depth, and canopy cover included as fixed effects, and 'site' included as a random effect. Interactions between forest type and each continuous predictor (surface area, water depth, and canopy cover) were also initially included. Variance inflation factors (VIFs; Fox 2008) suggested a fair amount of collinearity in the full model, with VIF's > 10 for the main effect of forest type and also for the interaction between forest type and water depth. In addition, interactions between forest type and water depth and canopy cover were not statistically significant (at the $\alpha = 0.1$ level). Therefore, I also fit a reduced model that included a single interaction (between forest type and surface area). With both models, I used QQplots to assess the normality assumptions for the random effects and for the within group errors (Pinheiro and Bates 2000). Homogeneity of variance of the within group errors was also assessed using plots of residuals versus fitted values. Models were fit using the lme function in the nlme package of Program R (Pinheiro and Bates 2000, R Core Development Team 2009).

To facilitate interpretation of the model parameters, I subtracted the mean of all continuous covariates (water depth, surface area, and canopy cover) before fitting the models, and summarized the fitted models using component plus residual plots (Maindonald and Braun 2003). Let $X_{i,j}^{k}$ be the *j*th observation at the *i*th site for predictor *k* (*k* = 1, 2, or 3 for surface area, water depth, or canopy cover), β_k be the regression parameter associated with predictor *k*, and $\varepsilon_{i,j}$ be the within group residual (i.e., the difference between the observed and predicted hydroperiod, where the predicted hydroperiod incorporates the site-level intercept). Plotted points ($X_{i,j}^{k}, X_{i,j}^{k}\hat{\beta}_k + \varepsilon_{i,j}$) along with the fitted line given by ($X_{i,j}^{k}, X_{i,j}^{k}\hat{\beta}_k$), also are shown.

I analyzed 2 years (2008 and 2009) of pond hydrological data, and four years of hydroperiod data using simple linear regression (JMP 8.0, SAS Institute Inc. 2008). Relationships were considered significant at $R^2 \geq 0.20$ and p-value $\leq$ 0.05. Only figures representing a significant relationship contain a trend line. Linear regression was used to identify relationships between hydrology and features of ponds, the adjacent uplands, and precipitation.

RESULTS

Soils in Pond Basins

Despite the shortest distance between study ponds in the two study areas (Buena Vista and Paul Bunyan State Forests) being 45.5 km, the soils were found to differ between the two forests (Soil Table in Appendix A). The pond basins of the Buena Vista State Forest generally contained soil textures ranging from sandy loam to loam. Several ponds had soil horizons with silty clay loam and clay soils. The clay percentage of basins in the Buena Vista State Forest averaged 22.6 percent, and ranged from 8.5 to 56 percent. Soil texture was less variable among pond basins in the Paul Bunyan State Forest, which typically had soil textures of sandy loam, with loam averaging 15.8%, and clay ranging from 4.6 to 28.6%.

Hydroperiod

The soils along the delineated wetland boundary of the Buena Vista State Forest typically ranged from loamy sand to sandy loam. Horizons of clay and clay loam were also documented at the boundary of several ponds, mainly in C soil horizons. Clay percentage of the soils ranged from 5.3 to as high as 51.1 percent, averaging 20.1 percent. The soil textures along the delineated wetland boundaries in the Paul Bunyan State Forest were similar to that of the Buena Vista State Forest containing soil textures of loamy sand to sandy loam. Two sites also contained horizons with sandy soils containing 90 percent sand. Clay percentage of the soils along the wetland boundaries in the Paul Bunyan State Forest averaged 9.1 percent which was less than half as much as the Buena Vista Forest (20.1%), and ranged from 3.4 to 19.1 percent. The average clay percent of pond soils was compared to hydroperiod length, however, no relationship was detected (Figure 1.7. $R^2 = 0.004$, $P = 0.62$).

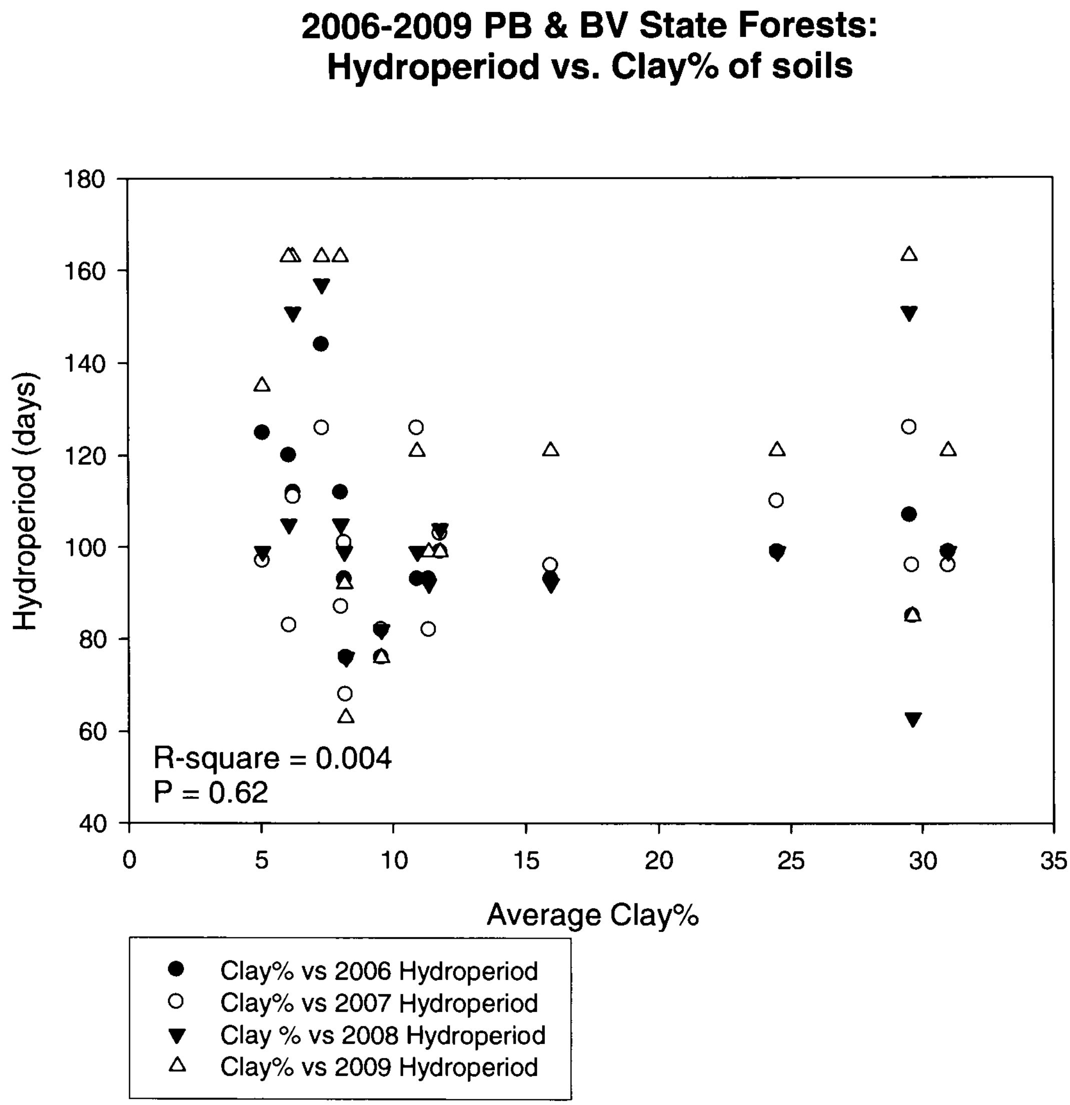

Figure 1.7. Hydroperiod length versus percent clay of pond soils.

Hydroperiod (consecutive days with standing water covering at least 20 percent of their basins) of clearcut sites was not significantly different for either of the four years when compared to other treatments (young-growth, middle-age growth, and old growth). The average hydroperiod for clear-cuts ranged from 110.8 consecutive days in 2006, to 134.8 days in 2009. Although clear-cuts on average had the longest hydroperiods, an old growth stand in the Paul Bunyan State forest typically had a longer hydroperiod than any of the young stands. I was unable to identify a significant relationship between age of adjacent stand and hydroperiod. Hydroperiods, average age of the adjacent stand, average hydroperiod and hydroperiod range difference between years 2006-2009 for each seasonal pond are listed in Table 1.1 for the Paul Bunyan State Forest and Table 1.2 for the Buena Vista State Forest.

Table 1.1. Hydroperiod of Paul Bunyan State Forest 2006-2009. Category represents stand-age category, PL = partially logged, CC = clearcut, YG = young-growth, MG = middle-age growth, OG = old growth.

Paul Bunyan State Forest								
Category	Ave. Stand-age 2006-2009	Pond	2006 Hydroperiod	2007 Hydroperiod	2008 Hydroperiod	2009 Hydroperiod	Individual Ave. Hydroperiod	Individual Hydroperiod Range Difference 2006-2009(days)
YG	32	PB-I-1	93	82	92	99	92	17
OG	82.5	PB-I-3	76	68	76	63	71	13
YG	28.5	PB-II-1	125	97	99	135	114	38
CC 1999-2000	7.5	PB-II-4	93	101	99	92	96	9
MG	42.5	PB-III-1	76	82	82	76	79	6
MG	41.5	PB-III-2	99	103	104	99	101	5
PL 2008	82	PB-III-3	112	111	151	163	125	40
CC 1999-2000	7.5	PB-III-4	144	126	157	163	148	37
PB Average Hydroperiod Range = 20.63 days								
PB Average Hydroperiod = 104.31 days								

Table 1.2. Hydroperiod of Buena Vista State Forest 2006-2009. Category represents stand-age category, PL = partially logged, CC = clearcut, YG = young-growth, MG = middle-age growth, OG = old growth.

Buena Vista State Forest

Category	Ave. Stand-age 2006-2009	Pond	2006 Hydroperiod	2007 Hydroperiod	2008 Hydroperiod	2009 Hydroperiod	Individual Ave. Hydroperiod	Individual Hydroperiod Range Difference 2006-2009(days)
YG	20.8	BV-I-1	120	83	105	163	118	80
MG	39.5	BV-I-2	112	87	105	163	117	76
OG	74	BV-II-3	99	96	99	121	104	25
CC 1999-2000	7.5	BV-II-4	99	110	99	121	107	22
YG	32	BV-III-1	93	126	99	121	110	33
MG	39.5	BV-III-2	93	96	92	121	101	29
PL 2005-2006		BV-III-3	85	96	63	85	82	33
CC 1999-2000	7.5	BV-III-4	107	126	151	163	137	56
BV Average Hydroperiod Range = 44.25 days								
BV Average Hydroperiod = 109.34 days								

Seasonal ponds in the study ranged in surface area from 145 m^2 to 3,160 m^2 (Table 1.3). Thirteen of the 16 ponds had surface areas ≤ 2,000 m^2. Pond surface area was positively associated with hydroperiod in the Paul Bunyan State Forest (p-value = 0.03), and an opposite, yet still significant negative pattern between pond surface area and hydroperiod was evident in the Buena Vista State Forest (Preliminary Model: Table 1.4. Final Model: p-value < 0.01, Figure 2b, Table 1.5) (Figure 1.8b).

Table 1.3. Surface area of seasonal ponds (meters^2).

Paul Bunyan State Forest		Buena Vista State Forest	
Pond	Surface Area(m^2)	Pond	Surface Area(m^2)
PB-I-1	145	BV-I-1	1765
PB-I-3	1394	BV-I-2	1080
PB-II-1	1078	BV-II-3	439
PB-II-4	864	BV-II-4	2091
PB-III-1	1128	BV-III-1	1165
PB-III-2	1501	BV-III-2	1414
PB-III-3	3049	BV-III-3	1483
PB-III-4	3160	BV-III-4	597

Table 1.4. Preliminary Model, Full Model: Linear mixed-effects model fit by REML.

Full Model

Linear mixed-effects model fit by REML

Random Effects:Site

Fixed Effects: Hydroperiod ~ State Forest + Zmax(cm) + Surface Area (m^2) + Canopy Cover

	Value	Std.Error	DF	t-value	p-value
(Intercept)	104.57	3.1972	49	32.71	<0.0001
Forest	-1.48	3.7879	49	-0.39	0.7
Zmax (cm)	0.82	0.1811	49	4.54	<0.0001
Surface Area (m^2)	0.01	0.0036	49	1.66	0.10
Canopy Cover	-0.35	0.1172	49	-3.02	0.004
Forest:Surface Area (m^2)	-0.03	0.0077	49	-4.34	<0.0001
Forest:Zmax (cm)	-0.33	0.2099	49	-1.55	0.13
Forest:Canopy Cover	-0.26	0.1780	49	-1.48	0.15

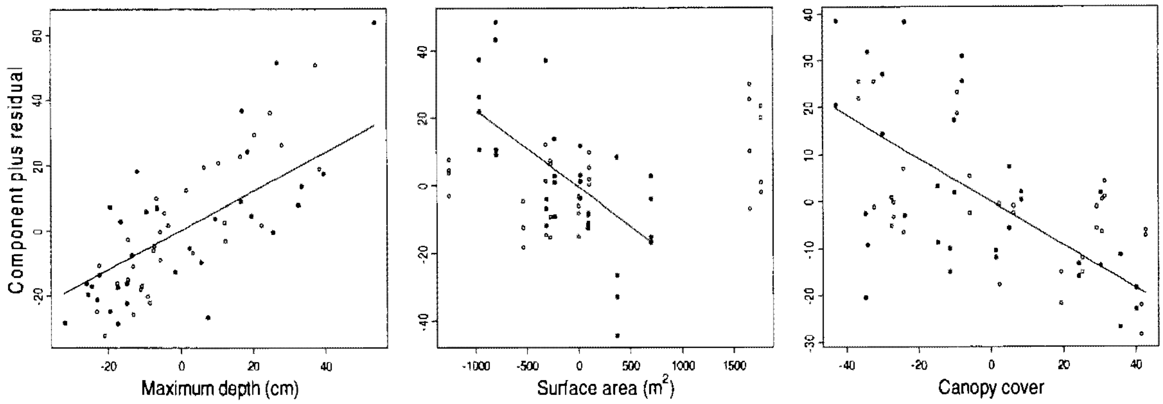

Figure 1.8. Component plus residual plots from the fitted reduced model. To aid in interpretation, I subtracted the mean of each continuous variable (water depth = 54cm, surface area = 1297 m^2, canopy cover = 69%). Solid circles = Buena Vista State Forest, Open circles = Paul Buynan State Forest 1.8a) Hydroperiod vs. Zmax (cm), 1.8b) Hydroperiod vs. Pond Surface Area (m^2) (Solid circles and dark lines correspond to Buena Vista State Forest (forest type = 1). Open circles and gray line [middle panel only] correspond to Paul Bunyan State Forest. (forest type = 0)). 1.8c) Hydroperiod vs. Canopy Cover.

Table 1.5. Final Model, Reduced Model: Linear mixed-effects model fit by REML.

Reduced Model					
Linear mixed-effects model fit by REML					
Random Effects:Site					
Fixed Effects: Hydroperiod ~ State Forest + Zmax (cm) + Surface Area (m^2) + Canopy Cover + State Forest:Surface Area (m^2)					
	Value	Std.Error	DF	t-value	p-value
(Intercept)	104.90	3.0935	51	33.91	<0.0001
Forest	-0.49	3.8391	51	-0.127	0.1
Zmax (cm)	0.60	0.1048	51	5.709	<0.0001
Surface Area (m^2)	0.01	0.0033	51	2.234	0.03
Canopy Cover	-0.46	0.0918	51	-5.001	<0.0001
Forest:Surface Area (m^2)	-0.03	0.0068	51	-4.494	<0.0001

I identified a significant positive relationship between maximum pond depth (cm) and hydroperiod (p-value < 0.0001) in the final reduced model. Because I observed no interaction between forest and maximum depth (p-value = 0.13) I used a final common slope model that included ponds in both forests.

I also compared maximum pond depth to pond surface area to determine if ponds with a larger surface area were likely to be deeper but detected no relationship (Figure 1.9. $R^2 = 0.1$, p-value = 0.23).

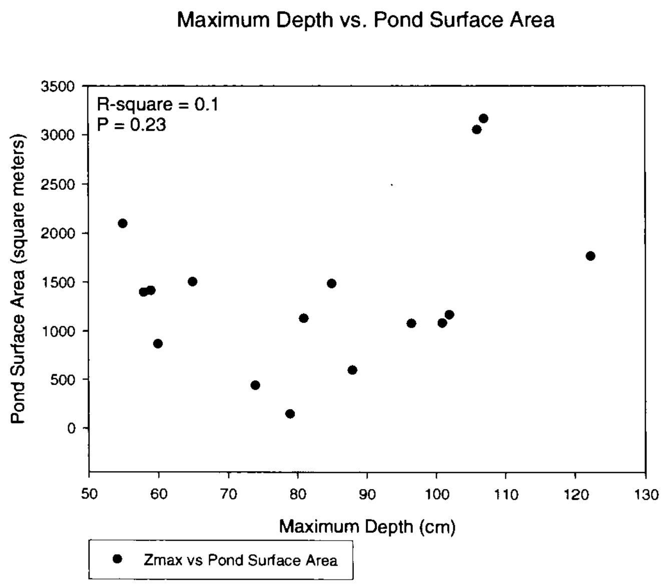

Figure 1.9. Maximum depth of seasonal ponds (n=16) compared to pond surface area (m^2).

Canopy cover is strongly influenced by age of adjacent stand (Hanson et al. 2009). I observed no influence of forest on canopy cover (p-value = 0.15) in the full model (Table 1.4), thus suggesting use of a common slope in the final model to relate canopy closure over study ponds to hydroperiod. A significant relationship occurred between canopy cover and hydroperiod (p-value < 0.0001) (Figure 1.8c, Table 1.5) in the reduced model, suggesting that canopy cover may influence hydroperiod length.

Generally the seasonal ponds in the Paul Bunyan State Forest had a larger range in hydroperiod within years (68 day range in 2006 and a 100 day range in 2009) when compared to the study ponds in the Buena Vista State Forest (35 day range in 2006 and an 78 day range 2009). The shortest range in hydroperiods within years in the Paul Bunyan sites occurred in 2006 with the shortest hydroperiod being 76 days in an old growth site and the longest being 144 days in a clearcut site; a difference of 58 days. The longest range in hydroperiod among the Paul Bunyan sites occurred in 2009 and ranged from 63 days (same old growth as in 2006) to 163 days (same clearcut as 2006); a difference of 100 days. The year 2008 was the only year in the study where the Paul Bunyan sites (shortest hydroperiod: 76 days; longest hydroperiod: 157 days) had a shorter range in hydroperiod than the Buena Vista State Forest ponds (shortest hydroperiod: 63 days; longest hydroperiod 151 days). Among the Paul Bunyan State Forest seasonal ponds, there was an old growth site that consistently had the shortest hydroperiod throughout the study ranging from 63 days in 2009 to 76 days in 2006 and 2008. There was also a clearcut site among the Paul Bunyan sites that consistently had the longest hydroperiod throughout the four year study, ranging from 126 days in 2007 to 163 days in 2009. Of the individual ponds in the Paul Bunyan State Forest the pond that had the narrowest hydroperiod range was of middle age growth with a variation of 5 days in hydroperiod length throughout the 4 years. The site with the highest variation in hydroperiod was an old growth site until trees were clearcut to the ponds edge during the second half of the third year. After tree-harvest the site was removed from analysis. Hydroperiod varied by 40 days between the first 3 years before the adjacent stand was harvested. Overall the sites of the Paul Bunyan State Forest had an average range of about 21 days throughout the four years, compared to the Buena Vista State Forest that had a 4 year average hydroperiod range of 44 days. Making generalizations of seasonal ponds is difficult due to their variation in hydroperiod from year to year. For example in the year 2009, four of the seasonal ponds in the Paul Bunyan State Forest had the shortest hydroperiod that was recorded during the four year study, while the other four seasonal ponds had the longest hydroperiod that was recorded among the 4 years, in that same year. Range or variation, of individual hydroperiod length across four years is compared to the individual average hydroperiod of the four years by forest in Figures 1.10 and 1.11. Both state forests showed a positive relationship, however the relationship was only significant for the Paul Bunyan State Forest (Figure 1.10. $R^2 = 0.62$, $P = 0.02$). The range of individual hydroperiod is regressed against the individual average hydroperiod of the fifteen ponds in both forests in Figure 1.12. The individual hydroperiod range difference is correlated with individual average hydroperiod for the fifteen ponds ($R^2 = 0.35$, $P = 0.02$).

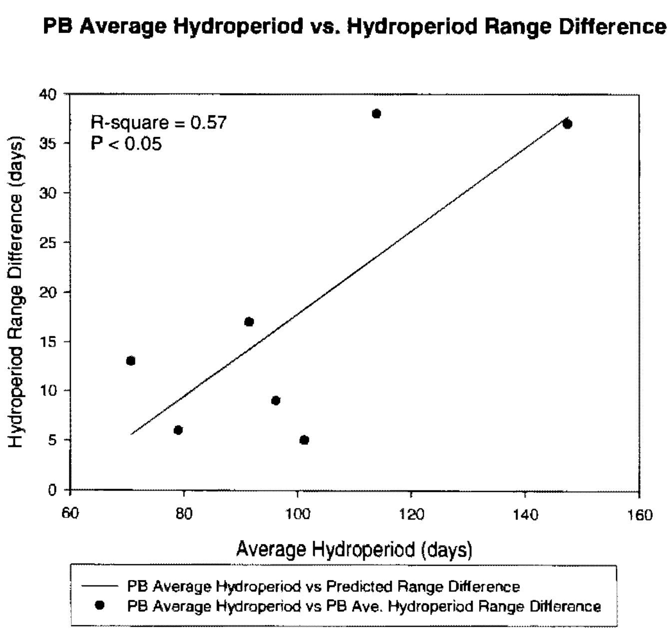

Figure 1.10. Average hydroperiod of each seasonal pond in the Paul Bunyan State Forest (n = 7) from 2006 through 2009 compared to the range (individual seasonal pond variation in hydroperiod length in days). Old-growth site was removed due to tree-harvest.

BV Average Hydroperiod vs. Hydroperiod Range Difference

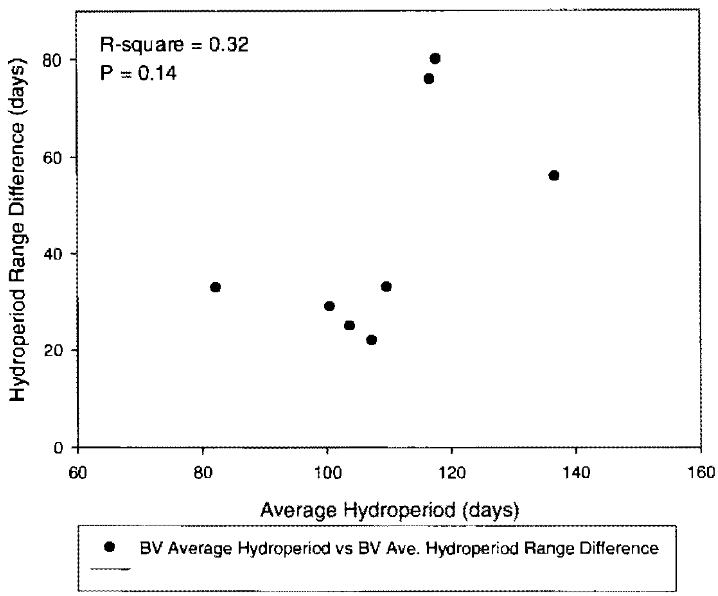

Figure 1.11. Average hydroperiod of each seasonal pond in the Buena Vista State Forest (n = 8) from 2006 through 2009 compared to the range (individual seasonal pond variation in hydroperiod length in days).

PB & BV Individual Average Hydroperiod 2006-2009 vs. Individual Hydroperiod Range Difference

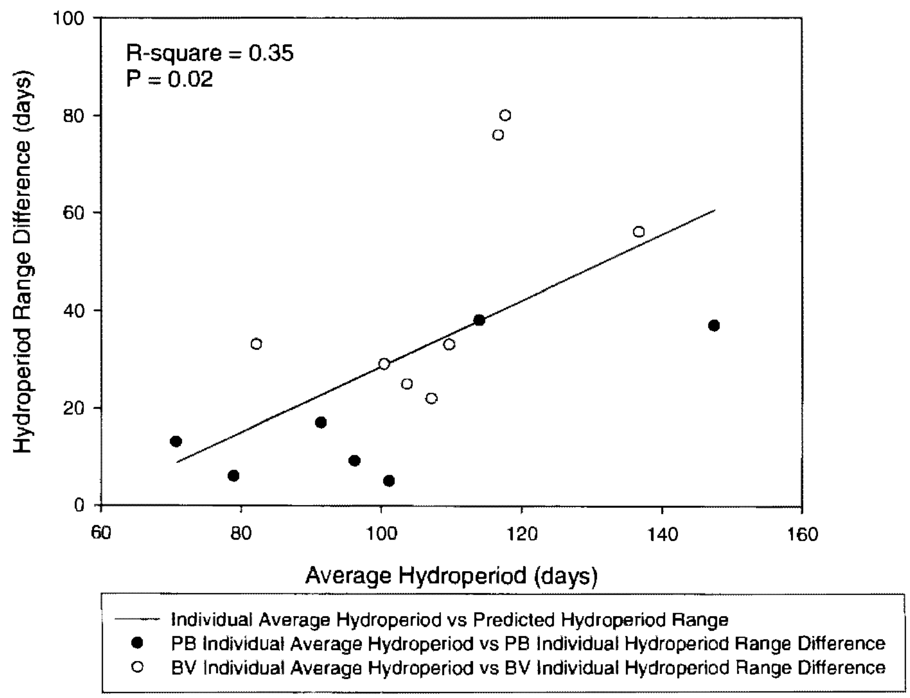

Figure 1.12. Average hydroperiod of each seasonal pond in the Paul Bunyan (n = 7) and Buena Vista State Forest (n = 8) from 2006 through 2009 compared to the range (individual seasonal pond variation in hydroperiod length in days).

The narrowest hydroperiod range among the Buena Vista Forest ponds occurred in 2006, ranging from 85 to 120 days, a difference of only 35 days. The widest range in hydroperiod among the Buena Vista Forest ponds occurred in 2008, ranging from 63 to 151 days, a difference of 88 days. Of the eight ponds in the Buena Vista State Forest a clearcut site had the longest hydroperiod 3 out of the 4 years, while another site which was also a clearcut site had the shortest hydroperiod 3 out of the 4 years in the study.

Precipitation

Precipitation volume was measured at 3 locations within each state forest. Precipitation was collected weekly from mid-May through mid-October in 2008 and 2009 (Precipitation Table in Appendix A). The average precipitation for the Paul Bunyan State Forest in 2008 was approximately 38 cm, and 2009 was approximately 30 cm. The average for the Buena Vista State Forest was approximately 40 cm in 2008 and approximately 29 cm in 2009.

Weekly precipitation was compared to weekly change in water-level in each pond within each State Forest (Figures 1.13-1.16). There was a significant positive relationship between weekly precipitation totals and weekly changes in pond-level during 2008 in both the Buena Vista State Forest (Figure 1.14, $R^2 = 0.38$, $P < 0.0001$), and Paul Bunyan State Forest (Figure 1.13, $R^2 = 0.26$, $P < 0.0001$). In 2009, a significant relationship between weekly precipitation and weekly changes in pond-level was detected but only in the Paul Bunyan State Forest (Figure 1.15, $R^2 = 0.32$, $P < 0.0001$).

2008 PB State Forest Weekly Change in Pond-level vs Weekly Precipitation

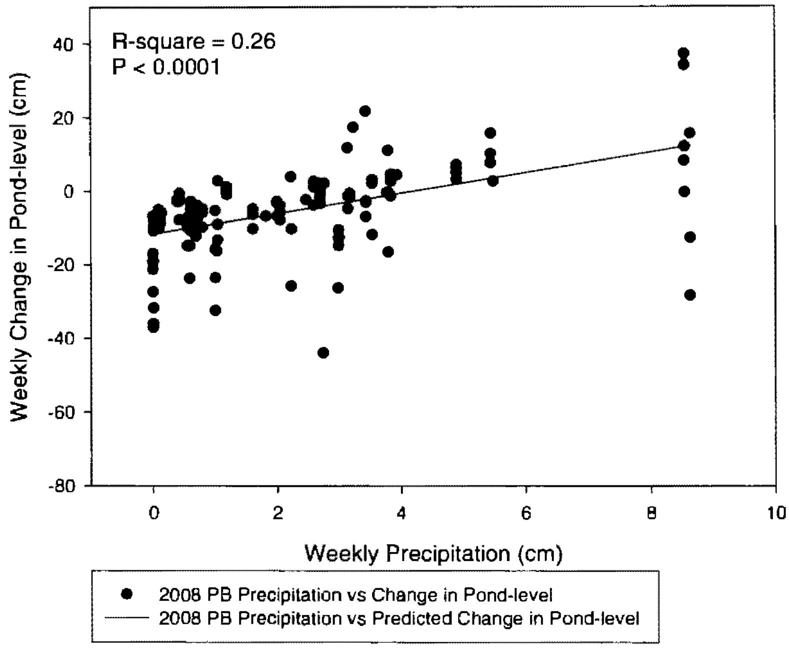

Figure 1.13. Comparing weekly change in pond-level and weekly precipitation in the Paul Bunyan State Forest in 2008.

2008 BV State Forest Weekly Change in Pond-level vs Weekly Precipitation

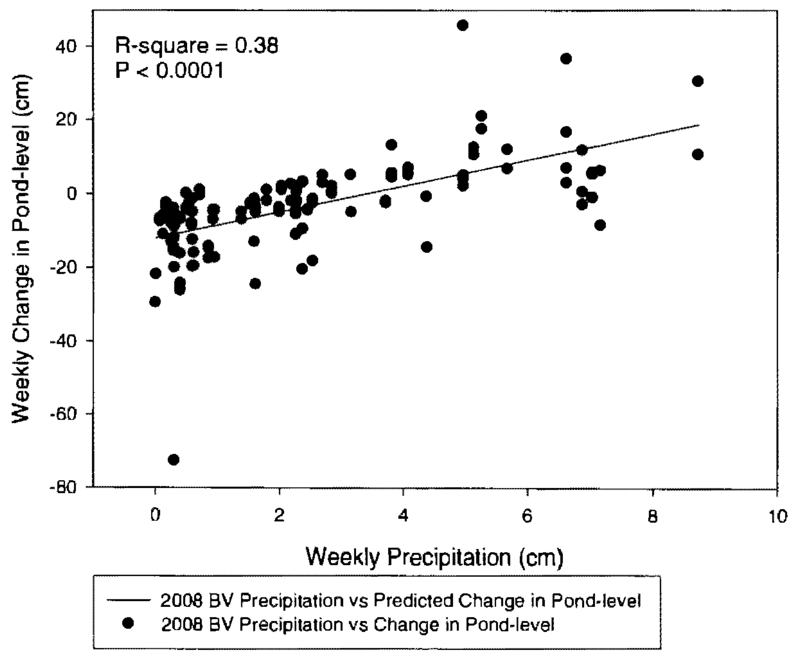

Figure 1.14. Comparing weekly change in pond-level and weekly precipitation in the Buena Vista State Forest in 2008.

2009 PB State Forest Weekly Change in Pond-level vs. Weekly Precipitation

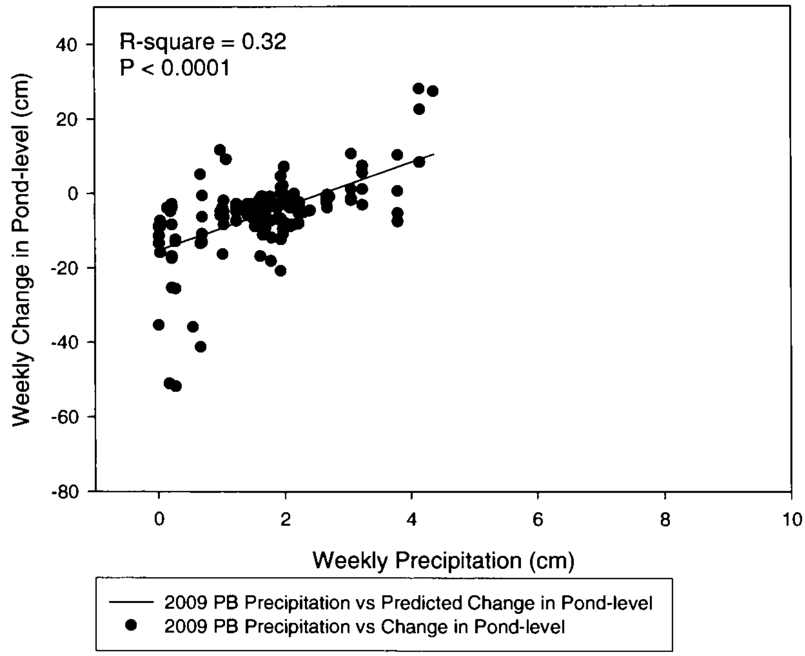

Figure 1.15. Comparing weekly change in pond-level and weekly precipitation in the Paul Bunyan State Forest in 2009.

2009 BV State Forest Weekly Change in Pond-level vs Weekly Precipitation

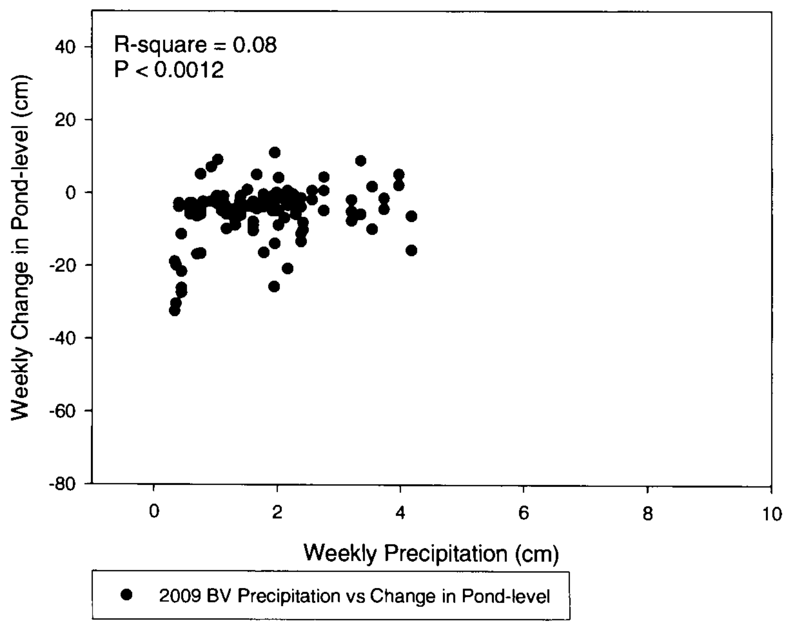

Figure 1.16. Comparing weekly change in pond-level and weekly precipitation in the Buena Vista State Forest in 2009.

Weekly precipitation was combined by year and compared to weekly change in water-level in each pond within the Paul Bunyan State Forest for each month (May – October) (Figures 1.17-1.22). There was a significant positive relationship between weekly precipitation totals and weekly changes in pond-level in the months of June (Figure 1.18, R^2 = 0.65, P < 0.0001), July (Figure 1.19, R^2 = 0.4, P < 0.0001), August (Figure 1.20, R^2 = 0.57, P < 0.0001), and September (Figure 1.21, R^2 = 0.23, P < 0.01). There was a non-significant relationship between change in pond-level and weekly precipitation for the months of May (Figure 1.17, R^2 = 0.03, P = 0.40), and October (Figure 1.22, R^2 = 0.12, P = 0.09) in the Paul Bunyan State Forest.

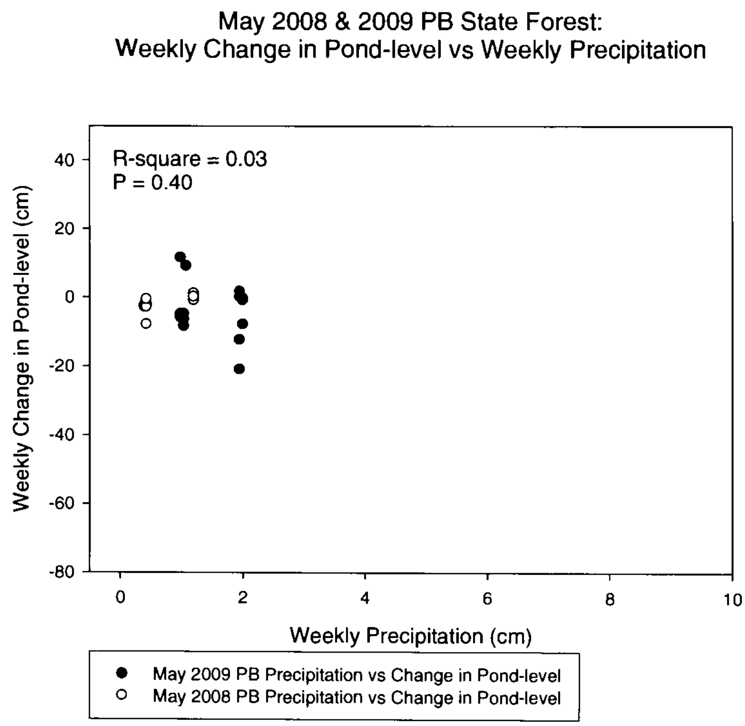

Figure 1.17. Comparing weekly change in pond-level and weekly precipitation during the month of May in the Paul Bunyan State Forest in 2008 and 2009.

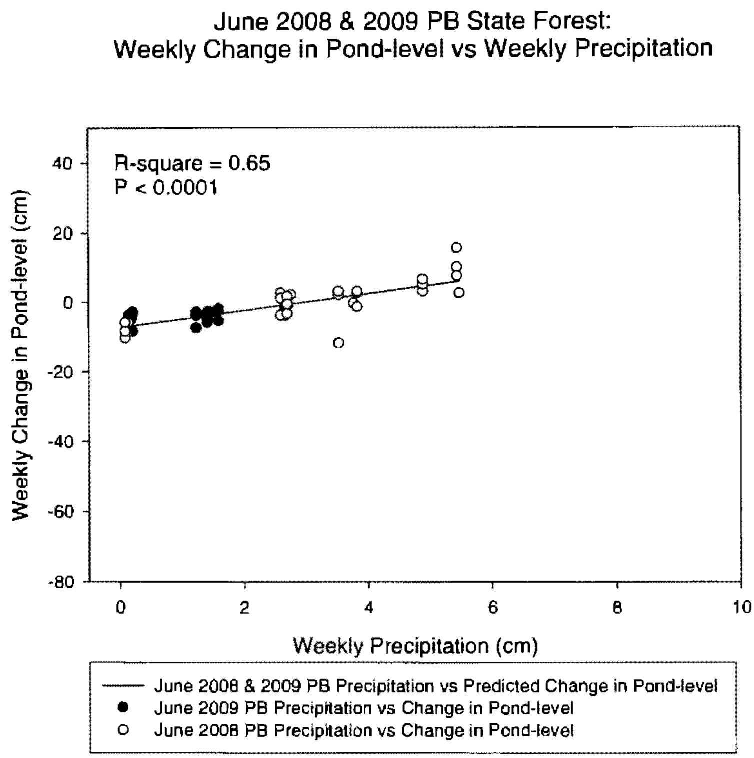

Figure 1.18. Comparing weekly change in pond-level and weekly precipitation during the month of June in the Paul Bunyan State Forest in 2008 and 2009.

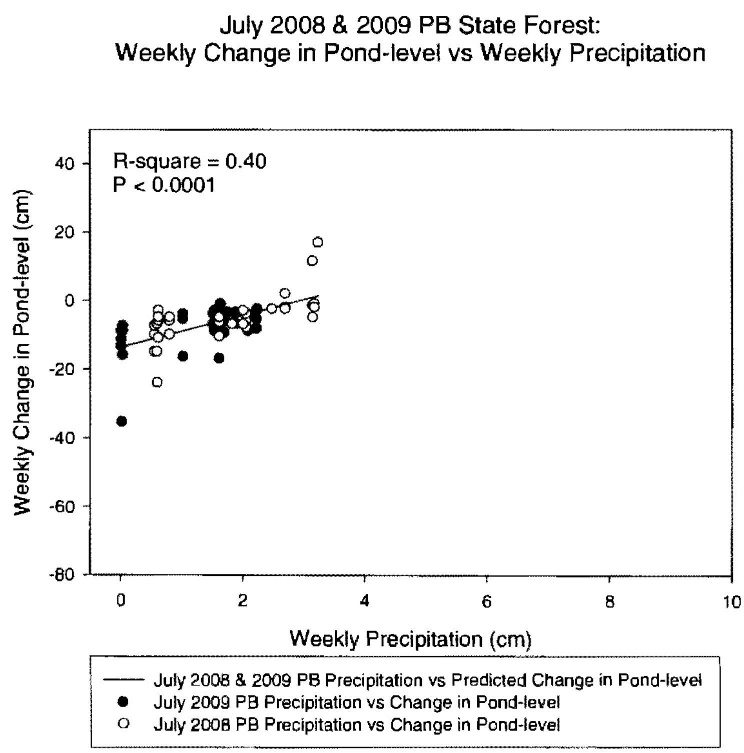

Figure 1.19. Comparing weekly change in pond-level and weekly precipitation during the month of July in the Paul Bunyan State Forest in 2008 and 2009.

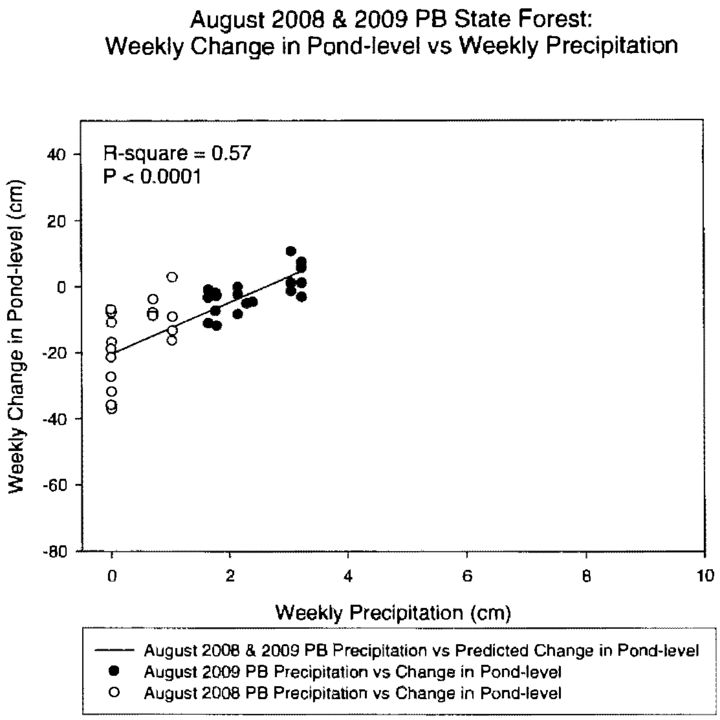

Figure 1.20. Comparing weekly change in pond-level and weekly precipitation during the month of August in the Paul Bunyan State Forest in 2008 and 2009.

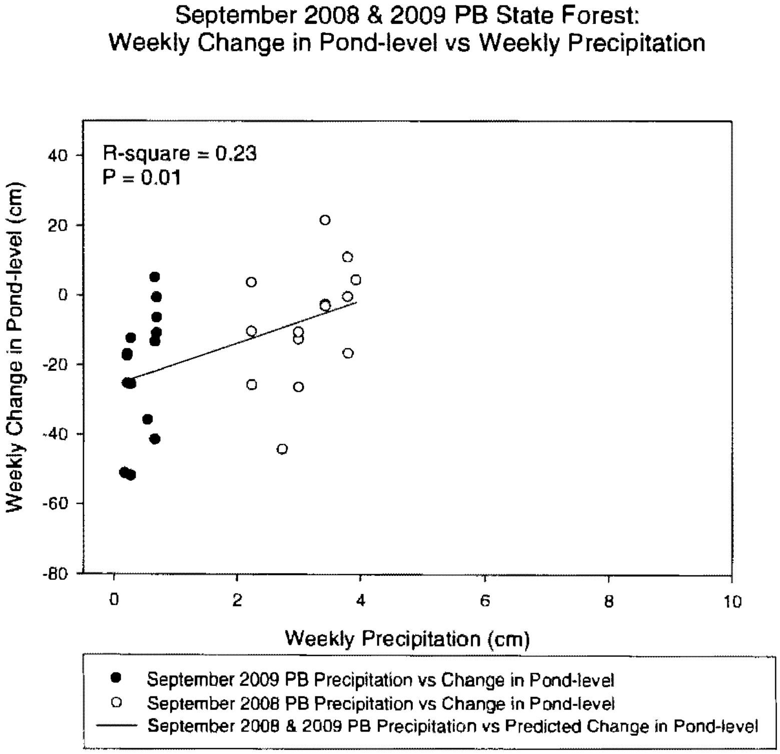

Figure 1.21. Comparing weekly change in pond-level and weekly precipitation during the month of September in the Paul Bunyan State Forest in 2008 and 2009.

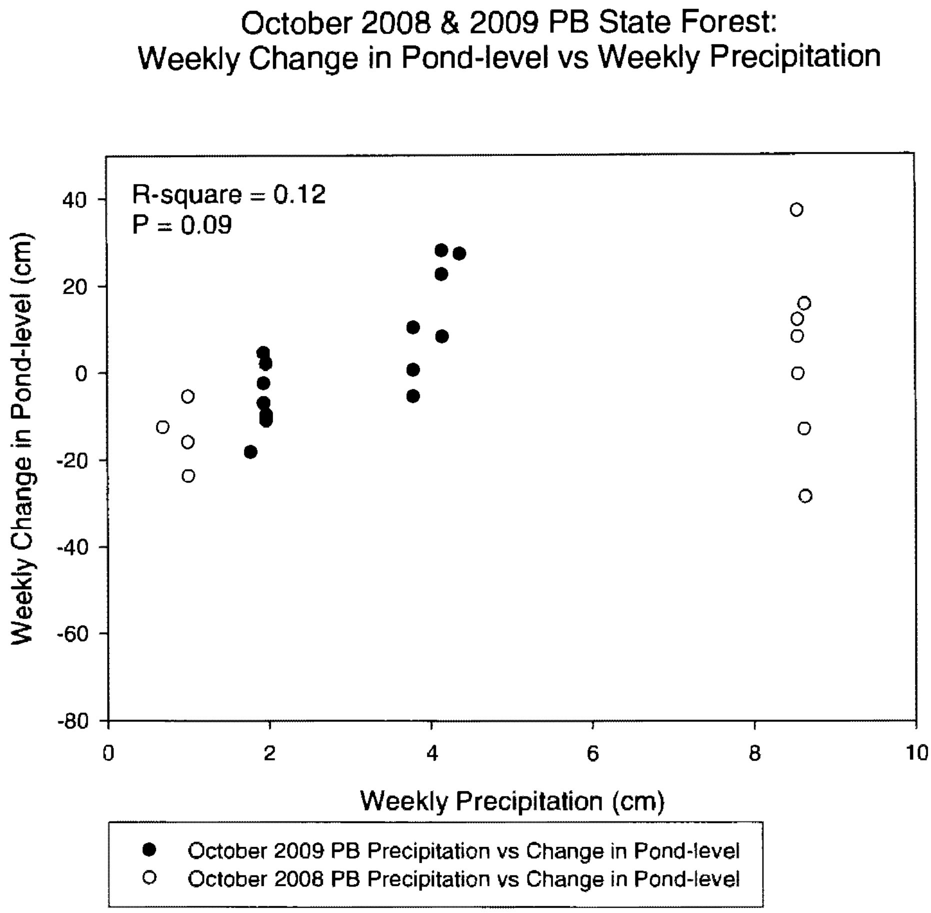

Figure 1.22. Comparing weekly change in pond-level and weekly precipitation during the month of October in the Paul Bunyan State Forest in 2008 and 2009.

Weekly precipitation was combined by year and compared to weekly change in water-level in each pond within the Buena Vista State Forest for each month (May – October) (Figures 1.23-1.28). There was a significant positive relationship between weekly precipitation totals and weekly changes in pond-level in the months of June (R^2 = 0.59, P < 0.0001), July (R^2 = 0.24, P < 0.0001), August (R^2 = 0.25, P = 0.0008), September (R^2 = 0.74, P < 0.0001), and October (R^2 = 0.61, P < 0.0001). May was only month in the Buena Vista State Forest that had non-significant relationship between weekly change in pond-level and weekly precipitation (R^2 = 0.02, P < 0.49).

May 2008 & 2009 BV State Forest:
Weekly Change in Pond-level vs Weekly Precipitation

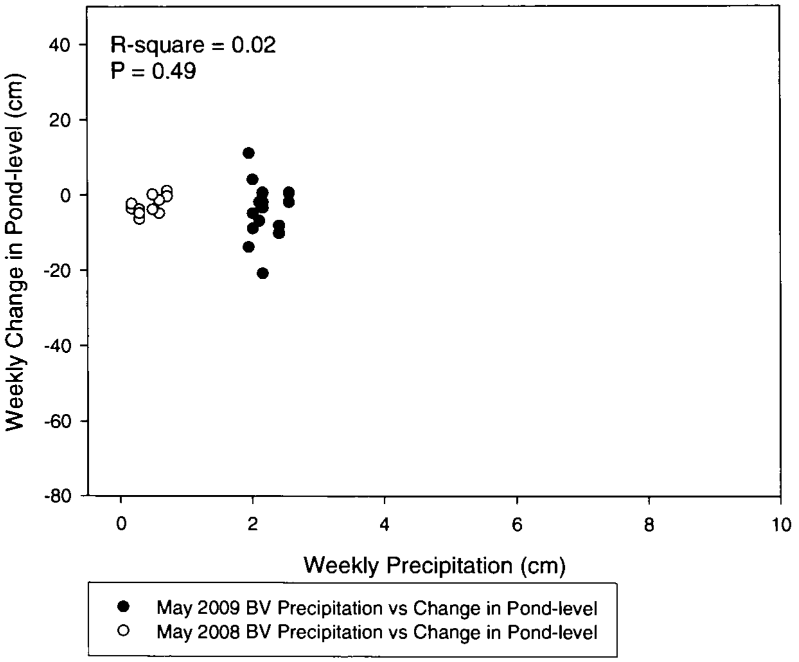

Figure 1.23. Comparing weekly change in pond-level and weekly precipitation during the month of May in the Buena Vista State Forest in 2008 and 2009.

June 2008 & 2009 BV State Forest:
Weekly Change in Pond-level vs Weekly Precipitation

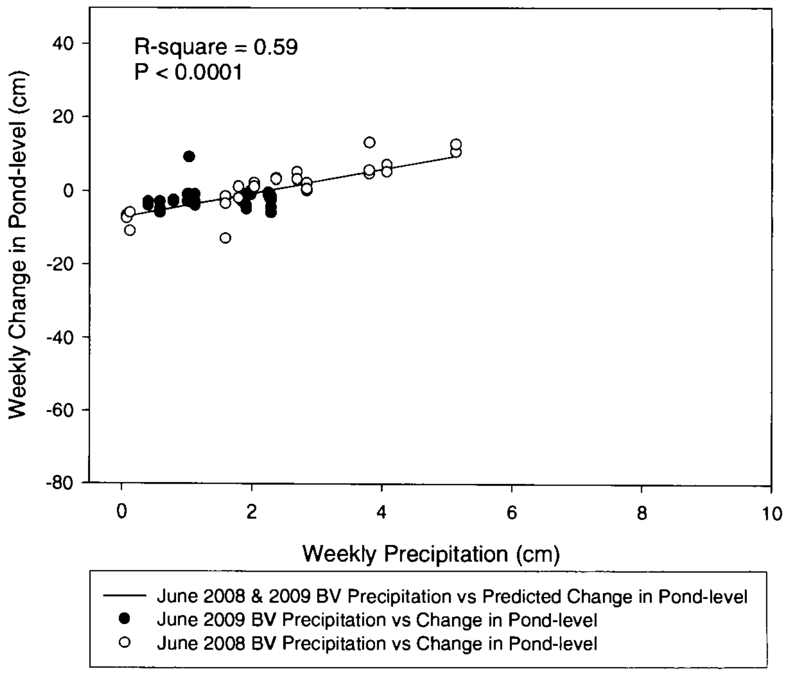

Figure 1.24. Comparing weekly change in pond-level and weekly precipitation during the month of June in the Buena Vista State Forest in 2008 and 2009.

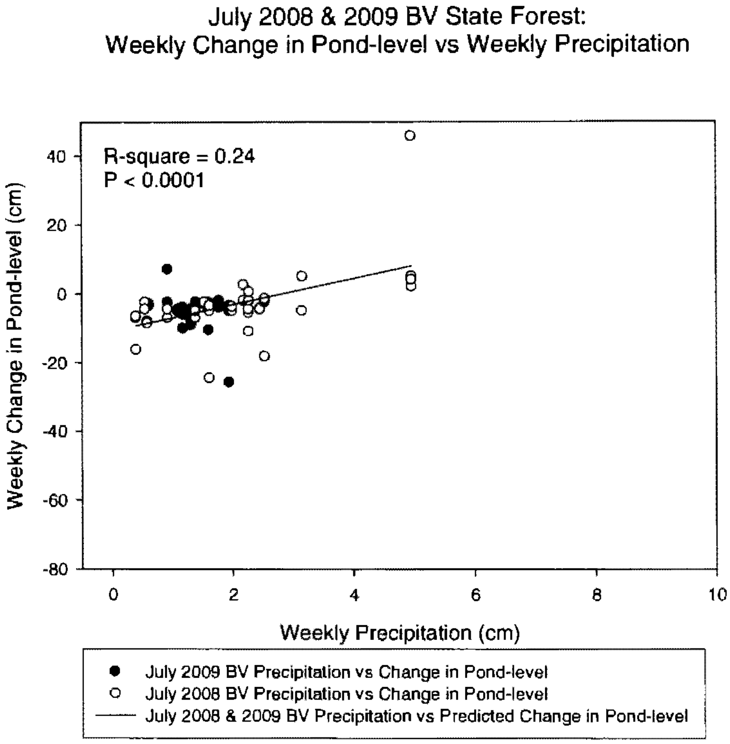

Figure 1.25. Comparing weekly change in pond-level and weekly precipitation during the month of July in the Buena Vista State Forest in 2008 and 2009.

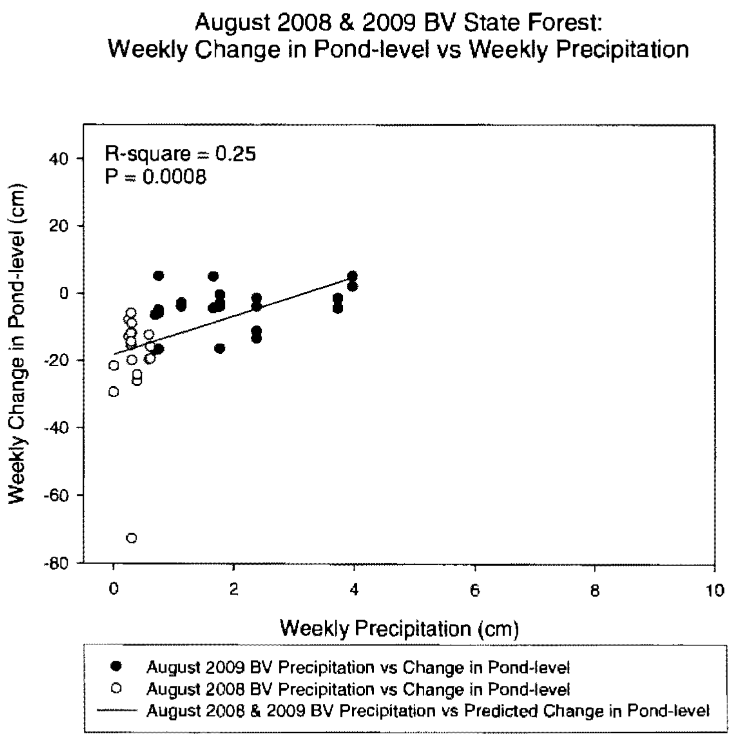

Figure 1.26. Comparing weekly change in pond-level and weekly precipitation during the month of August in the Buena Vista State Forest in 2008 and 2009.

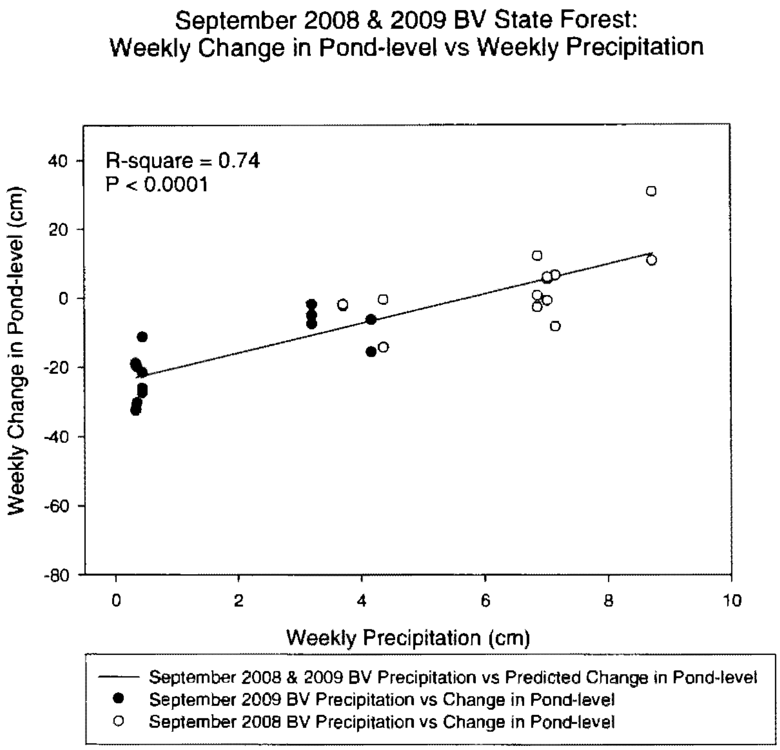

Figure 1.27. Comparing weekly change in pond-level and weekly precipitation during the month of September in the Buena Vista State Forest in 2008 and 2009.

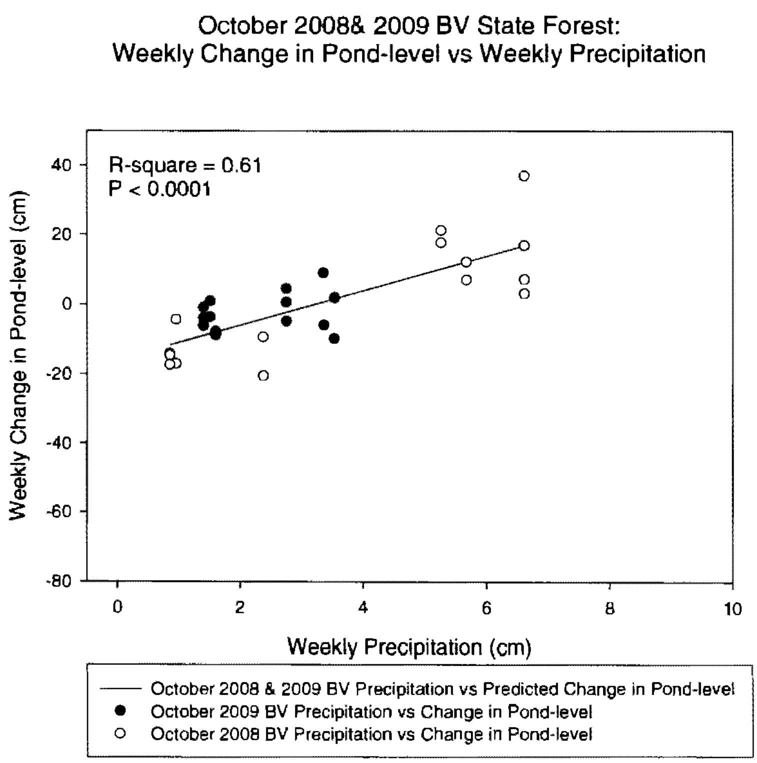

Figure 1.28. Comparing weekly change in pond-level and weekly precipitation during the month of October in the Buena Vista State Forest in 2008 and 2009.

Weekly precipitation was combined by year and forest and compared to weekly change in water-level in each pond for each month (May – October) (Figures 1.29-1.34). There was a significant positive relationship between weekly precipitation totals and weekly changes in pond-level in the months of June (Figure 1.30, $R^2 = 0.58$, $P < 0.0001$), July (Figure 1.31, $R^2 = 0.31$, $P < 0.0001$), August (Figure 1.32, $R^2 = 0.38$, $P < 0.0001$), September (Figure 1.33, $R^2 = 0.44$, $P < 0.0001$), and October (Figure 1.34, $R^2 = 0.26$, $P < 0.0001$). The only month to have a non-significant relationship between weekly change in pond-level and weekly precipitation with years and state forests combined was May (Figure 1.29, $R^2 = 0.026$, $P < 0.26$).

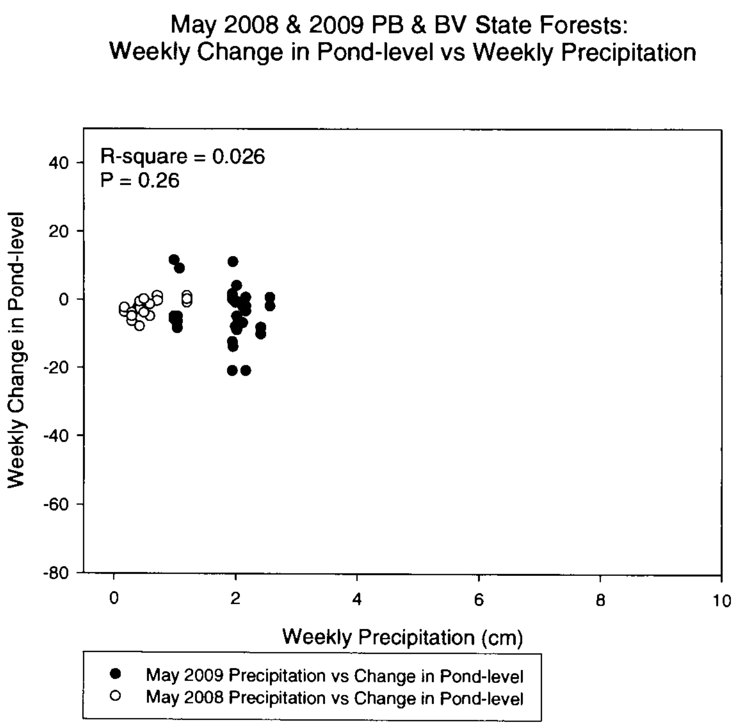

Figure 1.29. Comparing weekly change in pond-level and weekly precipitation during the month of May in the Buena Vista, and Paul Bunyan State Forest in 2008 and 2009.

June 2008 & 2009 PB & BV State Forests:
Weekly Change in Pond-level vs Weekly Precipitation

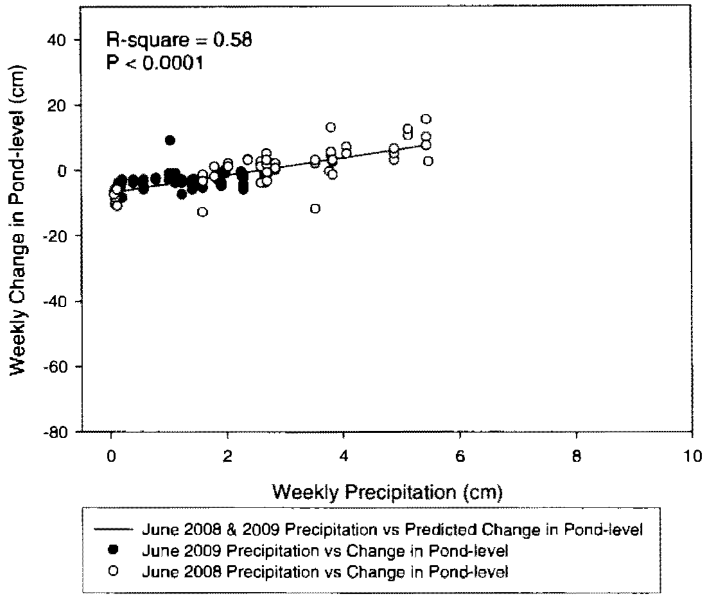

Figure 1.30. Comparing weekly change in pond-level and weekly precipitation during the month of June in the Buena Vista, and Paul Bunyan State Forest in 2008 and 2009.

July 2008 & 2009 PB & BV State Forests:
Weekly Change in Pond-level vs Weekly Precipitation

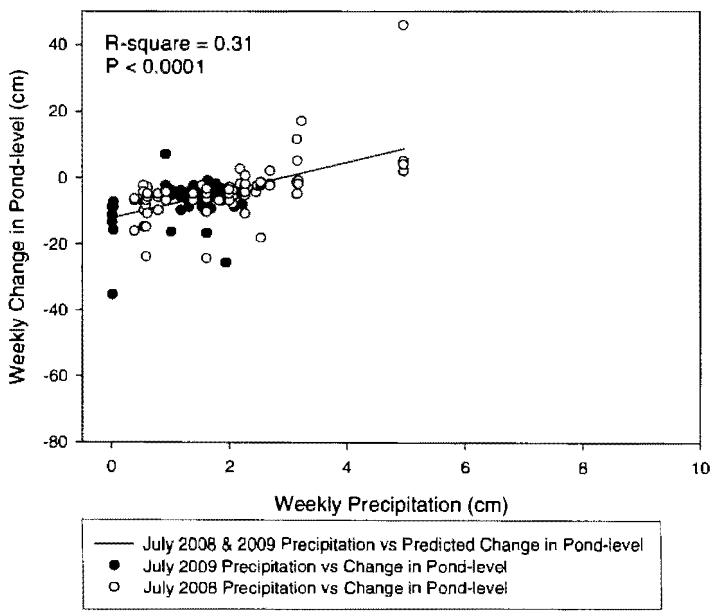

Figure 1.31. Comparing weekly change in pond-level and weekly precipitation during the month of July in the Buena Vista, and Paul Bunyan State Forest in 2008 and 2009.

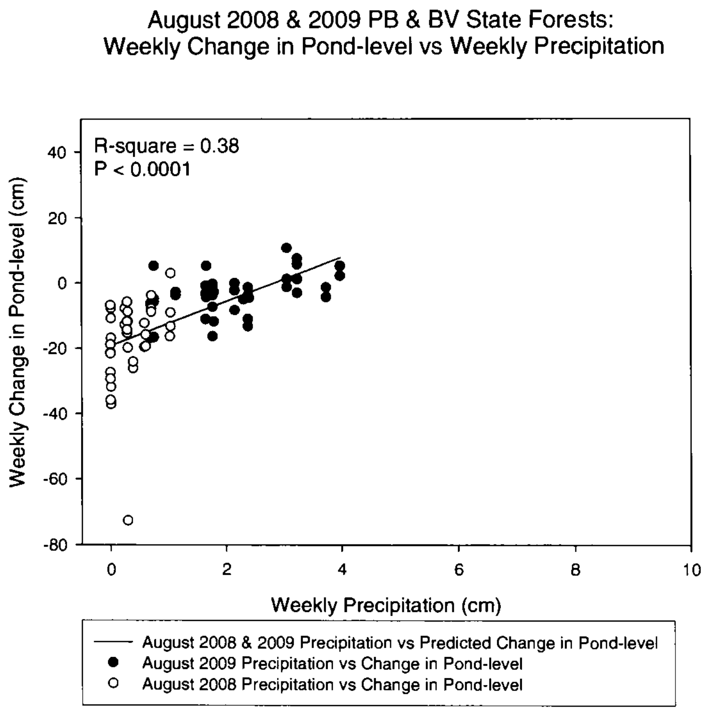

Figure 1.32. Comparing weekly change in pond-level and weekly precipitation during the month of August in the Buena Vista, and Paul Bunyan State Forest in 2008 and 2009.

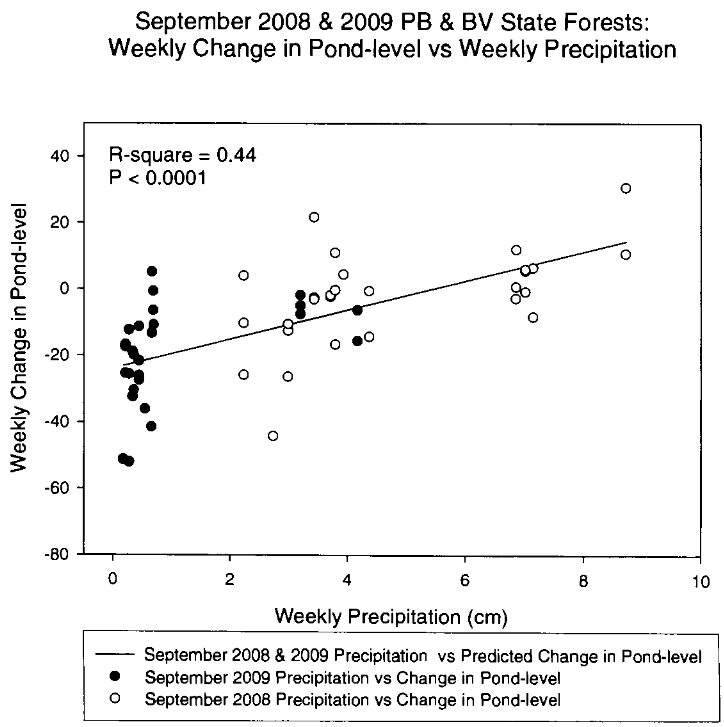

Figure 1.33. Comparing weekly change in pond-level and weekly precipitation during the month of September in the Buena Vista, and Paul Bunyan State Forest in 2008 and 2009.

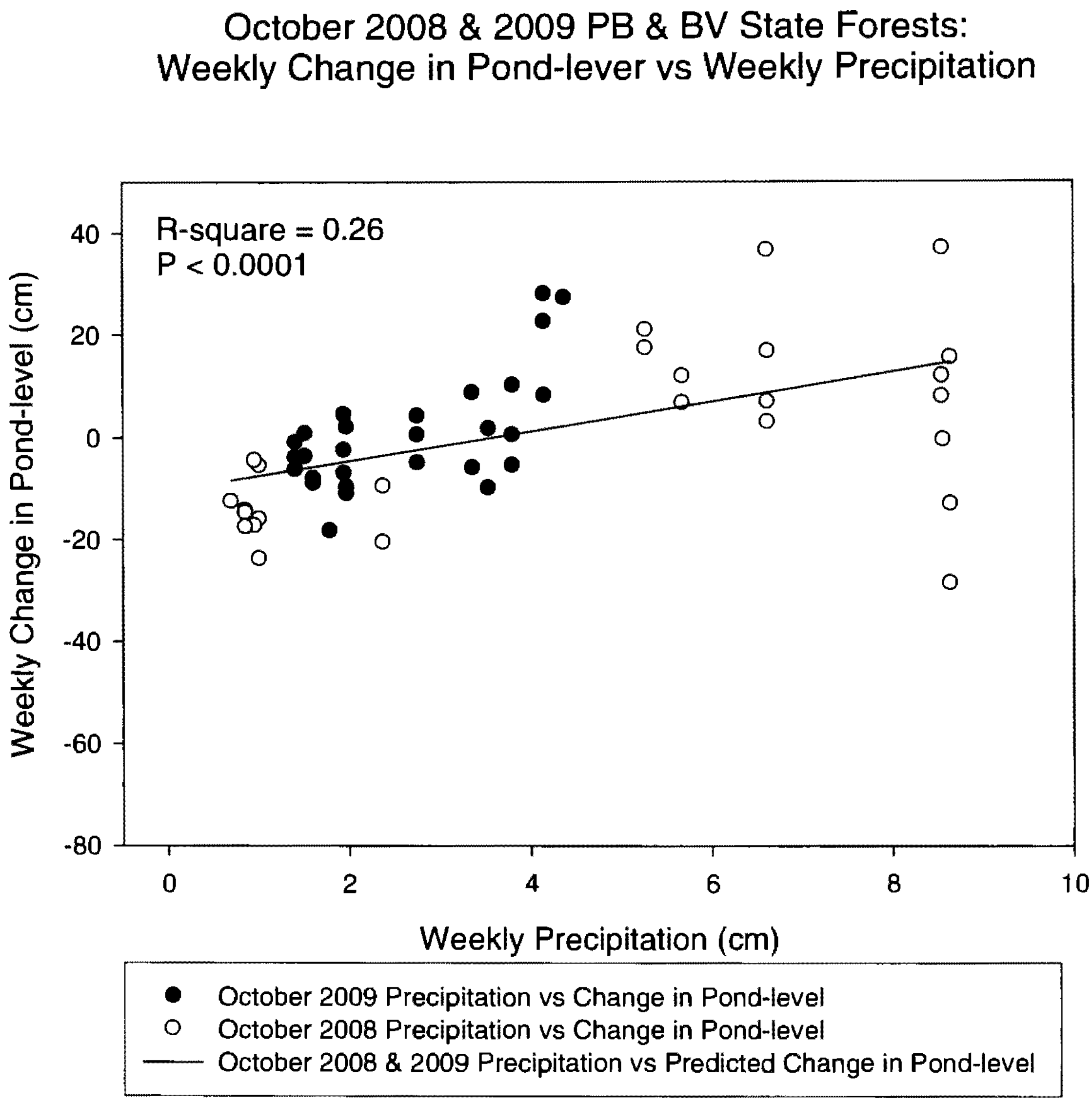

Figure 1.34. Comparing weekly change in pond-level and weekly precipitation during the month of October in the Buena Vista, and Paul Bunyan State Forest in 2008 and 2009.

Wetland Function/Classification

Piezometer nest results indicate that high, but variable, water exchange occurs between the 16 study ponds and groundwater. The hydrologic function of the ponds varied from recharge, to flow-through, to perched (Table 1.6). Among the 16 seasonal ponds, 4 ponds in the Paul Bunyan and 5 ponds in the Buena

Vista State Forests functioned as recharge ponds. An example of a piezometer nest showing recharge is given in Figure 1.35.

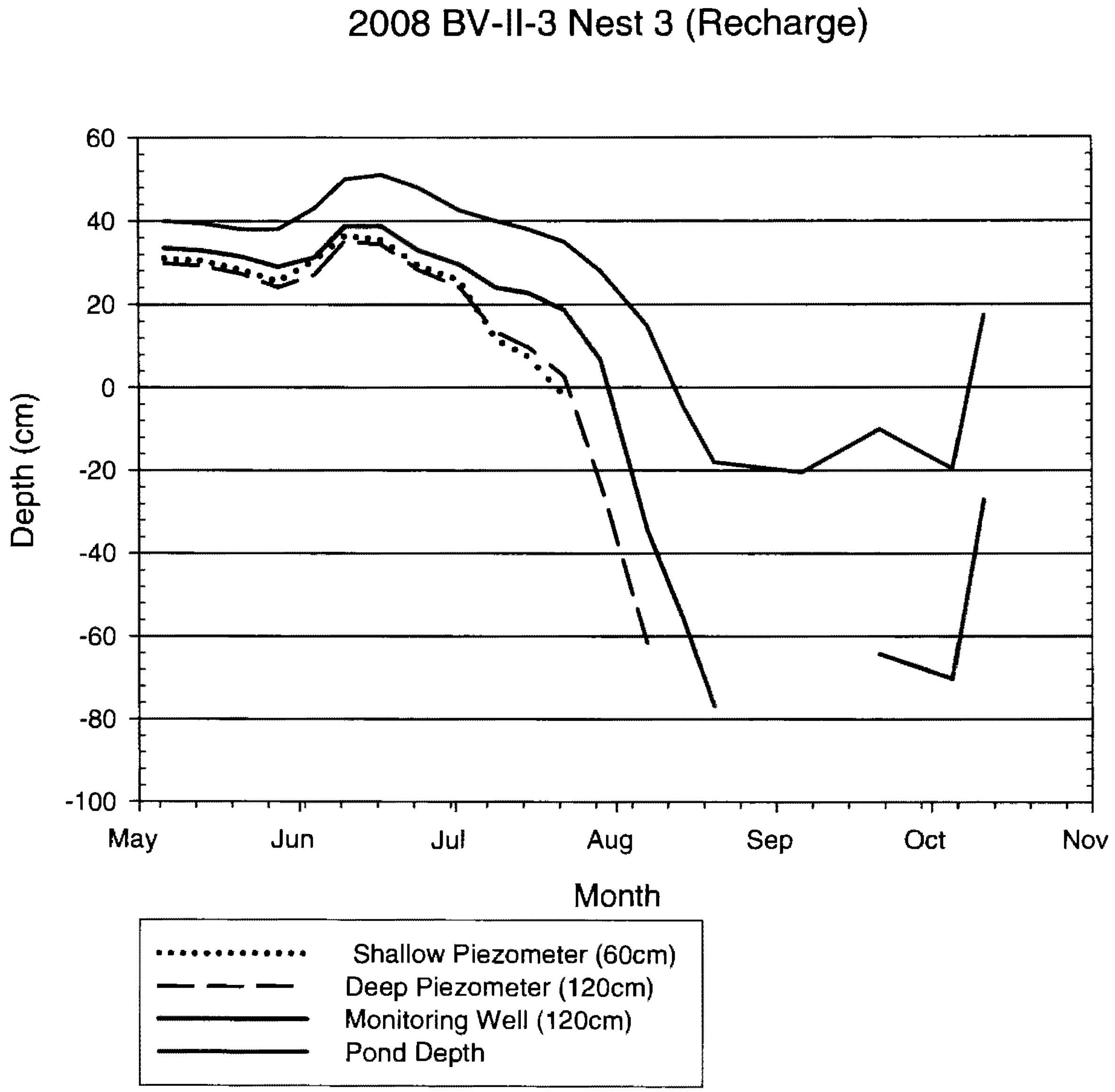

Figure 1.35. Piezometer nest showing groundwater recharge. Piezometer and well water-levels are below pond water-levels showing that pond water is recharging groundwater.

Table 1.6. Hydrologic Functions of each seasonal pond in the Paul Bunyan and Buena Vista State Forest.

Paul Bunyan State Forest		Buena Vista State Forest	
Pond	Hydro. Function	Pond	Hydro. Function
PB-I-1	Recharge	BV-I-2	Recharge
PB-I-3	Recharge	BV-II-3	Recharge
PB-III-1	Recharge	BV-III-1	Recharge
PB-II-1	Flow-Through	BV-III-2	Recharge
PB-II-4	Flow-Through	BV-III-3	Flow-Through
PB-III-2	Flow-Through	BV-I-1	Flow-Through
PB-III-3	Flow-Through	BV-II-4	Perched
PB-III-4	Flow-Through	BV-III-4	Perched

In 2008 13 of the 16 seasonal ponds, and in 2009, 10 of the 16 seasonal ponds had groundwater discharging into their basins. In these cases, formation of ephemeral groundwater mounds caused a hydraulic gradient to form towards the ponds (Figure 1.36). These ephemeral groundwater mounds formed due to snowmelt and high precipitation rates during early spring and lasted from 1 to 8 weeks. Discharge lasted for as long as 13 to 19 weeks. Such groundwater mounds were much more ephemeral for recharge ponds than for flow-through ponds, and generally disappeared with increasing seasonal evapotranspiration. In flow-through ponds groundwater mounds lasted much longer if not throughout the growing season. The groundwater mounds along the perimeters of flow-through ponds did however decrease in elevation and may have been influenced by increasing evapotranspiration. Groundwater mounds typically rose again in the fall; likely due to increased precipitation and decreasing evapotranspiration.

2008 BV-III-1 Nest 4 (Discharge/Recharge)

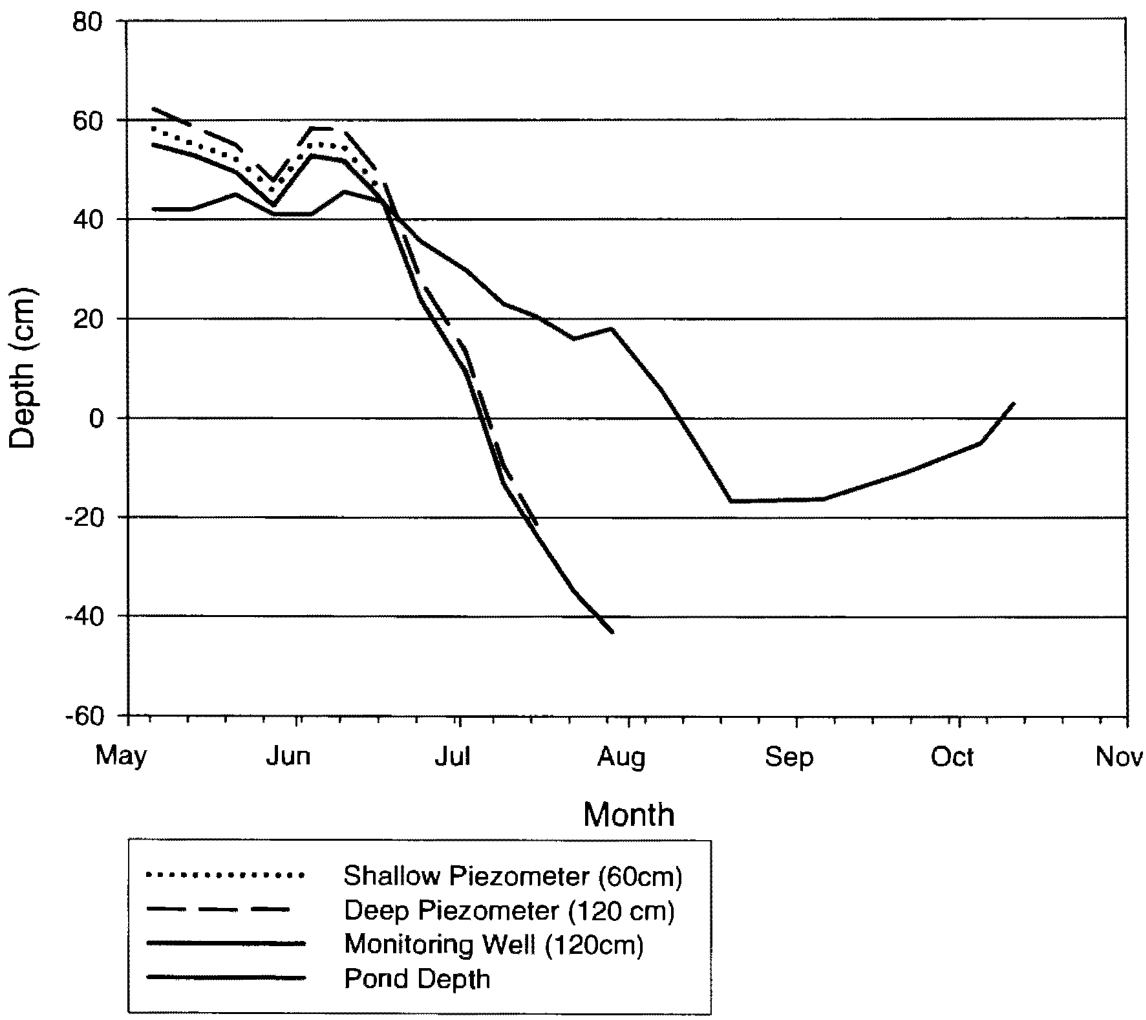

Figure 1.36. Discharge during beginning of season due to formation of ephemeral groundwater mounds along pond perimeter. Groundwater mounds were indicated by elevated groundwater levels in piezometers and wells compared to standing water levels in pond basins. Once water levels in well and piezometers fell below pond water level, pond water begins to recharge the groundwater and the pond then switches from discharge to recharge.

Five of the 16 seasonal ponds in the study were classified as flow-through. Ponds that were classified as flow-through had at least one piezometer nest displaying groundwater discharge during the entire time or significant portion of the time the pond basin contained standing water, and at least one other piezometer nest indicating that pondwater was recharging the groundwater.

The relationship between duration of groundwater discharge and length of pond hydroperiod differed between the two forests. Ponds in the Paul Bunyan State Forest showed a positive correlation between hydroperiod length and duration of groundwater discharge both years (2008 $R^2 = 0.61$, p-value = 0.02, Figure 1.37, 2009 $R^2 = 0.66$, p-value = 0.01, Figure 1.39). No significant relationship of this sort was detected in the Buena Vista State Forest for either year (Figure 1.38 and Figure 1.40). One flow-through pond in the Buena Vista State Forest exhibited groundwater discharged for 9 weeks in 2008 and 11 weeks in 2009, yet had the shortest hydroperiod of all study ponds in the Buena Vista State Forest (63 days in 2008, and 85 days in 2009). Because the pond is flow-through, the shortened hydroperiod reflected an imbalance between rates of groundwater discharge and pond water recharge, with pond water recharging at a higher rate.

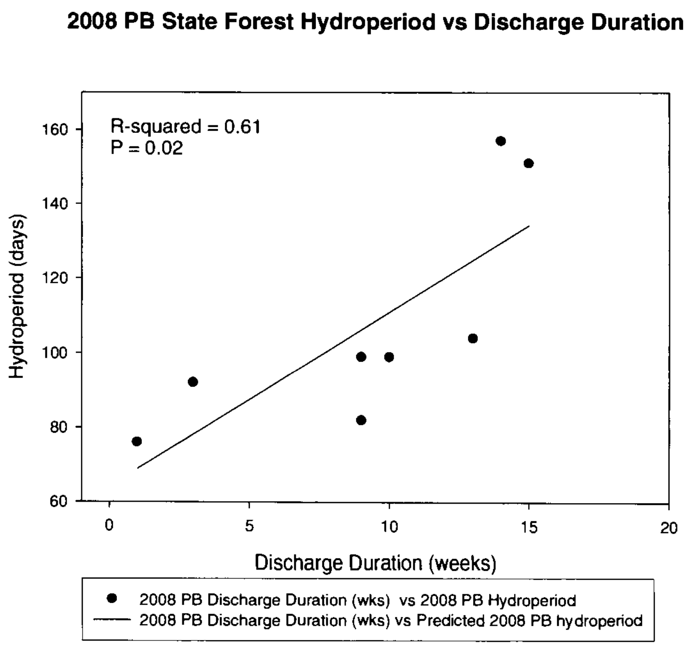

Figure 1.37. Influence of groundwater discharge duration on hydroperiod in the Paul Bunyan State Forest in 2008 (n = 8).

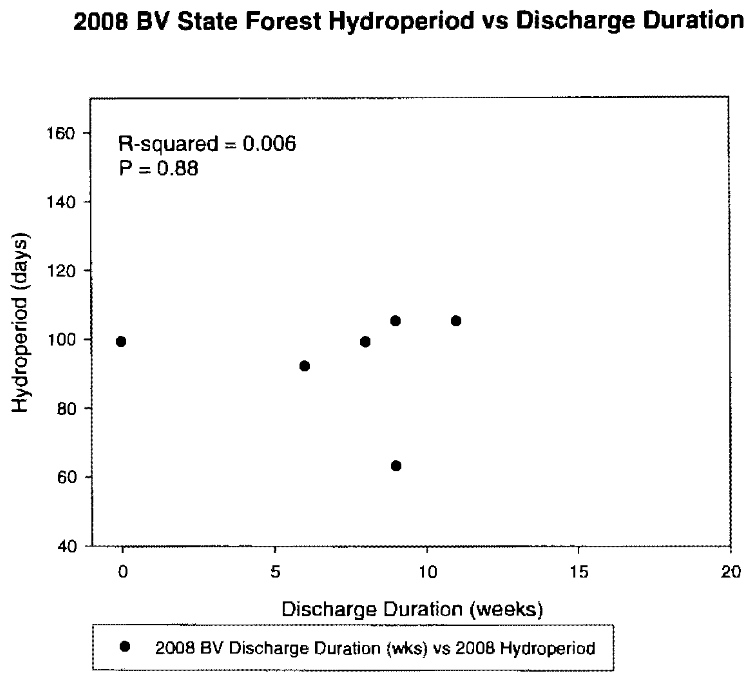

Figure 1.38. Influence of groundwater discharge duration on hydroperiod in the Buena Vista State Forest in 2008 (n = 6, 2 ponds in the Buena Vista State Forest are perched and there for did not exhibit groundwater discharge).

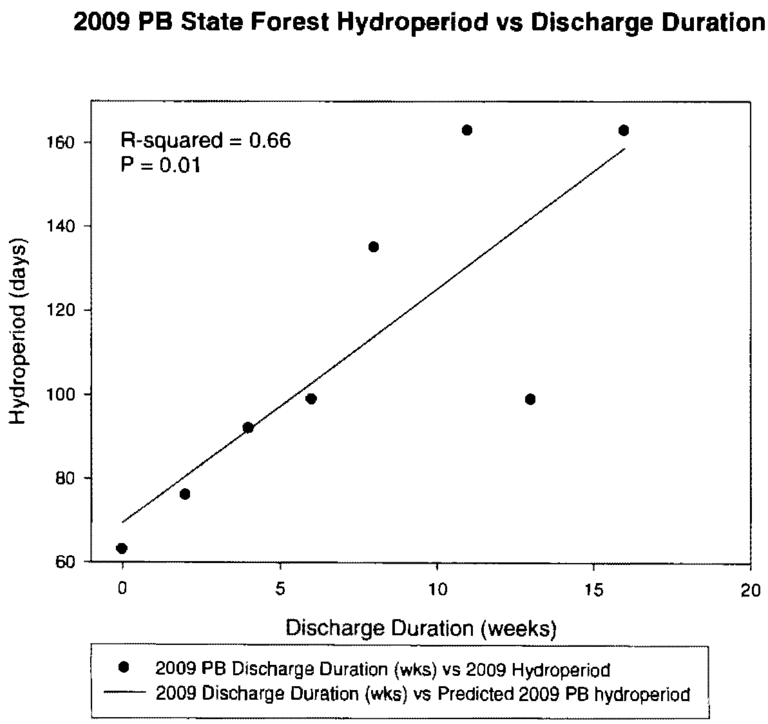

Figure 1.39. Influence of groundwater discharge duration on hydroperiod in the Paul Bunyan State Forest in 2009 (n = 8).

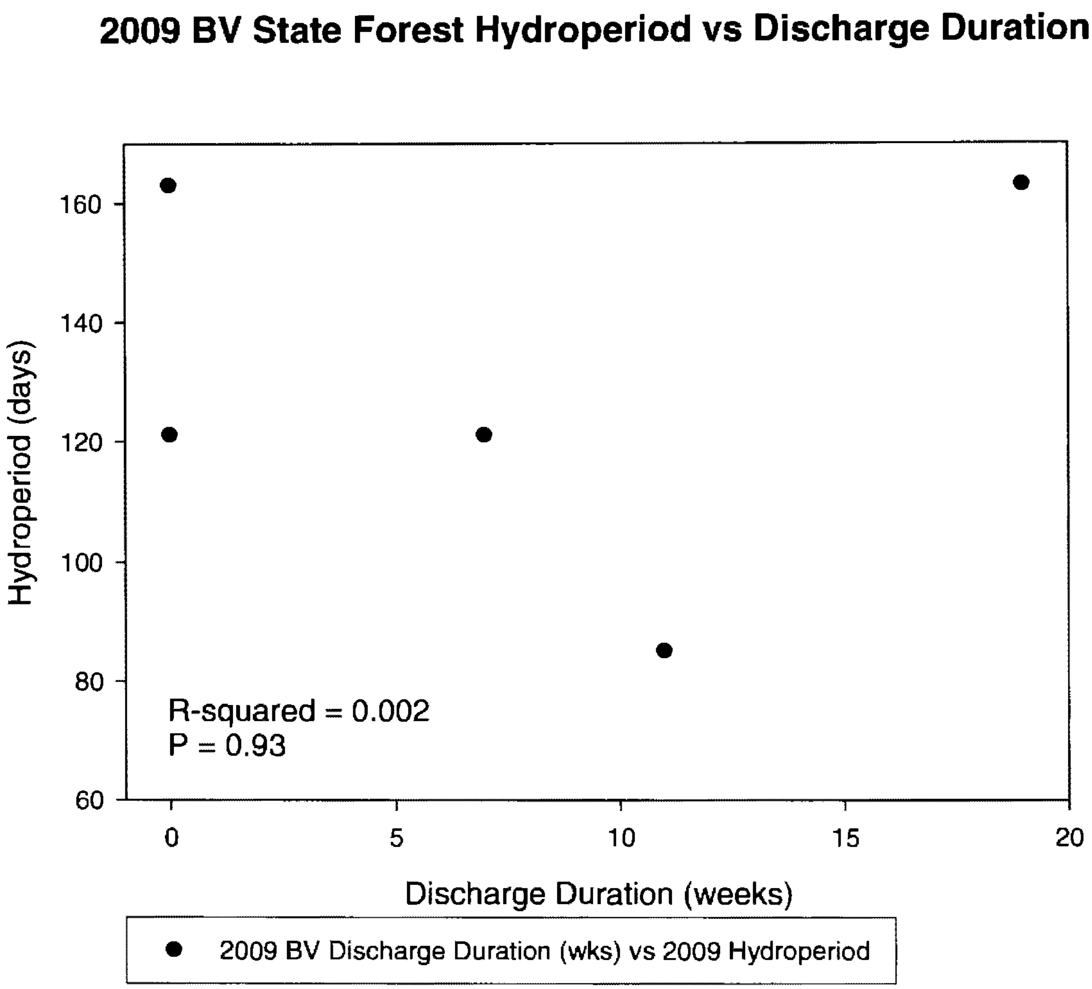

Figure 1.40. Influence of groundwater discharge duration on hydroperiod in the Buena Vista State Forest in 2009 (n = 6, 2 ponds in the Buena Vista State Forest are perched and there for did not exhibit groundwater discharge). (2 ponds exhibited identical discharge duration and hydroperiod length making it appear in the figure as though there are 5 ponds).

Only two of the 16 study sites, both located in the Buena Vista State Forest, were classified as perched ponds due to weak correspondence between pond water and groundwater fluctuations (e.g. Figure 1.41). This very limited relationship between changes in pond water-levels and groundwater dynamics is likely due to the soil profiles of the two basins, both having C horizons with clay levels as high as 51%.

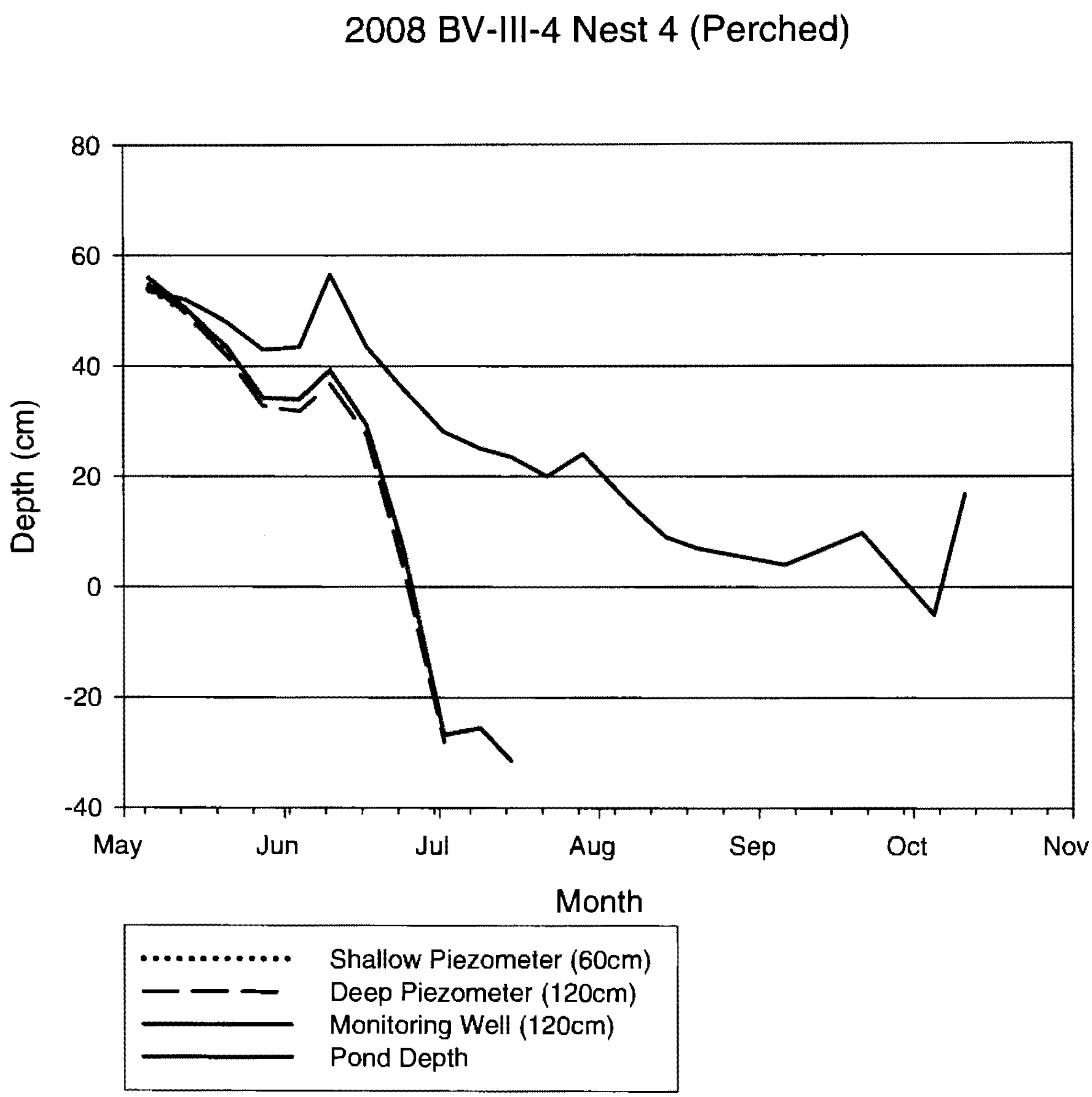

Figure 1.41. Piezometer nest representing a perched wetland. Standing water remains in pond basin for an extended period of time while groundwater levels recede below piezometers and monitoring well.

Precipitation can influence both local groundwater and pond water levels. Influence of precipitation can also depend on the connection between these two entities. For each hydrological function category, weekly precipitation totals were compared to changes in pond water level (Figures 1.42, 1.43: recharge ponds, Figures 1.44, 1.45: flow-through ponds, Figures 1.46, 1.47: perched ponds). For recharge ponds, there was only a weak correlation between weekly precipitation and change in pond level in both 2008 ($R^2 = 0.24$, $P < 0.0001$, Figure 1.42), and in 2009 ($R^2 = 0.19$, $P < 0.0001$, Figure 1.43). A significant positive relationship was found between weekly precipitation and change in pond-level in flow-through ponds in 2008 ($R^2 = 0.37$, $P < 0.0001$, Figure 1.44), and a weaker yet still significant relationship was seen in flow-through ponds in 2009 ($R^2 = 0.22$, $P < 0.0001$, Figure 1.45). Perched ponds showed a stronger relationship between precipitation and change in pond level both years (2008 $R^2 = 0.57$, $P < 0.0001$, Figure 1.46; 2009 $R^2 = 0.36$, $P = 0.0003$, Figure 1.47).

2008 Recharge Ponds Weekly Change in Pond-level vs Weekly Precipitation

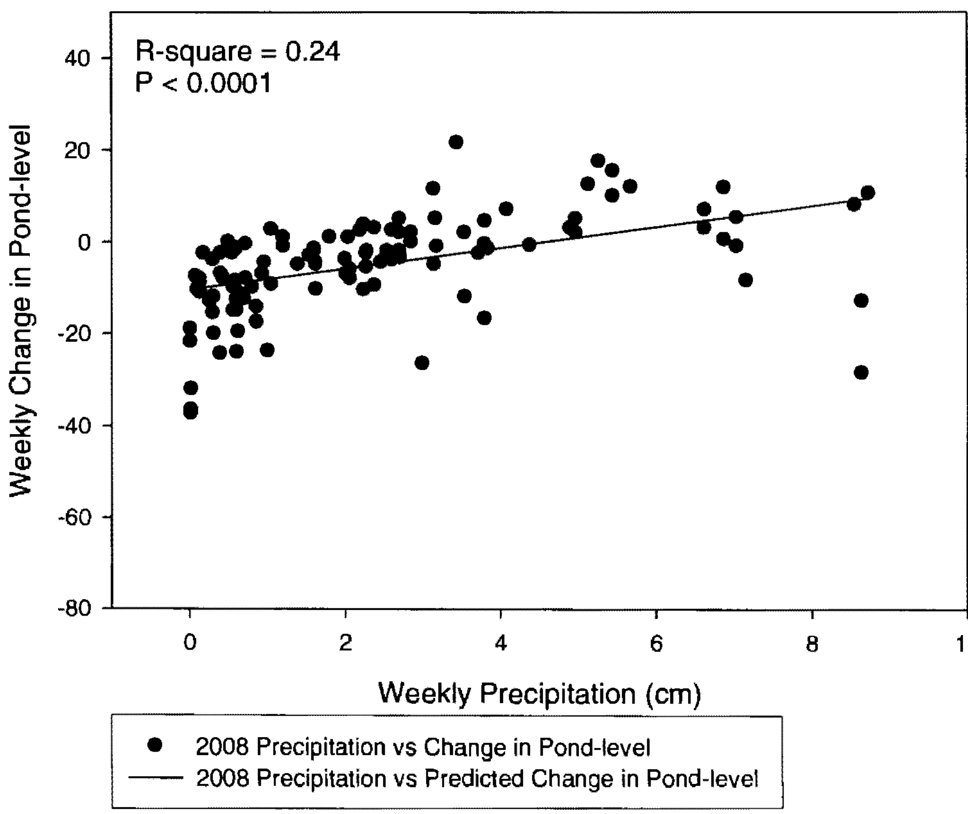

Figure 1.42. Relationship between weekly change in pond-level of recharge ponds with weekly precipitation in 2008 (n = 7, Ponds located in both Buena Vista and Paul Bunyan State Forests).

2009 Recharge Ponds Weekly Change in Pond-level vs. Weekly Precipitation

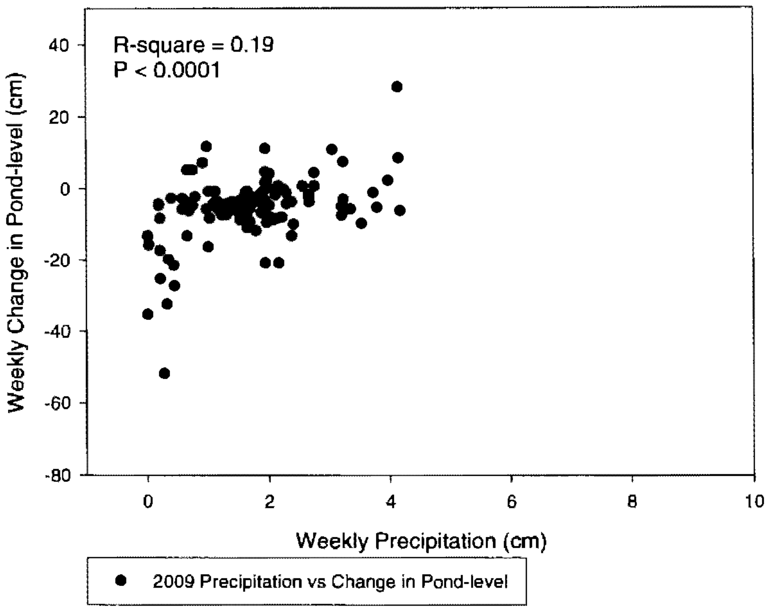

Figure 1.43. Relationship between weekly change in pond-level of recharge ponds with weekly precipitation in 2009 (n = 7, Ponds located in both Buena Vista and Paul Bunyan State Forests).

2008 Flow-Through Ponds Weekly Change in Pond-level vs Weekly Precipitation

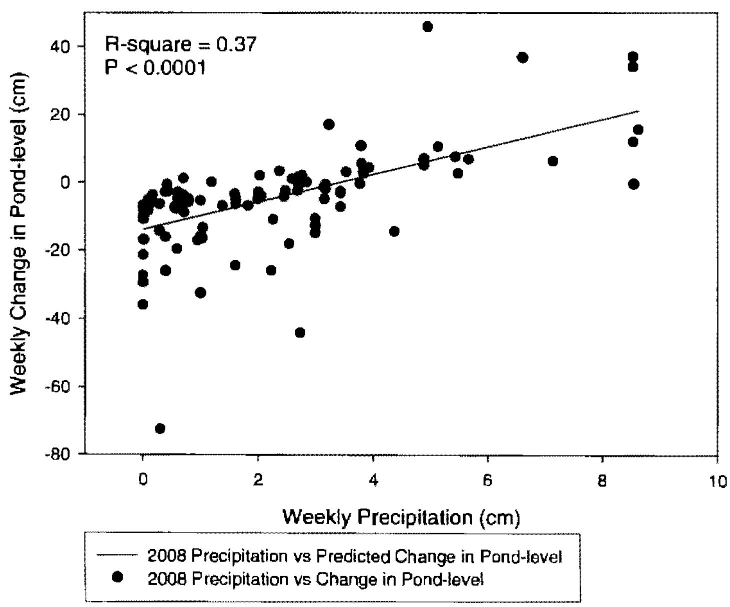

Figure 1.44. Relationship between weekly change in pond-level of flow-through ponds with weekly precipitation in 2008 (n = 7, Ponds located in both Buena Vista and Paul Bunyan State Forests).

2009 Flow-Through Ponds Weekly Change in Pond-level vs. Weekly Precipitation

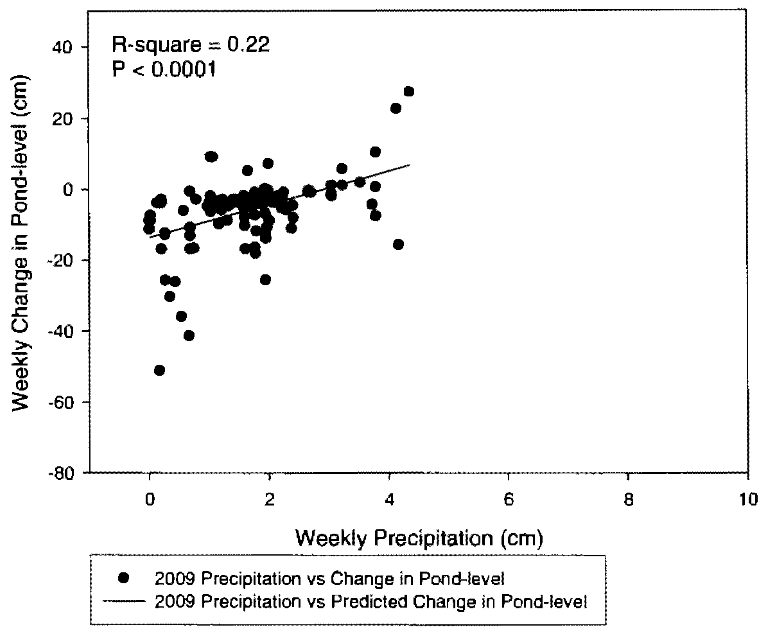

Figure 1.45. Relationship between weekly change in pond-level of flow-through ponds with weekly precipitation in 2009 (n = 7, Ponds located in both Buena Vista and Paul Bunyan State Forests).

2008 Perched Ponds Weekly Change in Pond-level vs. Weekly Precipitation (n=2)

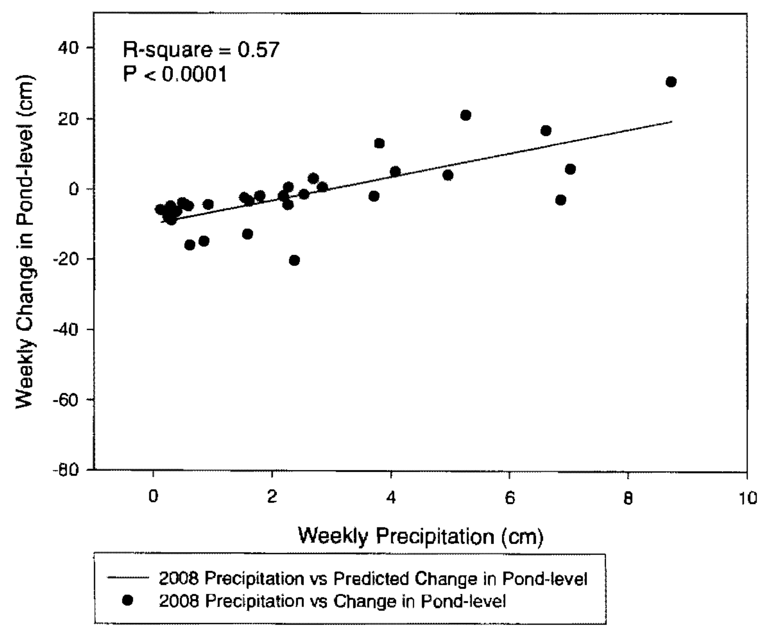

Figure 1.46. Relationship between weekly change in pond-level of perched ponds with weekly precipitation in 2008 (n = 2, both ponds are located in the Buena Vista State Forest).

2009 Perched Ponds Weekly Change in Pond-level vs. Weekly Precipitation

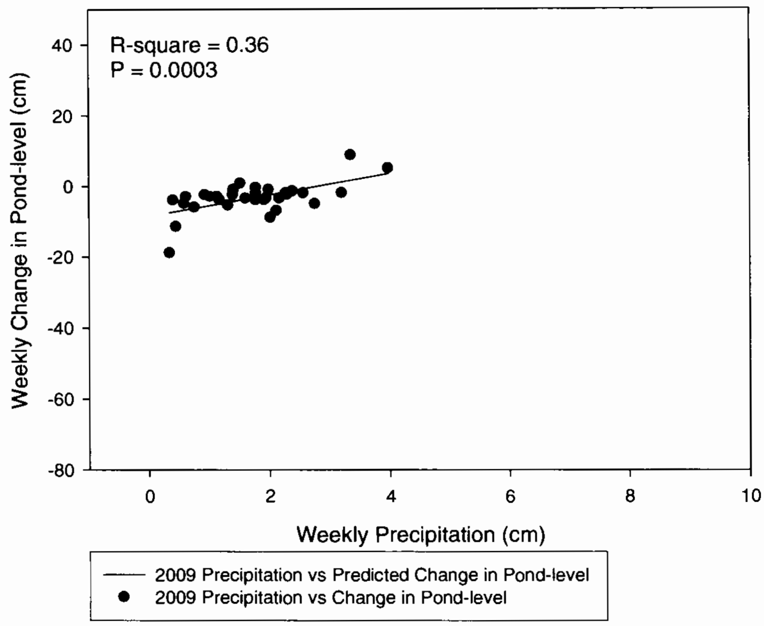

Figure 1.47. Relationship between weekly change in pond-level of perched ponds with weekly precipitation in 2009 (n = 2, both ponds are located in the Buena Vista State Forest).

DISCUSSION

Basin morphology may have a greater influence on the hydroperiod of seasonal ponds located in the Paul Bunyan State Forest, than those in the Buena Vista State Forest. Maximum depth was found to significantly influence hydroperiod duration in both state forests, with deeper ponds typically having longer hydroperiods. Pond area had a weaker, yet still significant influence on hydroperiod in the Buena Vista State Forest, with relatively larger ponds having shorter hydroperiods. The opposite relationship was observed in the Paul Bunyan State Forest, where ponds with larger areas typically had longer hydroperiods. Brooks et al. (1998) found that hydroperiod generally increased with increasing pond surface area. My findings suggest that maximum depth has a greater influence on hydroperiod than does pond surface area. Similarly, Brooks and Hayashi (2002), report that the relationship between hydroperiod and surface area in their study was not as strong as the relationship between hydroperiod and pond depth. This study suggests that the degree of influence is subject to regional variation. Brooks and Hayashi (2002) suggest that pools deeper than 1 meter in depth tend to be more semi-permanent to permanent, because deeper ponds often contain larger volumes of water. Maximum depth was also moderately and positively correlated to pond surface area in their study, however my seasonal ponds did not exhibit a relationship between maximum depth and pond surface area.

Aust et al. (1997) studied tree harvesting techniques in the southeastern USA and found evidence of hydrologic responses to harvested sites recovering to near pre-harvest conditions in as little as seven years. *Populus* spp. dominate the forested landscape in Minnesota's Laurentian Mixed Forest. These fast growing trees may also cause evapotranspiration rates to recover to near pre-harvest rates within 7 years after tree harvest, or less. Palik et al. 2001 also failed to find relationships between age of adjacent stand and abiotic characteristics of seasonal ponds seven years after tree harvest in northern Minnesota USA.

I interpreted percent canopy cover to be a possible proxy variable or surrogate of evapotranspiration. I was not surprised to see a significant negative correlation between percent canopy cover and hydroperiod length. Adjacent vegetation has been found to influence hydroperiod length through evapotranspiration and can account for significant water loss (Brooks and Hayashi 2002; Brooks 2004; Miller 1971; Hanes and Stromberg 1998). Adjacent vegetation can induce hydraulic gradients through evapotranspiration in adjacent upland soils causing pond water to recharge adjacent upland soils (Brooks and Hayashi 2002; Brooks 2005; Hanes and Stromberg 1998; Hayashi et al.1998; Meyboom 1966; Phillips and Shedlock 1993). In my study I used percent canopy cover as a proxy of the transpiring biomass to predict hydroperiod in the Paul Bunyan State Forest. The high clay content of soils in the Buena Vista State Forest may reduce the influence of evapotranspiration on hydroperiod length, specifically in the two perched seasonal ponds. Evaporation alone will not cause most ponds to become dry. Water levels may fall dramatically, and ponds often become dry during the early summer, suggesting water loss is occurring through groundwater recharge (Brooks and Hayashi 2002). Groundwater recharge may be a contributing factor to variability of hydroperiod length, and may explain why some ponds show weak relationships to environmental variables such as canopy cover, pond area, depth, and precipitation rates.

Brooks (2004) found a positive correlation between weekly pond water level change and precipitation in a study that included only four seasonal ponds. In my study of sixteen sites, ponds in the Paul Bunyan and Buena Vista State Forests displayed a positive trend between weekly precipitation totals and weekly change in pond level each year. The relationship was significant for each forest both years, however in 2009, precipitation was a poor predictor of change in pond level in the Buena Vista State Forest. When comparing the relationship between pond level dynamics and weekly precipitation, May was the only month showing no significant relationship in either forest, and also when all sites were combined. This weak relationship between precipitation and pond levels in May could result from the influence of snowmelt on pond levels. Thus groundwater may have considerable influence on water levels in seasonal ponds in both the Paul Bunyan and Buena Vista State Forests particularly in the early spring months. Cole et al. (1997) found that water levels in wetlands driven by groundwater were less responsive to precipitation events. Although I only had two examples, water levels in perched ponds appeared to be more responsive to precipitation events than water levels in recharge or flow-through ponds. The low permeability of the soils adjacent to perched seasonal ponds can lead to brief surface flow, particularly during heavy precipitation events, increasing the influence of precipitation on pond water levels. The weak correlation between precipitation and pond level in recharge ponds is likely due to pond water recharging the groundwater, and thus reducing pond level responses to precipitation. A similar, but relatively stronger response is also seen in flow-through seasonal ponds. Precipitation responses of flow-through seasonal ponds are also likely due to groundwater recharge, but stronger because of groundwater discharge occurring at other locations within the pond basin. Particularly heavy precipitation events may increase the rate at which groundwater is discharging into flow-through seasonal ponds.

My results suggest a high degree of spatial and temporal variability in water exchange between seasonal ponds and groundwater. There is pronounced spatial variability in groundwater exchange with seasonal ponds in the Buena Vista State Forest. This is likely due to the higher clay content of the Buena Vista State Forest soils compared to the Paul Bunyan State Forest. A majority of the ponds within both forests contained areas within their basins exhibiting groundwater discharge particularly early in the spring due to ephemeral groundwater mounds along the delineated wetland boundary. The positive correlation between duration of groundwater discharge and hydroperiod length in the Paul Bunyan State Forest is not surprising, but I am unaware of other studies demonstrating this relationship. The weaker correlation between groundwater discharge and hydroperiod length in the Buena Vista State Forest is likely due to the spatial variability of groundwater influence. A seasonal flow-through pond in the Buena Vista State Forest exhibited a long duration of discharge but a relatively short hydroperiod both years likely had a different region of the pond exhibiting an area of groundwater recharge that surpassed the magnitude of groundwater discharge. This relationship with the groundwater likely caused the pond to have a shorter hydroperiod than expected when comparing duration of discharge to hydroperiod. More than half of the ponds exhibited at least some localized groundwater discharge for more than 5 weeks during the two year study. I classified just under half of the ponds as flow-through and a majority of those ponds are located in the Paul Bunyan State Forest. The limited connection between groundwater and the two perched ponds suggests that water levels in these two ponds are highly influenced by spring snowmelt, precipitation patterns, and surface evaporation. This is supported by the relationships exhibited in Figures 46 and 47. The soil horizons in the two perched ponds have high levels of clay which can act as an impermeable/semi-impermeable layer, decreasing the influence groundwater can have on pond water levels. Therefore ponds that are perched, or exhibit little to no relationship to groundwater, have water levels that reflect precipitation, surface runoff, and possibly evapotranspiration along the adjacent wetland boundary.

Brooks and Hayashi (2002) suggest that wetlands with limited connectivity to groundwater are typically more ephemeral compared to wetlands that are influenced by groundwater, and pond water-levels reflect the differences between precipitation and evaporation. However, the two perched ponds in our study, despite limited connectivity to groundwater, typically have extended hydroperiods.

Failure to detect more significant environmental influences on hydroperiod in ponds of the Buena Vista State Forest may have several causes. Weak relationships may be due to localized groundwater influence that I was not able to identify using only 5 piezometer nests per pond. A reason for finding stronger correlations between seasonal ponds and environmental variables in the Paul Bunyan State Forest may be due to the differing soil characteristics and topography. Watersheds that contain steep slopes, which are characteristic of the Paul Bunyan State Forest, typically have a stronger influence on water levels in ponds (Hanes and Stromberg 1998). Another interesting variable that may influence groundwater interactions with seasonal ponds that I was did not study is the influence of recent (< seven years) tree harvest adjacent to seasonal ponds. Peck and Williams (1987) found groundwater levels to increase in response to forest clearing in Australia. My groundwater study began eight years after tree harvest allowing hydrologic responses to adjacent tree harvest to recover to near pre-harvest conditions (Palik et al. 2001).

My findings suggest seasonal pond responses to environmental influences can differ from region to region, even at distances of <50 km. Brooks (2004) also found differing responses between ponds, precipitation and evapotranspiration rates making it difficult to create a general seasonal pond hydrologic model that could be applied to all seasonal ponds. Seasonal ponds in my study with relatively longer hydroperiods were found to be more variable in hydroperiod length particularly in the Paul Bunyan State Forest. Groundwater influence is likely to add to the complexity of seasonal pond responses to weather related variables such as precipitation and evapotranspiration rates, causing water-levels within pond basins to respond uniquely to precipitation and evapotranspiration rates.

Due to the importance of precipitation and evapotranspiration rates on the hydrology of seasonal forest ponds, these wetlands are prone to the effects of climate change (Brooks 2005). Future climate change is predicted to bring increasing temperatures, and increase evapotranspiration (Brooks 2005). Increased evapotranspiration will likely cause pools to dry earlier, which may increase the frequency of reproductive failure in amphibian populations (Brooks 2004, 2005). Areas will likely experience a loss of wetlands, in particular smaller ponds, leading to a decrease in wetland density. Greater inter-wetland distance, would impede dispersal of amphibians, and other aquatic animals, and may lead to local extirpations (Brooks 2004; Gibbs 1993). Lower wetland density could also affect local aquatic invertebrate communities and impact invertebrates that fly among waterbodies and use seasonal ponds as reproductive sites. Precipitation events are also expected to decrease in frequency, resulting in extended dry periods (Brooks 2005).

Seasonal ponds host aquatic invertebrate communities that are unique when compared to permanent bodies of water, therefore these wetlands are important contributors to regional biodiversity (Williams 2005). Despite their size, even small, shallow, seasonal ponds are important as habitat for pond-breeding fauna (Brooks and Hayashi 2002). Further studies are needed to better understand variability in groundwater interactions in seasonal ponds, particularly groundwater influences on the biotic communities that inhabit seasonal ponds.

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PAPER 2. ENVIRONMENTAL INFLUENCES ON INVERTEBRATE COMMUNITY COMPOSITION OF SEASONAL FOREST PONDS IN NORTH CENTRAL MINNESOTA

ABSTRACT

Seasonal ponds are common throughout northern Minnesota's forested areas. Seasonal ponds typically flood due to snow-melt and high precipitation rates in early spring, then dry by mid-late summer. The dynamic hydroperiod, typical of seasonal ponds, creates a unique fishless habitat hosting an abundance of endemic aquatic species. Hydroperiod has long been considered a major controller of biological communities in seasonal ponds, but few data are available for testing hydrological linkages among seasonal ponds, their surrounding watersheds and their resident invertebrate communities. To test influences of hydrological pond function on invertebrate communities, I placed peizometers and monitoring wells in 8 sites in the Buena Vista State Forest in Beltrami County, MN, and 8 sites in the Paul Bunyan State Forest in Hubbard County, MN (16 sites total). Water levels were monitored weekly from spring melt until ponds dried and water tables fell below readable depths. Invertebrate communities were sampled weekly during 2008, and 2009. Results indicate that high, but variable water exchange occurs between seasonal ponds and ground water. Patterns in pond invertebrate communities were related to hydrological function and hydroperiod, and appear consistent between the 2 forest areas, suggesting that many invertebrates are generalist users of these areas.

LITERATURE REVIEW

Seasonal ponds are a common type of wetland in regions that have experienced continental glaciation (Brooks 2005), including like northern Minnesota (Hanson et al. 2009). Seasonal ponds are shallow depression wetlands underlain by bedrock or semi-impervious soil horizons (Brooks 2005). Seasonal ponds typically have small catchments and no permanent overland connection to other bodies of water (Brooks and Hayashi 2002; Brooks 2004, 2005; Tiner et al. 2002). Due to their hydrologic isolation, these aquatic systems are influenced directly by precipitation, evapotranspiration, and their connection to groundwater (Brooks and Hayashi 2002; Brooks 2005). In particular the relationship between seasonal ponds, and surface-groundwater exchange is poorly understood (Brooks 2005; Sun et al. 2000). Mitch and Gosselink (2000) suggest the hydrologic classification of a wetland, (e.g. recharge, discharge) is one of the most important characteristics of a wetland. However, the importance of groundwater contribution varies from wetland to wetland. The influence of surface-groundwater exchange on a wetland can vary depending on the relative position in the landscape and geologic conditions (Brooks 2005). There is even less known about the influence of surface-groundwater exchange on invertebrate communities in seasonal ponds.

Seasonal ponds are typically inundated in early spring due to snowmelt, saturated soils, elevated water-tables, and high precipitation rates. The high water input associated with early spring generally exceeds evapotranspiration rates, causing the pond basins to fill with water. Seasonal ponds generally become dry by mid to late summer (Brooks 2005; Mansell et al. 2000). Water-tolerant species dominate the plant community in these basins (Brooks 2005). The length of inundation, the number of consecutive days the pond basin contains standing water, is referred to as the hydroperiod (Mitch and Gosselink 2000). Particularly in the spring, ephemeral groundwater mounds can form adjacent to seasonal ponds forming a hydraulic gradient towards the pond. When this occurs, groundwater will discharge into the pond (Phillips and Shedlock 1993; Hanes and Stromberg 1998). During dry periods especially in the summer the groundwater mounds disappear due to falling water table levels and an increase in evapotranspiration rates, causing the hydraulic gradient to shift towards the adjacent uplands. When this occurs water levels in the ponds will begin to decrease due to pond water recharging the groundwater. Decreasing water levels generally occur during the months of June, July and August when temperatures may be highest and adjacent forests have maximum leaf area (Brooks 2004, 2005). In the fall, precipitation rates typically increase and exceed evapotranspiration rates. Transpiration rates diminish as leaf area decreases due to falling temperatures (Brooks 2004). These harsh conditions promote seasonal inundation, however, seasonal ponds support rich and diverse invertebrate communities with high seasonal variability, that are distinctly unique when compared to invertebrate communities of permanently flooded wetlands (Brooks 2000; Brooks, and Hayashi 2002; Batzer et al. 2004; Miller et al. 2008; Williams 2005). The uniqueness of aquatic invertebrate communities found in seasonal ponds increases their importance in maintaining a regions' biodiversity (Williams 2005). The environmental influence that sets invertebrate communities of seasonal ponds apart from permanently flooded wetlands is duration of flooding, or hydroperiod (Batzer et al. 2004; Brooks 2000; Collinson et al. 1995; Williams 2005). Schneider (1999), studying seasonal ponds with short hydroperiods in Wisconsin found invertebrate communities composed primarily of taxa with adaptations to drying or abiotic conditions, while seasonal ponds with extended hydroperiods contained invertebrate communities with structures associated to biotic interactions such as predation and competition. The duration of ponding in seasonal ponds is rather difficult to predict; therefore the invertebrates inhabiting these systems must develop adaptations (Batzer et al. 2004). The adaptations can include the ability to avoid desiccation by moving by flight from pond to pond, or having an accelerated life cycle which allows them to emerge, mature and reproduce before pond desiccation occurs (Batzer et al. 2004; Williams 1996, 2005). Other adaptations include the production of resting eggs, and the ability to enter dormancy as an immature. Several studies have found aquatic invertebrate richness to increase with increasing hydroperiod length (Batzer et al. 2004; Brooks 2000; Hanson et al. 2009). Hanson et al. (2009) reported a weak positive relationship between hydroperiod length and taxon richness. Brooks (2000) reported similar findings, but the relationship was only significant between ponds with the shortest and longest hydroperiods. Batzer et al. (2004) also found a relationship between taxon richness and hydroperiod length, however the relationship was due to rare taxa only occurring in ponds with extended hydroperiods, and found little influence of hydroperiod length on wide spread taxa. Hanson et al. (2009) also report that hydroperiod had a significant influence on invertebrate community composition in their 24 seasonal ponds, however there was little variance within the invertebrate community explained by hydroperiod. Findings by Batzer et al. (2004), and Brooks (2000) suggest the influence of hydroperiod can even carry over to the following year. Brooks (2000) found that a year with unusually short hydroperiods can cause a reduction in benthic invertebrate abundance early in the following year. When this occurs it is possible that reductions are due to a shift towards invertebrates that have increased desiccation tolerance, however in the study by Brooks (2000) there was little affect on community composition.

Hydroperiod has been shown to be related to pond size which includes water depth and surface area (Brooks 2000, 2005; Brooks and Hayashi 2002; Williams 2005). Large pond basins typically promote longer hydroperiods when compared to ponds with smaller basins. Ponds with longer hydroperiods are associated with higher amphibian reproductive rates (Brooks 2005). When considering the importance of smaller wetlands one must also take into consideration that ponds with longer hydroperiods also promotes or favors the presence of predatory fish, which can have strong negative impacts on seasonal pond fauna which have adapted to low predation pressures (Brooks 2005). In a study conducted by Brooks, surface area was found to be positively related to habitat diversity. Therefore, as pond size increases so does habitat diversity and the ponds ability to support a diverse invertebrate community (Brooks 2000).

Seasonal ponds are generally small, < 1 meter in depth and typically range from 0.1 to 0.25 ha in size, rarely approaching 1.0 ha (Palik et al. 2001, 2004; Brooks 2005). Due to the small size of seasonal ponds they generally have a high perimeter-to-area ratio which can influence length of hydroperiod and increase the sensitivity of the inhabiting invertebrate communities to disturbances in the adjacent uplands (Palik et al. 2001, 2004; Brooks 2005; Williams 2005). Disturbances to upland vegetation such as tree harvest can decrease leaf litter input and therefore possibly influence macroinvertebrate communities in seasonal ponds (Batzer et al. 2004; Palik et al. 2001, 2005; Hanson et al. 2009; Williams 2005). The dry phase of seasonal ponds while excluding predacious fish, also promotes aerobic decomposition of plant and leaf litter (Brooks 2005). Leaf detritus is the most abundant food resource in ponds, however studies have failed to find a significant relationship between invertebrate communities and amount of leaf litter entering seasonal ponds (Batzer et al. 2004; Palik et al. 2001; Williams 2005). In a study on stream ecology, macroinvertebrate abundance and diversity in streams generally declined as leaf litter resources became limiting (Richardson 1991). The reason for the findings being different between streams and ponds may be due to an increase in sedge cover commonly observed in ponds shortly after tree harvest (Batzer et al. 2000, Hanson et al. 2009). Batzer et al. (2000) found a positive relationship between sedge cover and richness and abundance of terrestrial invertebrates. An increase in sedge cover would provide forage and cover for invertebrates, therefore muting affects of decreased levels of leaf litter entering the pond, and increase habitat diversity for aquatic invertebrates. Ponds in general are also nutrient sinks where as streams have constant fluctuating levels of nutrients due to water-flow. Canopy openness can be altered by tree harvest and is associated with stand age (Hanson et al. 2009; Palik et al. 2001).

Hanson et al. (2009) reported that canopy openness explained significant variance among aquatic invertebrate communities in their study ponds. A positive relationship was observed between taxon richness and canopy openness, suggesting the increase in invertebrate richness was possibly due to changes in light availability following tree harvest, and increased visibility of seasonal ponds to invertebrate taxa that disperse by flight such as adult Hemiptera, and Coleoptera (Williams 1996). Palik et al. (2001) also reported a positive response of algal feeding invertebrates to increased canopy openness. Hanson et al. (2009) did find that age of adjacent stands influenced taxon richness of invertebrates in their study ponds; however their data was collected 1 to 5 years following tree harvest. Studies suggest the influence of age of adjacent forest may become minimal as little as 15 to 20 years after tree harvest (Batzer et al. 2000; Palik et al. 2001).

Seasonal ponds are quite dynamic due to their seasonal inundation which creates a unique fishless habitat that many species of amphibians and invertebrates rely on for reproduction (Brooks 2005; Egan and Paton 2004). As an example of how dynamic seasonal ponds can be, Hanson et al. (2009) reported different significant environmental variables from year to year during their two study periods. The inconsistently significant environmental variables included hydroperiod, maximum depth, total alkalinity, and total phosphorous. Canopy openness was the only environmental variable to consistently explain significant invertebrate community variance during both study periods.

A majority of past studies on seasonal ponds found that most relationships between invertebrates and environmental variables were weak or non-significant

(Batzer et al. 2000, 2004; Hanson et al. 2009; Palik et al. 2001). Hanson et al. (2009) speculate these weak relationships between invertebrate communities and environmental variables may be due to a high tolerance of the invertebrates to extreme and variable environmental conditions. Batzer et al. (2000, 2004) suggest that invertebrate communities with adaptations to high habitat variation should be expected to show weak relationships with environmental variables. Any environmental changes that are associated with tree harvest may fall well within natural variation in environmental conditions. These findings may also be due to the timing of sampling as well as a limited sampling schedule. Most studies only include 2 to 4 sampling periods with 2 weeks to a month or more between the sampling periods (Batzer et al. 2000, 2004; Brooks 2000; Hanson et al. 2009; Miller et al. 2009). The large amounts of time between sampling periods and low number of sampling periods in a season may limit the ability to detect changes that may occur in patterns among invertebrate communities during inundation of seasonal ponds. (Batzer et al. 2000, 2004; Hanson et al. 2009). A study involving other regional (MN) seasonal ponds found invertebrate communities to dramatically shift in composition in as little as 2 to 3 months ranging from May 1 to July 11 (Miller et al. 2008). These dramatic shifts in community composition create high temporal variability which is the major source of variation in invertebrate communities in seasonal ponds (Miller et al. 2008). Because the invertebrate communities inhabiting seasonal ponds are adapted to a dynamic system it is likely that changes among these communities can occur rapidly and will likely be missed by only sampling 2 to 4 times during an entire season (Batzer et al. 2004).

Invertebrate communities inhabiting seasonal ponds display such high within-year variability that patterns within invertebrate communities are difficult to discern resulting in the difficulty of developing models. For these reasons it is advised to target temporal variation among invertebrate communities by developing sampling and analysis strategies that would detect these changes within invertebrate communities (Miller et al. 2008). Scientists familiar with the high temporal variability typical of invertebrate communities inhabiting seasonal ponds encourage conducting simultaneous sampling of invertebrates from multiple seasonal ponds, and also to mirror the sampling dates from one year to the next (Miller et al. 2008).

Based on literature, information is lacking on relationships between groundwater and invertebrate community composition in seasonal ponds. Many papers mention the importance of groundwater influence on seasonal ponds (Brooks and Hayashi 2002; Colburn 2004, Mitch and Gosselink 2000; Sun et al. 2000) but few studies (if any) actually investigate the influence of surface-groundwater exchange on invertebrate communities in seasonal ponds (Colburn 2004).

Study Objectives

The following objectives were pursued to explain variability among seasonal pond invertebrate communities. My first objective was to define the hydrologic function of each seasonal pond. This was done using piezometer nests deployed along the delineated wetland boundary and within each pond to indicate the relationship between groundwater (e.g. discharging or recharging) and the standing water within the pond basin. Second, to overcome temporal variation among invertebrate communities in seasonal ponds I simultaneously sampled sixteen ponds weekly over a period of 7 to 8 weeks per year to identify taxa and any changes within the community that may have occurred throughout the entire wet season. Finally, I assessed environmental variables that have been shown to exhibit some influence on invertebrate communities such as hydroperiod, canopy cover, stand-age, pond surface area, and maximum pond depth.

MATERIALS AND METHODS

The study was conducted on 16 seasonal ponds, with eight sites located in the Buena Vista State Forest in Beltrami County, MN about 8 km or 5 miles north of Bemidji and eight sites in the Paul Bunyan State Forest which is located in Hubbard County, MN about 30 km or 18.5 miles south of Bemidji (Figure 2.1). The 16 seasonal ponds were selected from a larger study of 24 sites previously established by MNDNR in 1999 (Figure 2.2). These sites are surrounded by stands predominantly composed of aspen (*Populus* spp.) (Almendinger and Hanson 1998), and each site contains stands of aspen trees of relatively similar age. Sites were each assigned to one of 4 groups based on the age of adjacent aspen stand. [Group 4 contained sites with adjacent stands ranging from clearcut to ≤ 9 years of age.] Group 1 contained sites with adjacent stands of young growth ranging from 10 – 34 years of age, group 2 consisted of sites with adjacent stands of middle age growth ranging from 35 – 59 years of age and group 3 (control group) included old growth stands ≥ 60 years of age.

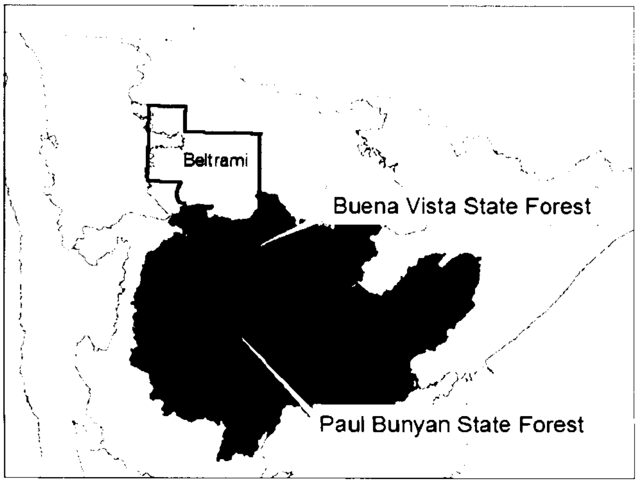

Figure 2.1. North Central area of Minnesota showing the locations of the Beuna Vista State Forest and Paul Bunyan State Forest. The blue shaded area is the upper portion of the Mississippi River watershed. (Minnesota Department of Natural Resources, layer wshd_lev08py3, 2007).

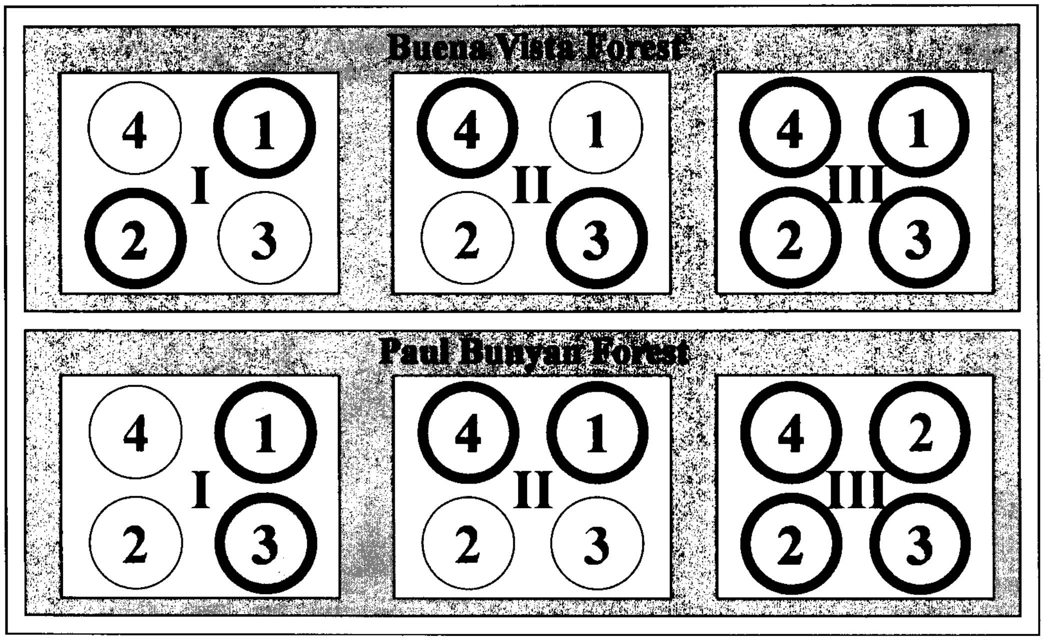

Figure 2.2. Sixteen sites (in bold, eight in each forest) selected from a larger study which included 24 sites. 1 = young growth (10-34 yrs.), 2 = middle age growth (35-59 yrs.), 3 = old gowth (> 60 yrs.), 4 = clearcut < 9 years of age.

Invertebrate Sampling

Sampling of aquatic invertebrates was conducted during 2008 and 2009. The sampling of aquatic invertebrates began after snow melt when pond basins contained standing water. The starting date for invertebrate sampling for both years happened to fall on May 14^{th} and was conducted weekly until the beginning of July when the first ponds happened to go dry, giving a total of eight sampling dates per seasonal pond. All ponds were sampled on the same day.

Two surface activity traps (SATs) (Figure 2.3.) (Hanson et al. 2000) were used to sample semi-aquatic and aquatic invertebrates in each pond. The benefits of using SATs to sample invertebrates are their ability to sample invertebrates that are associated with the water surface (Culicidae, Corixidae, Gerridae, Gyrinidae, ect) as well as those found in the water column (Crustacea taxa, Ephemeroptera, etc.).

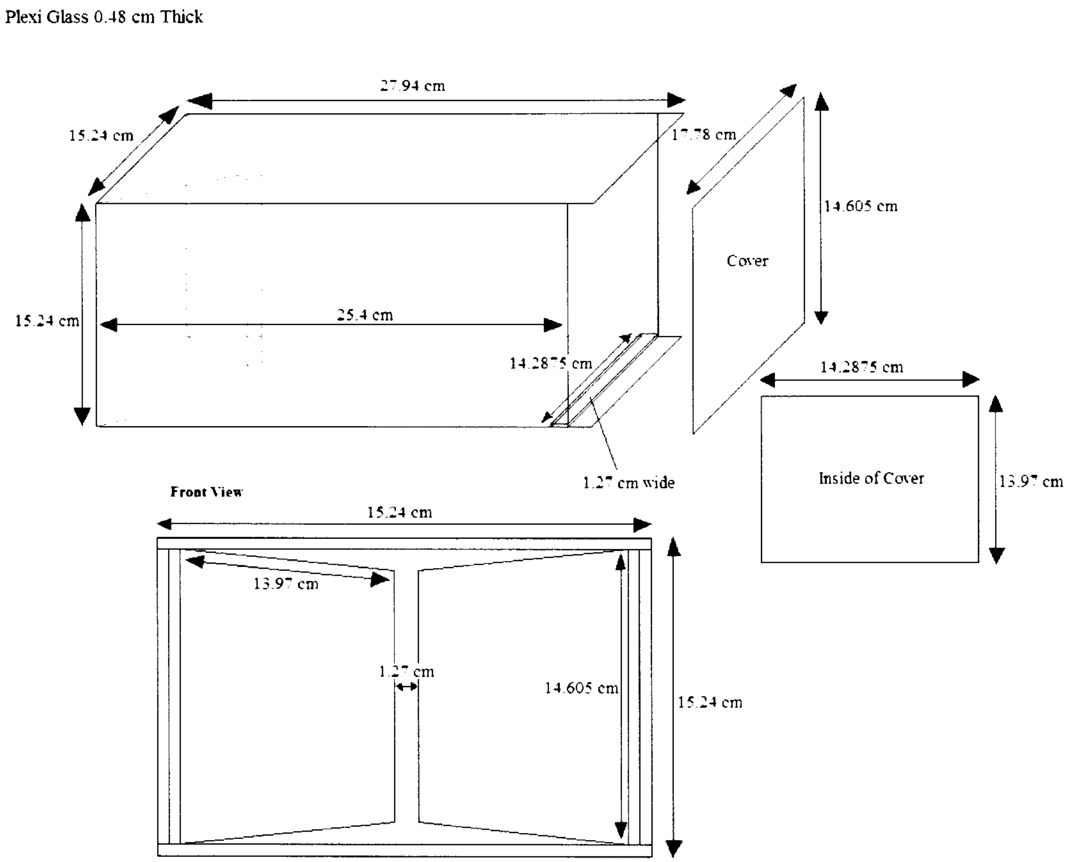

Figure 2.3. Surface Activity Trap (SAT) constructed of 0.48 cm thick transparent plexiglass.

Two transects, each containing one SAT, were randomly selected in each pond. The first transect contained an SAT that was deployed one quarter of the distance to the center of the pond. The second transect contained an SAT that was deployed three quarters of the distance to the center of the pond. SATs were positioned along margins of hydrophytes if present otherwise SATs were deployed in open water (Hanson et al. 2009). SATs were held in position using PVC frames anchored into pond sediments. SATs were deployed for 24 hours before emptying contents. Contents from each trap were condensed using a 0.4 mm mesh condensing beaker and preserved using 70 percent ethanol. Invertebrates were sorted and identified using stereomicroscopes in the lab. Insects were typically identified down to family while crustaceans were identified down to genus using Merrit et al. (2008), and Thorp and Covich (2001). The recorded numbers of invertebrates of the two SATs in each pond per sampling period were combined to represent a single taxon richness value of each pond for each weekly sampling period. For analysis I grouped invertebrates into 20 taxonomic categories or feeding guilds similar to Hanson et al. (2009). The seasonal ponds in my study were also included in the study by Hanson et al. (2009). By grouping the invertebrates into the same feeding guilds it allowed me to compare similarities and differences between my results and theirs, and most importantly identify consistent relationships between the two studies. Studying feeding guilds also helped me identify patterns in the invertebrate community structure (McCune and Grace 2002).

Soil Nutrients

At each pond, soil samples were collected using a soil corer from locations in the deepest point of each pond and from one randomly chosen location along the delineated wetland boundary. Soil core samples were collected and analyzed in a lab for particle size, pH, phosphorous, nitrogen, carbon, and exchangeable cations including $AlCl_3$, $CaCl_2$, CdCl, CuCl, $FeCl_3$, KCl, $MgCl_2$, $MnCl_2$, NaCl, $NiCl_2$, $PbCl_2$, SCl_2, and $ZnCl_2$.

Canopy Cover

Percent canopy cover was assessed using a spherical densiometer. Two transects were randomly chosen in each pond and intersected at the center.

Percent canopy cover readings were conducted at five locations on each transect, with the third reading of each transect being at the center of the pond.

Pond Surface Area

Pond perimeters were plotted using a global positioning system with an external antenna to increase accuracy. The GPS data points were uploaded into the geographic information system software (ArcGIS 9.2, Environmental Systems Research Institute Inc., 2007) to estimate the surface area of each pond in square meters.

Hydroperiod

A staff gauge was installed in the deepest point of each seasonal pond (Figure 2.4.) and constructed of 2.54 cm diameter PVC piping. The staff gauge was used to measure the standing water level within the seasonal pond basin. Once the water level receded below ground level the center monitoring well was used to estimate the groundwater level immediately below the pond basin. Pond water level readings began soon after spring snow melt, and were conducted weekly throughout the spring and summer. Starting in September pond water level readings were taken every other week until the ground froze or until water levels sunk below the readable depth of the center monitoring well. This data was used to assess the hydroperiod (consecutive days ponded) for each seasonal pond of each year. I defined the hydroperiod onset as the first date the pond was visited in which at least 20 percent of the pond basin contained standing water. The hydroperiod ended on the first date when less than 20 percent of the seasonal pond basin contained standing water, or when the standing water in the seasonal pond froze, usually occurring in late October or early November. Mean differences of hydroperiods were compared among the different stand-age treatments. Hydroperiods were also compared to approximate age of adjacent stands, as well as pond surface area, maximum depth, groundwater discharge duration, and percent canopy cover.

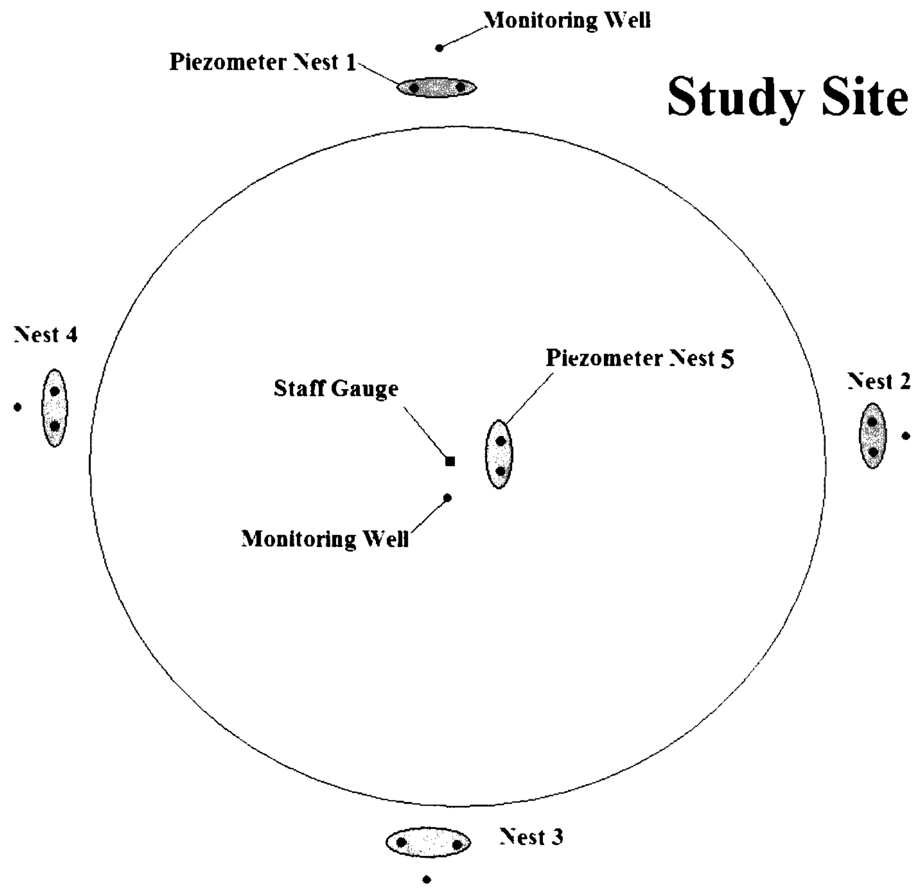

Figure 2.4. General layout of piezometer/monitoring well nests, and staff gage in each of the study sites within the Buena Vista State Forest, Beltrami County, MN, and the Paul Bunyan State Forest, Hubbard County, MN.

Groundwater

Monitoring of the upper most limit of the groundwater was conducted through the use of the piezometers and monitoring wells. The water levels in the piezometers were used in conjunction with the water levels in the monitoring wells to track and estimate the predominant function of each wetland (discharge, recharge, flow-through, perched). Piezometers (Figure 2.5) and monitoring wells (Figure 2.6) were installed following the methods of Sprecher (2000) in each of the 16 seasonal ponds. Five piezometer nests, each containing one shallow piezometer (60cm), one deep piezometer (120cm) and one monitoring well (120cm), were deployed at each site (Figure 2.4). Four piezometer nests were installed at 4 locations along the delineated wetland boundary and a fifth piezometer nest was installed at the deepest point of the seasonal pond in close proximity to the staff gauge. The piezometers in the pond center were installed with extended PVC pipe extensions for the top openings to remain above the standing water level in the seasonal pond.

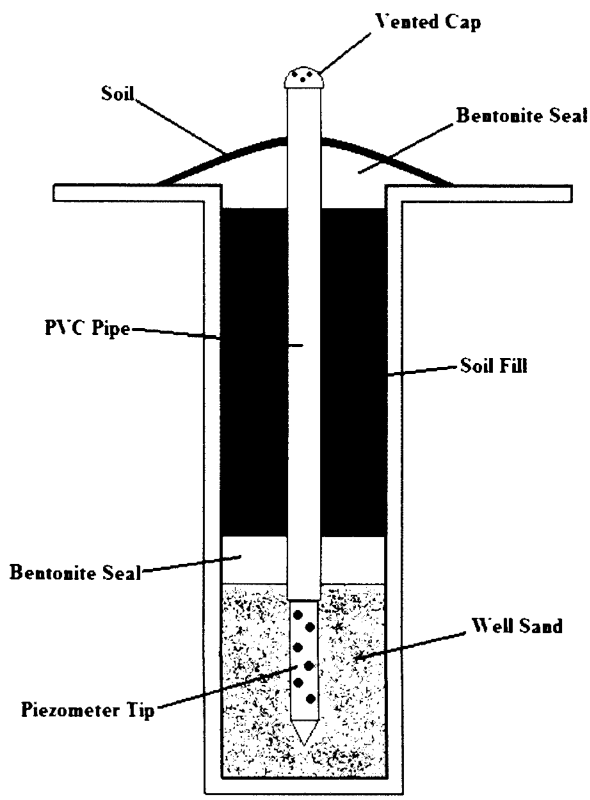

Figure 2.5. Piezometer installation in ground.

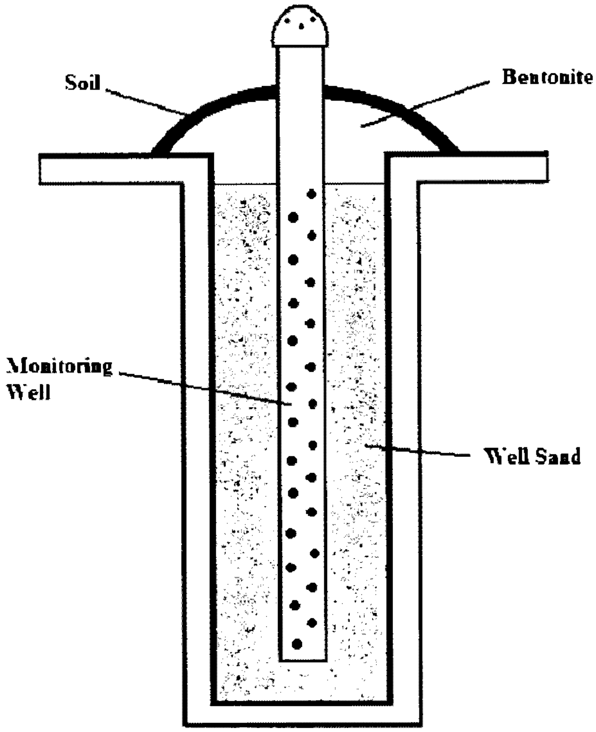

Figure 2.6. Monitoring well installation in ground.

Piezometers were constructed using 2.54 cm diameter PVC piping glued to prefabricated piezometer tips (Forestry Suppliers). Monitoring wells were also constructed of 2.54 cm diameter PVC piping with perforations made using a hand drill along 120 cm of the lower portion of the PVC pipe. A perforated PVC cap was added, closing the lower end of each well. Fabric socks were constructed from synthetic mesh fabric, and placed over the perforated portion of each monitoring well to prevent sand from entering the well through the perforations. Holes for the wells and piezometers were dug using a hand auger with a diameter of 7.62 cm. After each hole was dug approximately 0.5 liters of silica sand was poured into the bottom of the hole. The well or piezometer was then placed in the hole to the appropriate depth, and sand was poured until the piezometer tip or the perforated length of the well was covered allowing free flow of groundwater (Figure 2.5 & 2.6).

Bentonite was then added to form a top seal just above the perforated portion of the well or piezometer to prevent water seepage from above. Dredged soil was used to fill in around the remainder of pipe extension of the piezometer, and tamped firmly in place to limit air cavities. At piezometers, a second bentonite seal (Figure 2.5) was poured around the piping about 15.25 cm below the ground surface, until it formed a small mound just above the soils surface to further prevent any surface water seepage. The exposed top opening of each pipe was covered by a vented cap to prevent rain water or insects from effecting changing water levels within the pipes. Caps were vented to allow air movement due to changing water levels within the wells and piezometers.

Each piezometer and monitoring well was surveyed individually within each wetland permitting comparisons of water table elevation. The base (ground level) for each piezometer/monitoring well was surveyed, as was the location of the staff gauge to obtain its elevation in comparison to the deepest point of the pond. Groundwater depth readings were measured from the top of the pipe extension to the water level in the well or piezometer. The length of the pipe extension above ground was then subtracted to give the depth of water from the ground surface. The elevations of the piezometers and monitoring wells obtained through the surveys were then used to derive the elevations of the water levels in the piezometers and monitoring wells, in comparison to the deepest regions of each seasonal pond.

Groundwater level readings began soon after snow melt and shortly following ground thaw. Readings were recorded weekly throughout the spring, typically the beginning of May and into summer. In September groundwater level readings were recorded every other week until the ground froze typically in the beginning of November. Groundwater level readings were conducted using a pliable fabric measuring tape with a thimble attached to the end of it with the open side facing down. When the thimble contacted the water surface in the pipe, it would make a distinct popping noise allowing for easy and accurate water depth measurements.

Piezometers were used to measure the pressure head of the groundwater from the depth at which the lower perforated portions of the piezometers were located (Figure 2.5). Wells, which are perforated along the entire length below ground (Figure 2.6) were used to identify the actual level of the water table. The water levels in the piezometers were used in conjunction with the water levels in the monitoring wells to track and estimate the predominant function of each wetland (discharge, recharge, flow-through, perched). For example, when the water level in the piezometer indicates a positive head due to pressure differences (Figure 2.7. scenario B, water level is higher in piezometer than in monitoring well), it suggests there is an increase in hydraulic pressure at greater depths causing water to flow upwards (Sprecher 2000). The pressure then decreases as the water gets closer to the ground surface. If the water level in the piezometer indicates a negative head (Figure 2.7. scenario A, and C) which occurs when the water level in a piezometer is lower than the water level in the corresponding monitoring well, a negative hydraulic gradient has formed suggesting water is flowing into the ground ("recharge"). The downward movement of water causes a decrease in pressure with increasing depth causing water levels to be higher in the shallow piezometer and lower in the deep piezometer as seen in Figure 2.7, scenario A. For a wetland to be classified as a flow-through wetland the wetland must contain at least one piezometer nest that indicates groundwater discharge during the entire time or significant portion of the time the pond basin contains standing water, and at least one other piezometer nest indicating that pond water is recharging the groundwater. When this occurs the piezometer nests suggest that groundwater is discharging into the pond in one area of the pond basin, and pond water is then recharging the groundwater in another area of the pond basin. When there is little difference between the water levels in the monitoring well and two piezometers lateral groundwater flow is occurring.

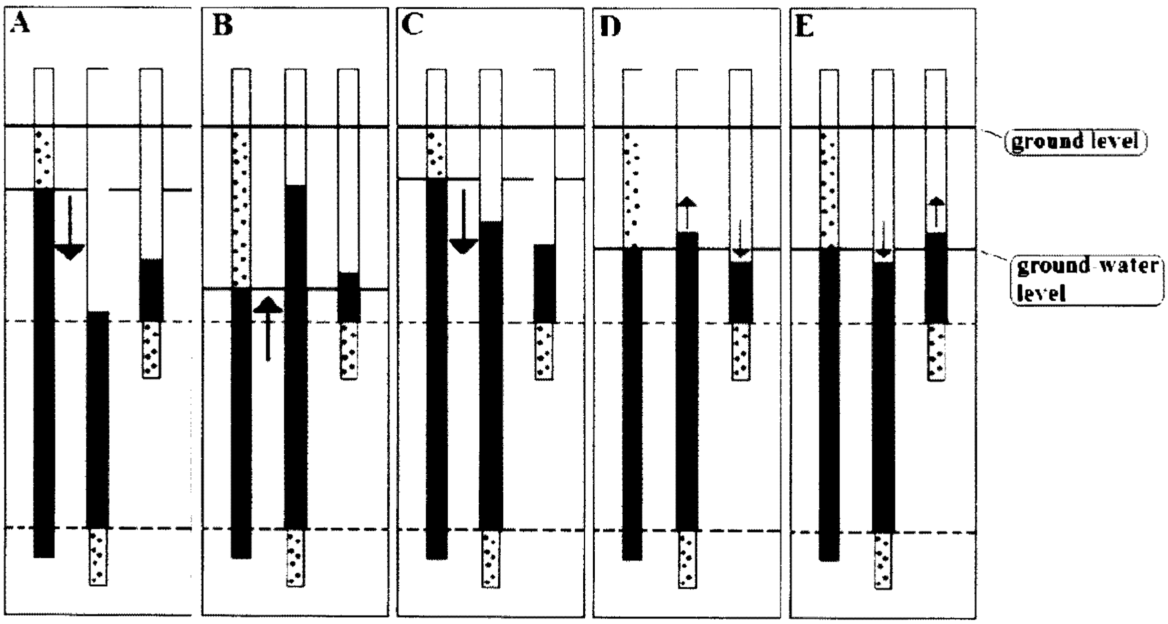

Figure 2.7. Piezometer and monitoring well scenarios encountered in the field. Scenario A: recharge, Scenario B: discharge, Scenario C: recharge, Scenario D & E: Transition between recharge and discharge.

A wetland may be perched or have limited connectivity to the groundwater due to an impermeable layer such as clay or bedrock. Impermeable layers can be located with soil assessments of the wetland. The water levels in the piezometers and wells may also suggest a perched wetland if subsurface levels behave independently of the standing water in the pond. For example, the peizometers and/or wells may become dry due to a falling water table and yet the pond still contains standing water in the basin. In some cases there can be different depths in the soils acting independently from one another such as in Figure 2.7, scenarios D and E. This is likely due to different soil horizons with different soil properties that the perforated portions of the piezometers intercept. In Figure 2.7 scenario D, the deep piezometer is showing discharge at that specific depth, while the shallow piezometer is showing recharge and just the opposite in Figure 2.7 scenario E. These differences can also result from impermeable layers located between the specific depths of the deep and shallow piezometer. Because different soil properties may be encountered at certain depths, soils were surveyed at all instrumented sites to allow interpretation of the hydrological data.

Statistical Analysis

I analyzed two years (2008 and 2009) of invertebrate relative abundance, and environmental data. Interannual relationships between invertebrate communities and environmental variables was analyzed using a direct gradient analysis (redundancy analysis, RDA) using Canoco 4.54 (Ter Braak and Smilauer 1997-2006). The use of RDA was appropriate due to preliminary detrended correspondence analysis (DCA) indicating that gradient lengths were < 2.0 standard deviations. Significant environmental variables used in the final models were identified using randomization (Monte Carlo) forward selection and had p-values ≤ 0.05.

Interannual and also intraannual patterns of invertebrate communities were analyzed using nonmetric multidimensional scaling (NMS) which is an indirect gradient analysis (McCune and Grace 2002). NMS was conducted using PC-ORD version 5.0, Multivariate Analysis of Exological Data (McCune and Mefford 1999-2005). I used Sorensen (Bray-Curtis) distance measures for the initial analysis, and 6 dimensions with 250 iterations. The final ordinations included 2 to 3 dimensions based on stress reduction. The final ordinations indicate chronological invertebrate community patterns within and among the two years between the treatments according to environmental variable such as between year differences (2008, 2009), state forest as a variable, maximum pond depth, percent canopy cover, hydroperiod, and hydrological pond function (ex: recharge, discharge, flow-through, and perched).

RESULTS

There were a total of eight sampling periods in 2008, and seven in 2009. A total of 76 invertebrate taxa were collected between the two study years. The 76 taxa is conservative because insects were typically identified down to family and crustaceans to genus, respectively. Invertebrate communities were mainly represented by insects and crustaceans. Predominant invertebrate taxa collected in the SATs included Diptera larva such as mosquitos (Culicidae), phantom midges (Chaoboridae), midges (Chironomidae), and water mites (Hydracarina). A variety of other aquatic invertebrates were captured including those belonging to the insect orders of Trichoptera, Coleoptera, Hemiptera, and Odonata, crustaceans including fairy shrimp (*Eubranchipus*), clam shrimp (Conchostraca), seed shrimp (Ostracoda), various cladocerans, copepods, as well as snails (Gastropoda) and fingernail clams (Sphaeriidae). Invertebrate communities were represented by members of all general feeding groups (Merrit et al. 2008).

Invertebrate Community Relationships with Environmental Variables

My objective was to identify relationships between environmental variables (Figure 2.8) and the structure and composition of invertebrate communities in seasonal forest ponds. Invertebrate communities within seasonal ponds were associated with several environmental variables during 2008, and 2009. Maximum pond depth, percent canopy cover, and hydroperiod were all significant sources of variance within invertebrate communities for both years, and each explained 14%, 12%, 11%, respectively during 2008 (Figure 2.9a, Table 1), and 19%, 11%, 9%, respectively during 2009 (Figure 2.9b, Table 2.1). Stand-age was not a significant source of variance among invertebrate communities.

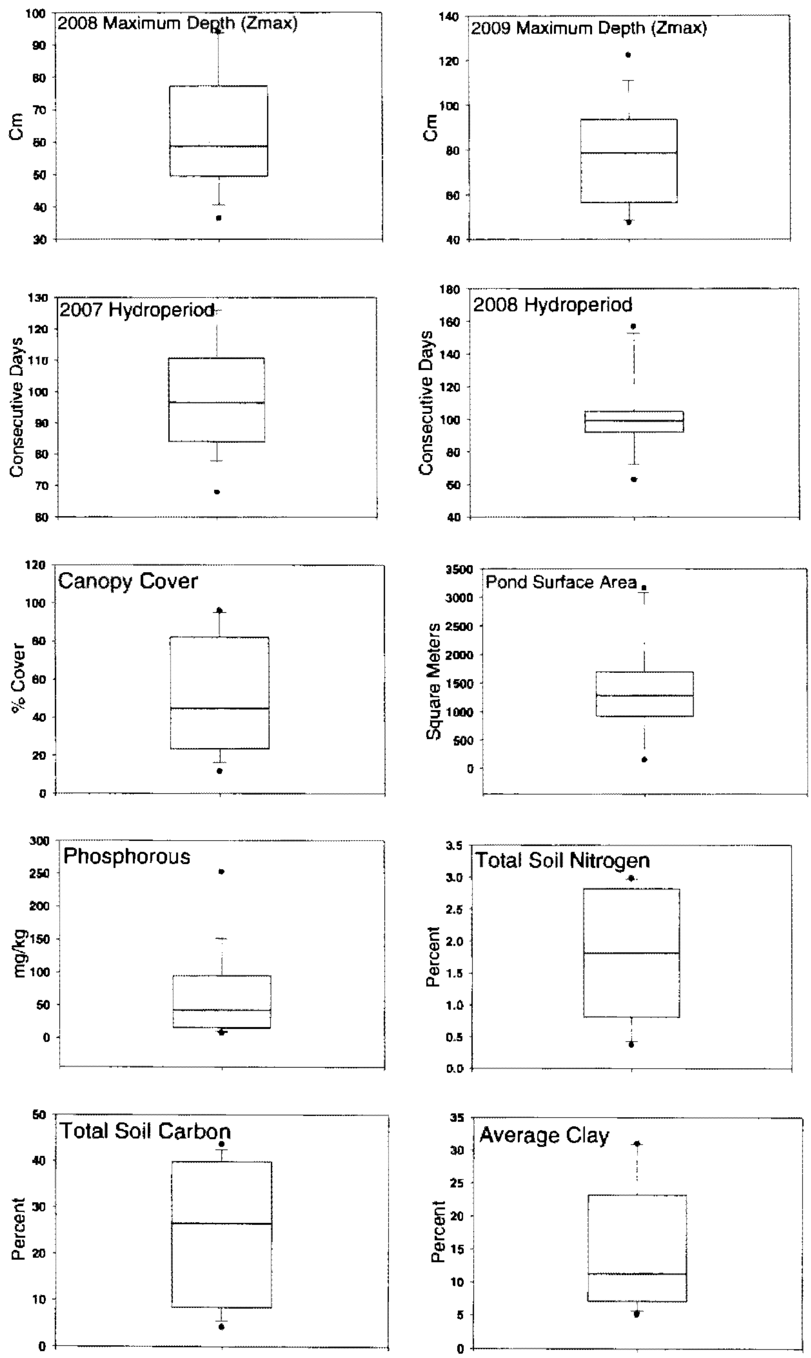

Figure 2.8. Environmental characteristics (maximum pond depth (Zmax), hydroperiod, %canopy cover, pond surface area, phosphorous(mg/kg), total soil nitrogen%, total soil carbon%, average clay%) observed in seasonal forest ponds. Box plots depict mean and range of values during 2008 and 2009.

Table 2.1. Results of final repeated measures partial redundancy analyses (rpRDA) of pond invertebrates using the three environmental variables that explained the most variance. Environmental variables were selected using forward selection. Significance was inferred at alpha = 0.05.

2008	Variance Explained	P-value	2009	Variance Explained	P-value
2008 Zmax	14%	0.024	2009 Zmax	19%	0.002
%Canopy Cover 2007	12%	0.028	%Canopy Cover 2008	11%	0.036
Hydroperiod	11%	0.054	Hydroperiod	9%	0.046
Total	37%			39%	

Several invertebrate groups were associated with at least one of three environmental variables (percent canopy cover, maximum depth, and hydroperiod) during the study years of 2008, and 2009 (Figure 2.9 and 2.10), however, only the significant and consistent relationships for both study years are listed in the results. Only Conchostraca were positively associated with increasing maximum depth during both 2008 and 2009. Several invertebrate groups, including both predatory and non-predatory Hemiptera, along with Chironomidae were negatively associated with increasing canopy cover. Odonata was the only group showing a strong association to sites with relatively longer hydroperiods. Two other invertebrate taxa also exhibited consistent, but less obvious associations with environmental variables including Hirudinea which was positively associated with increasing canopy cover, and Hydracarina which exhibited an opposite relationship to canopy cover.

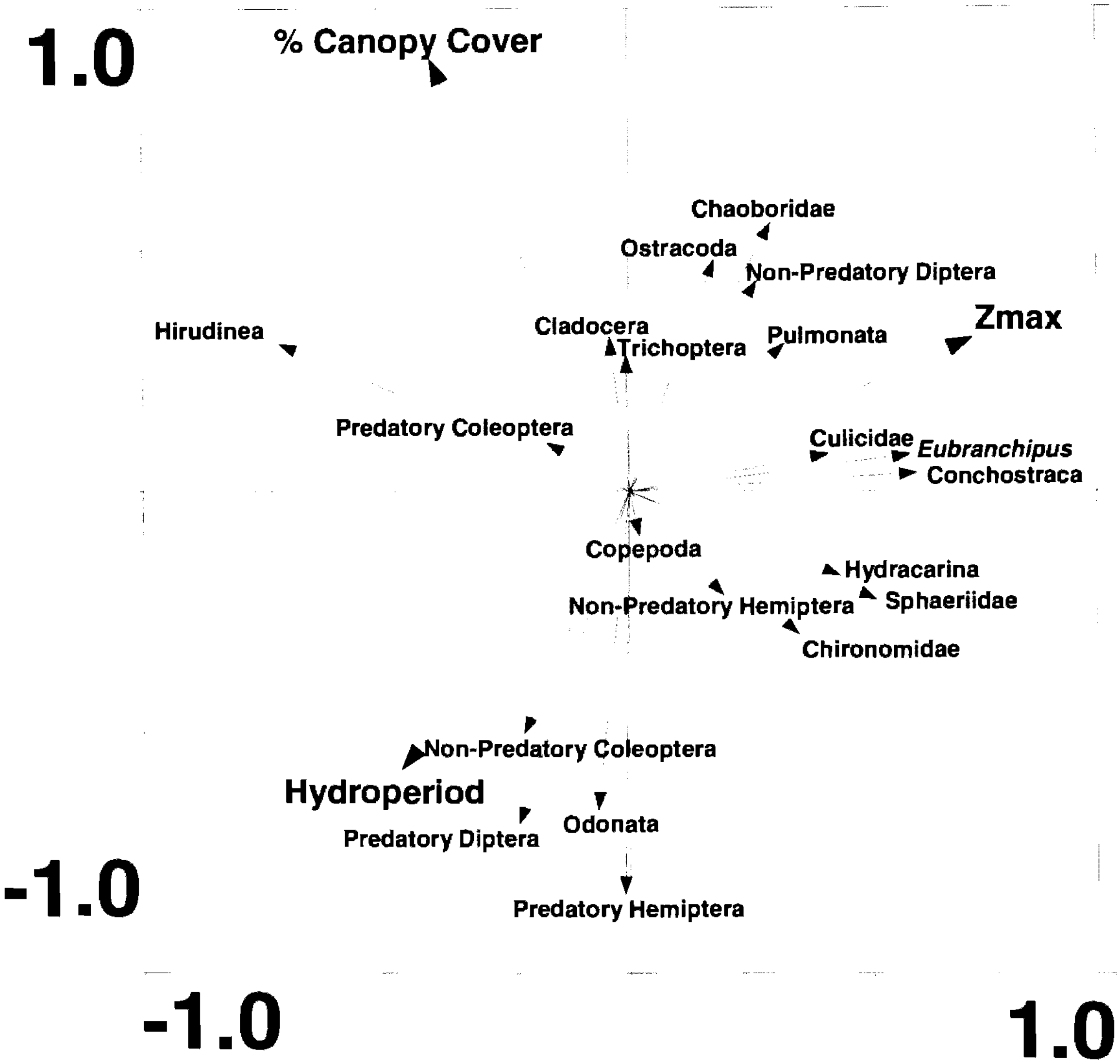

Figure 2.9. 2008 results. Plots of final repeated measures partial redundancy analysis (rpRDA) models of pond invertebrate communities using the three environmental variables that explained the most variance. Length of dashed vectors indicates strength of relationships between axes and environmental variables. Solid arrows indicate direction of sharpest increase in abundance of aquatic invertebrate groups.

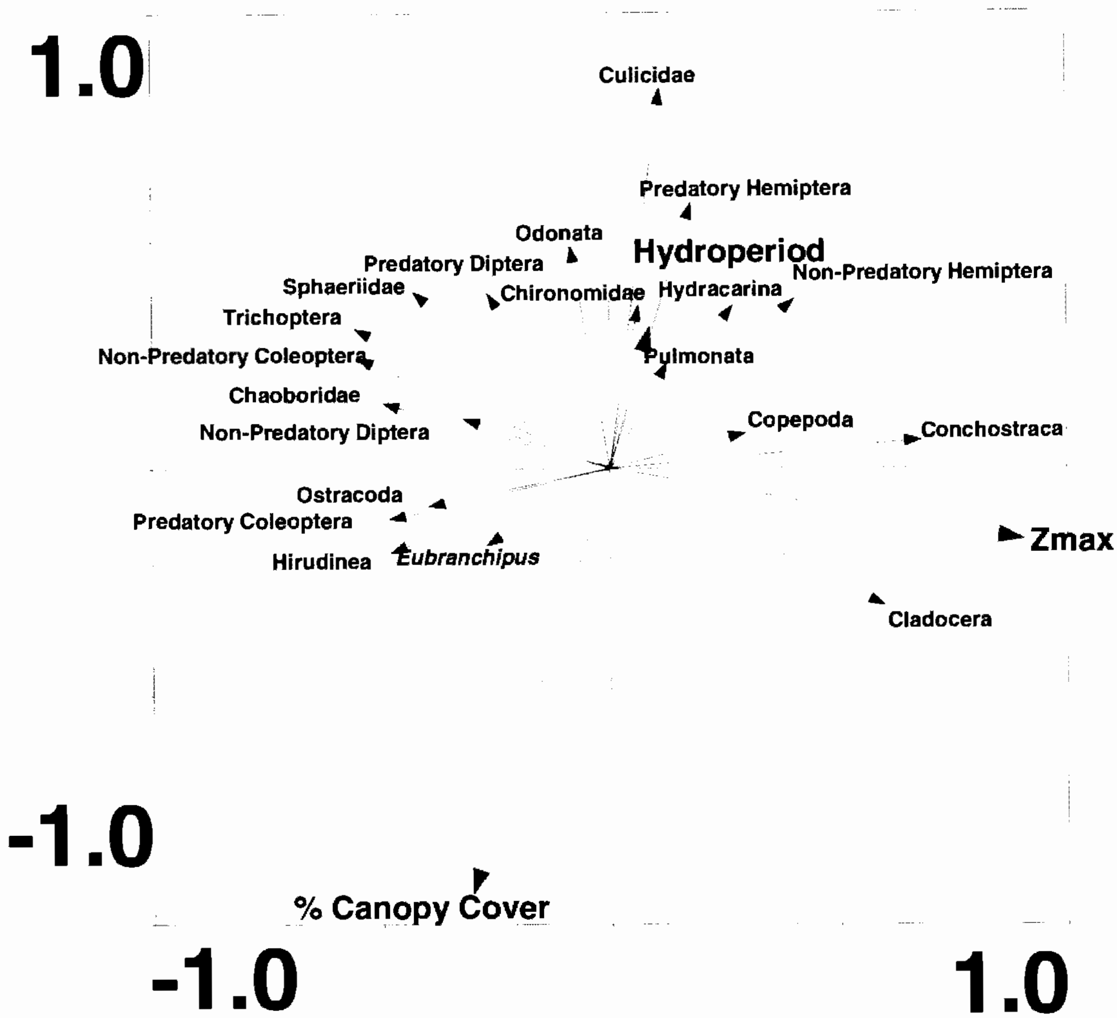

Figure 2.10. 2009 results. Plots of final repeated measures partial redundancy analysis (rpRDA) models of pond invertebrate communities using the three environmental variables that explained the most variance. Length of dashed vectors indicates strength of relationships between axes and environmental variables. Solid arrows indicate direction of sharpest increase in abundance of aquatic invertebrate groups.

Between-Year Differences

A non-metric multidimensional scale (NMS) was used to create an ordination using invertebrate community scores from 2008 and 2009 to display the interannual differences and similarities among invertebrate communities between 2008 and 2009 (Figure 2.11). NMS identified a two-dimensional solution (Table

2.2) with axis 1 explaining 79%, and axis 2 explaining 17% of the variance (cumulative $R^2 = 0.96$). Stress of the final ordination was 6.1, which is well below the recommended stress allowance (10.0-15.0) for a reliable model (McCune and Grace 2002). The observed pattern reveals there was a higher dissimilarity in invertebrate community composition during the early and mid-season sampling periods in 2008 and 2009. However, invertebrate community composition became more similar between years later in the season. The weighted average of the combined 2008 and 2009 scores of the invertebrate groups are represented by grey circles (Figure 2.11). The pattern in the following weighted average scores of the invertebrate groups *Eubranchipus,* Culicidae, and Trichoptera is because these groups were typically found in seasonal ponds during early spring. Other invertebrate groups appear to lump together, suggesting that these invertebrate groups were generalists, and were found in seasonal ponds throughout sampling periods.

Table 2.2. Summary of final 2-dimensional solution for non-metric multidimensional scaling (NMS) using site invertebrate community composition scores of 20 aquatic invertebrate groups found in seasonal ponds during 2008 and 2009.

	Stress in source data						
	Actual data (250 runs)			Monte Carlo tests (250)			
Axes	Minimum	Mean	Maximum	Minimum	Mean	Maximum	P-value
1	17.865	41.773	53.745	19.758	45.547	53.71	0.004
2	6.095	7.939	35.465	11.583	18.212	32.002	0.004

Values indicate dissimilarity (stress) with site scores and results summarized for actual and randomized (Monte Carlo) data. P-values indicate improvement in actual data in comparison to randomized data. Dimensions of final solution were determined through preliminary models with 6 axes (McCune and Grace 2002).

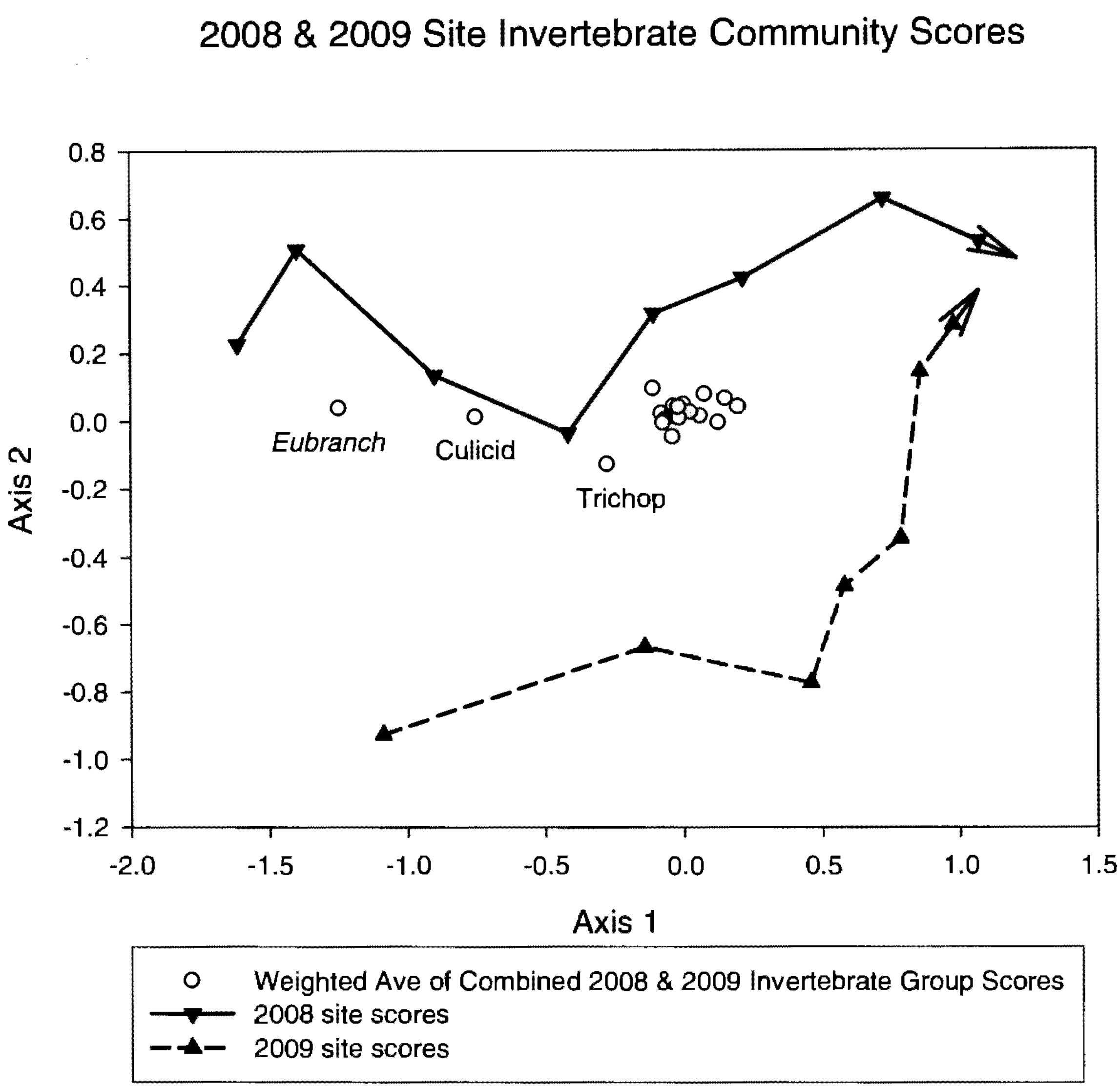

Figure 2.11. Invertebrate community scores by year from non-metric multidimensional scaling (NMS) during 2008 (solid black line) and 2009 (dashed black line). Lines connecting sampling periods form a chronosequence for each year. Arrows represent trajectory of invertebrate community composition through time. Grey circles represent weighted averages of the combined 2008 and 2009 invertebrate group scores (Eubranch: *Eubranchipus*, Culicid: Culicidae, Trichop: Trichoptera).

The invertebrate groups that showed moderate ($R^2 > 0.30$) to strong correlations with the NMS axes include aquatic insects (Culicidae, Diptera (mixed or non-predacious), Diptera (predacious), Trichoptera, Hemiptera (mixed or non-predacious), Hemiptera (predacious), Coleoptera (predacious)), Hydracarina, Crustaceans (*Eubranchipus,* Conchostraca, Copepoda), Mollusca (Pulmonata, Sphaeriidae), and Hirudinea (Table 2.3). The highest NMS axis correlations were for Culicidae (R^2 = 0.96, axis 1), *Eubranchipus* (R^2 = 0.81, axis 1), Copepoda (R^2 = 0.56, axis 1), Pulmonata (R^2 = 0.77, axis 2) and Hirudinea (R^2 = 0.75, axis 1). The invertebrate groups with higher R^2 values suggest the presence and abundance of these particular taxa have a greater influence on invertebrate community composition patterns observed in my final NMS ordination.

Table 2.3. Summary of R^2 values displaying linear correlations between invertebrate groups ($\log_{10}$ (n+1)), and 2 axes identified in final non-metric multidimensional scaling (NMS) model for years, 2008 and 2009.

Taxa		R^2 values	
		Axis 1	Axis 2
Insecta	Culicidae	0.96	0.00
	Chaoboridae	0.19	0.04
	Chironomidae	0.00	0.65
	Diptera (mixed or non predacious)	0.16	0.42
	Diptera (predacious)	0.10	0.45
	Trichoptera	0.47	0.28
	Hemiptera (mixed or non-predacious)	0.38	0.01
	Hemiptera (predacious)	0.15	0.41
	Coleoptera (mixed or non-predacious)	0.16	0.02
	Coleoptera (predacious)	0.19	0.50
	Odonata	0.18	0.05
Hydracarina		0.17	0.37
Crustacea	*Eubranchipus*	0.81	0.01
	Conchostraca	0.10	0.45
	Ostracoda	0.07	0.06
	Cladocera	0.35	0.00
	Copepoda	0.56	0.01
Mollusca	Pulmonata	0.04	0.77
	Sphaeriidae	0.35	0.18
Hirudinea		0.75	0.08

I not only wanted to identify possible differences between years but also by location (state forest). NMS identified a 2-dimensional solution (Table 2.4) with axis 1 explaining 28%, and axis 2 explaining 61% of the variance (cumulative R^2 = 0.90). Stress of the final ordination was 12.9, which is within the suggested guideline of 10.0-15.0 (McCune, and Grace 2002). The pattern in invertebrate community composition scores suggests that time had a stronger influence on invertebrate community composition than did pond location (Paul Bunyan or Buena Vista State Forests). The largest difference in invertebrate community composition was in the early spring. As time progressed invertebrate community composition began to converge in similarity to the point where differences were difficult to distinguish between both years, and forest. Again, the combined weighted average scores of 2008 and 2009 of the invertebrate groups are represented by grey circles (Figure 2.12).

Table 2.4. Summary of final 2-dimensional solution for non-metric multidimensional scaling (NMS) using site invertebrate community composition scores of 20 aquatic invertebrate groups found in seasonal ponds in the Buena Vista and Paul Bunyan State Forests during 2008 and 2009.

	Stress in source data						
	Actual data (250 runs)			Monte Carlo tests (250)			
Axes	Minimum	Mean	Maximum	Minimum	Mean	Maximum	P-value
1	24.287	48.434	55.777	36.145	49.825	55.777	0.004
2	12.866	13.84	39.15	19.337	23.956	39.15	0.004

Values indicate dissimilarity (stress) with site scores and results summarized for actual and randomized (Monte Carlo) data. P-values indicate improvement in actual data in comparison to randomized data. Dimensions of final solution were determined through preliminary test models with 6 axes (McCune and Grace 2002).

When comparing similarities and differences between forest by year, the main invertebrate groups that showed moderate (R^2 > 0.30) to strong correlations with NMS axes were aquatic insects (Culicidae, Diptera (mixed or non-predacious), Trichoptera, Hemiptera (predacious), Coleoptera (predacious), Crustaceans (*Eubranchipus*, Copepod), and Hirudinea (Table 2.5, Figure 2.12). The invertebrates with the highest correlations with the axes and also the taxa to have the highest influence on the observed pattern based on presence and abundance in my final NMS model include Culicidae (R^2 = 0.91, axis 2), Trichoptera (R^2 = 0.52, axis 1), Hemiptera (predacious) (R^2 = 0.59, axis 1), Coleoptera (predacious) (R^2 = 0.60, axis 1), and *Eubranchipus* (R^2 = 0.73, axis 2).

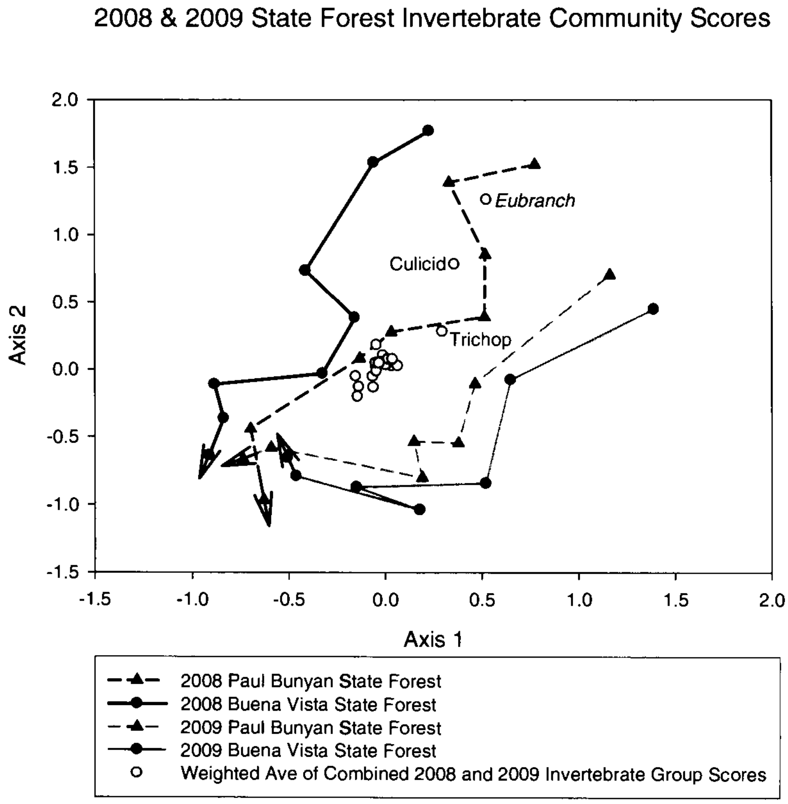

Figure 2.12. State forest invertebrate community scores from non-metric multidimensional scaling (NMS) during 2008 (black lines) and 2009 (grey lines). Treatments are divided by forest and include the Paul Bunyan State Forest (dashed lines), and the Buena Vista State Forest (solid lines). Lines connecting sampling periods form a chronosequence for each state forest during each year (2008, 2009). Arrows represent trajectory of invertebrate community composition through time. Grey circles represent weighted averages of the combined 2008 and 2009 invertebrate group scores (Eubranch: *Eubranchipus*, Culicid: Culicidae, Trichop: Trichoptera).

Table 2.5. Summary of R^2 values displaying linear correlations between invertebrate groups ($\log_{10}(n+1)$), and 2 axes identified in final non-metric multidimensional scaling (NMS) model for state forest.

Taxa		R^2 values	
		Axis 1	Axis 2
Insecta	Culicidae	0.36	0.91
	Chaoboridae	0.06	0.01
	Chironomidae	0.28	0.04
	Diptera (mixed or non predacious)	0.03	0.30
	Diptera (predacious)	0.29	0.02
	Trichoptera	0.52	0.26
	Hemiptera (mixed or non-predacious)	0.10	0.29
	Hemiptera (predacious)	0.59	0.04
	Coleoptera (mixed or non-predacious)	0.19	0.08
	Coleoptera (predacious)	0.60	0.03
	Odonata	0.00	0.15
Hydracarina		0.07	0.24
Crustacea	*Eubranchipus*	0.23	0.73
	Conchostraca	0.22	0.11
	Ostracoda	0.01	0.10
	Cladocera	0.03	0.28
	Copepoda	0.22	0.44
Mollusca	Pulmonata	0.16	0.19
	Sphaeriidae	0.30	0.15
Hirudinea		0.41	0.46

Maximum Pond Depth

A third set of ordinations were created to compare maximum depth/year invertebrate community composition scores to identify similarities and dissimilarities in community patterns between shallow (36.5 – 58 cm in 2008, 47.5 – 78 cm in 2009) and deep (59.5 – 94 cm in 2008, 79 – 122.25 cm in 2009) seasonal ponds during 2008 and 2009 (Figure 2.13). Maximum depth explained the most variance in invertebrate community composition using an RDA (direct or constrained ordination) in both 2008 and 2009. NMS identified a 2-dimensional solution (Table 2.6) with axis 1 explaining 55%, and axis 2 explaining 36% of the variance (cumulative $R^2 = 0.91$). Stress of the final ordination was 12.2, which is within the recommend stress level of 10.0-15.0 (McCune and Grace 2002) indicating that my model results were reliable. According to the NMS ordinations deep and shallow ponds exhibited similar patterns within years in invertebrate community composition during both 2008 and 2009. The invertebrate communities of deep and shallow ponds do follow similar trajectories, and differences and similarities between invertebrate communities inhabiting deep and shallow ponds were quite variable throughout the season. Interestingly, invertebrate community composition in shallow ponds in 2008 and 2009 was more similar to each other than to the invertebrate communities inhabiting deep ponds in the late sampling period. Most importantly pattern in invertebrate community composition again indicates that the majority of observed difference in pattern is due to year (time) rather than to influences of other environmental variables.

Table 2.6. Summary of final 2-dimensional solution for non-metric multidimensional scaling (NMS) using site invertebrate community composition scores of 20 aquatic invertebrate groups found in seasonal ponds comparing shallow and deep maximum depth during 2008 and 2009. Values indicate dissimilarity (stress) with site scores and results summarized for actual and randomized (Monte Carlo) data. P-values indicate improvement in actual data in comparison to randomized data. Dimensions of final solution were determined through preliminary test models with 6 axes (McCune and Grace 2002).

	Stress in source data						
	Actual data (250 runs)			Monte Carlo tests (250)			
Axes	Minimum	Mean	Maximum	Minimum	Mean	Maximum	P-value
1	22.938	45.606	55.777	32.523	49.588	55.777	0.004
2	12.165	13.534	39.15	20.203	24.298	31.083	0.004

Maximum Depth Invertebrate Community Scores

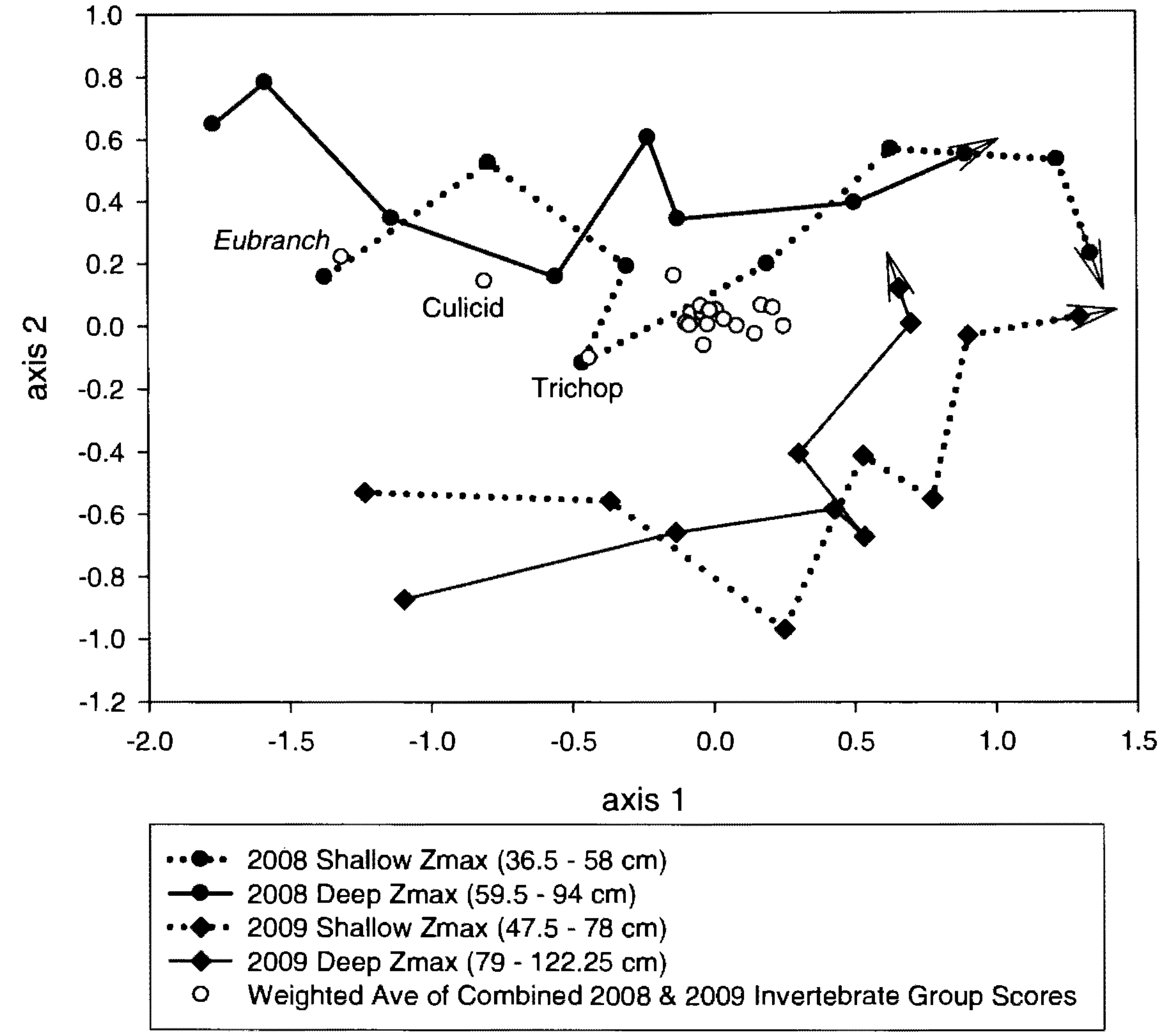

Figure 2.13. Maximum depth (Zmax) invertebrate community scores from non-metric multidimensional scaling (NMS) during 2008 (black lines) and 2009 (grey lines). Treatments include shallow Zmax (light dashed lines) and deep Zmax (solid lines). Lines connecting sampling periods form a chronosequence for ponds with shallow and deep maximum depths for each year (2008, 2009). Arrows represent trajectory of invertebrate community composition through time. Grey circles represent weighted averages of the combined 2008 and 2009 invertebrate group scores (Eubranch: *Eubranchipus*, Culicid: Culicidae, Trichop: Trichoptera).

The groups of invertebrates that showed moderate ($R^2 > 0.30$) to strong association with the NMS axes included aquatic insects (Culicidae, Diptera (mixed or non-predacious), Diptera (predacious), Trichoptera, Hemiptera (mixed or non-predacious), Hemiptera (predacious)), Hydracarina, Crustaceans (*Eubranchipus,* Conchostraca, Cladocera (other), Copepoda), Mollusca (Pulmonata), and Hirudinea (Table 2.7). The invertebrates with the highest R^2 values, suggesting considerable relationship to the observed pattern in my final NMS model, include Culicidae (R^2 = 0.89, axis 2), Trichoptera (R^2 = 0.53, axis 2), *Eubranchipus* (R^2 = 0.69, axis 2), Copepoda (R^2 = 0.51, axis 2), Pulmonata (R^2 = 0.74, axis 1), and Hirudinea (R^2 = 0.77, axis 2).

Table 2.7. Summary of R^2 values displaying linear correlations between invertebrate groups ($\log_{10}$ (n+1)), and 2 axes identified in final non-metric multidimensional scaling (NMS) model for maximum depth (Zmax).

Taxa		R^2 values	
		Axis 1	Axis 2
Insecta	Culicidae	0.09	0.89
	Chaoboridae	0.02	0.10
	Chironomidae	0.48	0.01
	Diptera (mixed or non predacious)	0.46	0.11
	Diptera (predacious)	0.33	0.03
	Trichoptera	0.09	0.53
	Hemiptera (mixed or non-predacious)	0.04	0.31
	Hemiptera (predacious)	0.14	0.33
	Coleoptera (mixed or non-predacious)	0.00	0.15
	Coleoptera (predacious)	0.18	0.24
	Odonata	0.06	0.07
Hydracarina		0.42	0.11
Crustacea	*Eubranchipus*	0.06	0.69
	Conchostraca	0.38	0.06
	Ostracoda	0.00	0.03
	Cladocera	0.01	0.40
	Copepoda	0.00	0.51
Mollusca	Pulmonata	0.74	0.01
	Sphaeriidae	0.06	0.28
Hirudinea		0.00	0.77

Canopy Cover

I wanted to assess similarities and differences in invertebrate community composition when compared to percent canopy cover. Using an NMS ordination (Figure 2.14) invertebrate scores were compared to three percent canopy cover categories, low (11-31%), medium (39-61%), and high % canopy cover (73-96%), between 2008 and 2009. Percent canopy cover was found to explain the second highest amount of variance using an RDA, in both 2008 and 2009. NMS identified a 2-dimensional solution (Table 2.8) with axis 1 explaining 23%, and axis 2 explaining 64% of the variance (cumulative $R^2 = 0.87$). Stress of the final ordination was 14.5 which is within the recommend stress level of 10.0-15.0, indicating my model results were reliable (McCune and Grace 2002). Shifts in invertebrate community composition followed similar trajectories in ponds that had low percent canopy cover during 2008 and 2009, and became even more similar later in the season. Ponds with high percent canopy cover also displayed invertebrate community composition trajectories that were similar to each other between 2008 and 2009, and also become more similar during the later sampling periods. The similarities between the low percent canopy scores of 2008 and 2009 reflect only minor differences between years. There were also only minor differences in invertebrate community composition scores between the sites in the high percent canopy cover treatment of 2008 and 2009.

Table 2.8. Summary of final 2-dimensional solution for non-metric multidimensional scaling (NMS) using site invertebrate community composition scores of 20 aquatic invertebrate groups found in seasonal ponds comparing percent canopy cover during 2008 and 2009. Values indicate dissimilarity (stress) with site scores and results summarized for actual and randomized (Monte Carlo) data. P-values indicate improvement in actual data in comparison to randomized data. Dimensions of final solution were determined through preliminary test models with 6 axes (McCune and Grace 2002).

	Stress in source data						
	Actual data (250 runs)			Monte Carlo tests (250)			
Axes	Minimum	Mean	Maximum	Minimum	Mean	Maximum	P-value
1	32.087	49.723	56.438	39.919	52.304	56.441	0.004
2	14.524	15.577	40.127	23.799	26.951	40.128	0.004

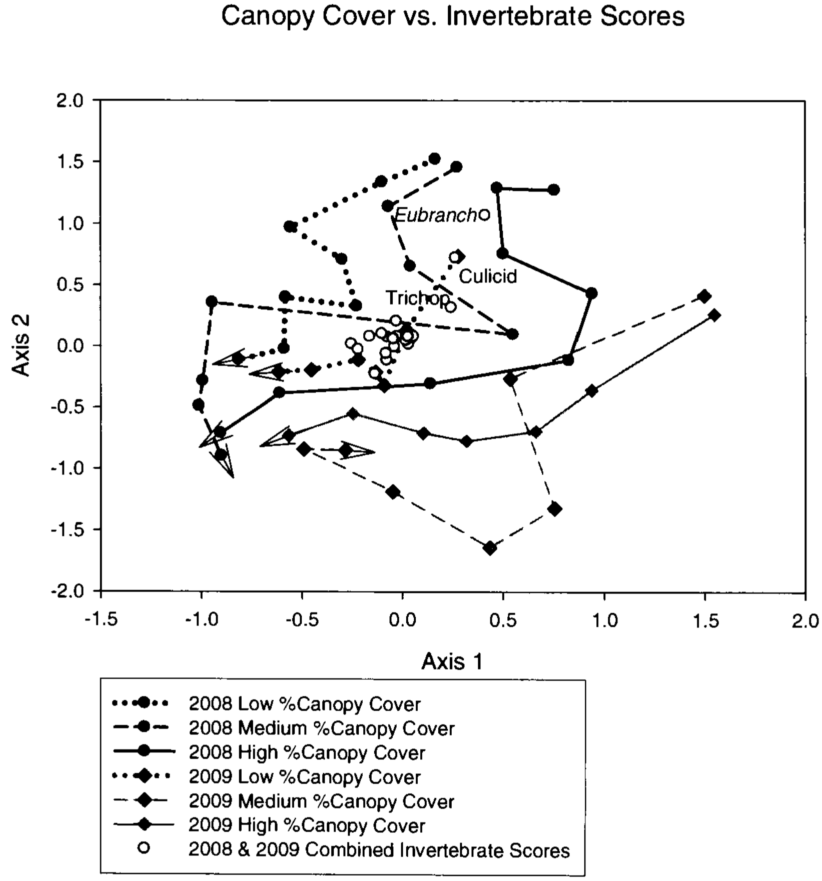

Figure 2.14. Percent canopy cover invertebrate community scores from non-metric multidimensional scaling (NMS) during 2008 (black lines) and 2009 (grey lines). Treatments include ponds with low % canopy cover (light dash lines), medium % canopy cover (heavy dash lines) and high % canopy cover (solid lines). Lines connecting sampling periods form a chronosequence for ponds within each treatment for each year. Arrows represent trajectory of shifts in invertebrate community composition through time. Grey circles represent weighted averages of the combined 2008 and 2009 invertebrate group scores (Eubranch: *Eubranchipus*, Culicid: Culicidae, Trichop: Trichoptera).

Invertebrate taxa that displayed moderate (R^2 >0.30) to strong correlations with NMS axes include aquatic insects (Culicidae, Chironomidae, Trichoptera, Hemiptera (predacious), Coleoptera (predacious)), crustaceans (*Eubranchipus,* Conchostraca, Cladocera, Copepoda), Mollusca (Pulmonata, Sphaeriidae), and Hirudinea (Table 2.9). Culicidae (R^2 = 0.88, axis 2), Hemiptera (predacious) (R^2 = 0.62, axis 1), *Eubranchipus* (R^2 = 0.58, axis 2), Conchostraca (R^2 = 0.60, axis 1), and Hirudinea (R^2 = 0.54, axis 2) had the highest R^2 values suggesting these taxa exhibited the most influence on the observed patterns in my final NMS model for percent canopy cover.

Table 2.9. Summary of R^2 values displaying linear correlations between invertebrate groups ($\log_{10}$ (n+1)), and 2 axes identified in final non-metric multidimensional scaling (NMS) model for percent canopy cover.

Taxa		R^2 values	
		Axis 1	Axis 2
Insecta	Culicidae	0.02	0.88
	Chaoboridae	0.03	0.08
	Chironomidae	0.45	0.10
	Diptera (mixed or non predacious)	0.07	0.26
	Diptera (predacious)	0.02	0.01
	Trichoptera	0.11	0.35
	Hemiptera (mixed or non-predacious)	0.03	0.15
	Hemiptera (predacious)	0.62	0.01
	Coleoptera (mixed or non-predacious)	0.13	0.12
	Coleoptera (predacious)	0.30	0.03
	Odonata	0.24	0.01
Hydracarina		0.19	0.28
Crustacea	*Eubranchipus*	0.02	0.58
	Conchostraca	0.60	0.13
	Ostracoda	0.00	0.15
	Cladocera	0.07	0.31
	Copepoda	0.01	0.39
Mollusca	Pulmonata	0.42	0.17
	Sphaeriidae	0.32	0.03
Hirudinea		0.08	0.54

Hydroperiod

Using an NMS ordination, which identified a 3-dimensional solution (Table 2.10), invertebrate community composition scores were compared to three hydroperiod length categories, short (68-87 days in 2008, 63-92 days in 2009), medium length (96-103 days in 2008, 99-105 days in 2009), and long (110-126 days in 2008, 151-157 days in 2009) in both 2008 and 2009 (Figure 2.15). The first three axes of the ordination explained approximately 54, 17, and 22% of the variance with a cumulative $R^2 = 0.94$. Using the recommended guideline of a mean stress value between 10.0 and 15.0 to indicate whether the model results were reliable (McCune and Grace 2002), stress of the final NMS ordination was identified at 9.2. Invertebrate community composition among all ponds, despite hydroperiod length, was similar to each other among years in the early sampling periods. As time progressed invertebrate community composition in ponds with relatively long hydroperiods began to diverge from ponds with short and medium hydroperiods. Invertebrate community composition in the early sampling periods in ponds with long hydroperiods were quite different from each other between years; however, in the later sampling periods invertebrate communities in ponds with relatively long hydroperiods became more similar to each other between years, especially in the last sampling period. The NMS ordination suggests there is little noticeable difference in invertebrate community composition among ponds with short and medium hydroperiods among years.

Table 2.10. Summary of final 3-dimensional solution for non-metric multidimensional scaling (NMS) using site invertebrate community composition scores of 20 aquatic invertebrate groups found in seasonal ponds comparing hydroperiod during 2008 and 2009. Values indicate dissimilarity (stress) with site scores and results summarized for actual and randomized (Monte Carlo) data. P-values indicate improvement in actual data in comparison to randomized data. Dimensions of final solution were determined through preliminary test models with 6 axes (McCune and Grace 2002).

	Stress in source data						
	Actual data (250 runs)			Monte Carlo tests (250)			
Axes	Minimum	Mean	Maximum	Minimum	Mean	Maximum	P-value
1	28.909	48.901	56.437	39.379	52.333	56.437	0.004
2	14.877	16.932	40.126	22.921	27.24	39.961	0.004
3	9.157	9.464	11.348	16.289	18.489	20.517	0.004

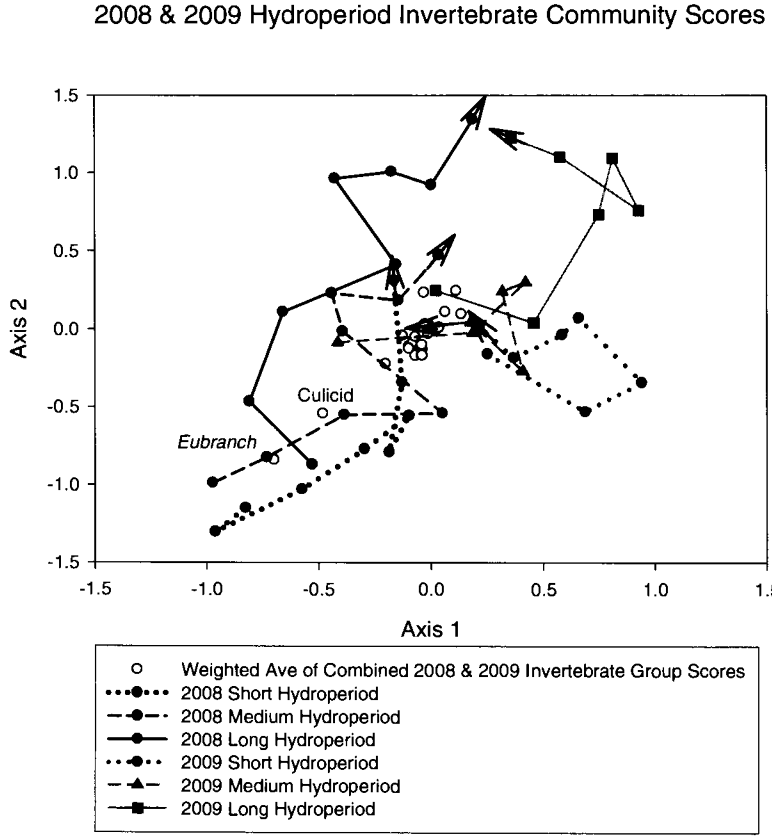

Figure 2.15. Hydroperiod invertebrate community scores from non-metric multidimensional scaling (NMS) during 2008 (black lines) and 2009 (grey lines). Treatments include ponds with short hydroperiod (light dash lines), medium hydroperiod (heavy dash lines) and long hydroperiod (solid lines). Lines connecting sampling periods form a chronosequence for ponds within each treatment for each year. Arrows represent trajectory of shifts in invertebrate community composition through time. Grey circles represent weighted averages of the combined 2008 and 2009 invertebrate group scores (Eubranch: *Eubranchipus*, Culicid: Culicidae).

Invertebrate groups that showed moderate ($R^2 > 0.30$) to strong associations with the NMS axes (Table 2.11) were aquatic insects Culicidae, Chironomidae, Diptera (mixed or non-predacious), Trichoptera, Hemiptera (predacious), Hydracarina, crustaceans (*Eubranchipus,* Ostracoda, Cladocera (other), Copepoda), Mollusca (Pulmonata), and Hirudinea. The highest axes correlations determined were for Culicidae ($R^2 = 0.58$, axis 1), Ostracoda ($R^2 = 0.65$, axis 2), Cladocera (other) ($R^2 = 0.74$, axis 2), and Hirudinea ($R^2 = 0.51$, axis 3), due to their high axes correlations, these invertebrate groups had the most pronounced influence on the observed pattern in the final NMS model.

Table 2.11. Summary of R^2 values displaying linear correlations between invertebrate groups ($\log_{10}$ (n+1)), and 3 axes identified in final non-metric multidimensional scaling (NMS) model for hydroperiod.

Taxa		R^2 values		
		Axis 1	Axis 2	Axis 3
Insecta	Culicidae	0.58	0.43	0.40
	Chaoboridae	0.20	0.21	0.06
	Chironomidae	0.34	0.26	0.07
	Diptera (mixed or non predacious)	0.31	0.23	0.01
	Diptera (predacious)	0.03	0.00	0.17
	Trichoptera	0.02	0.06	0.39
	Hemiptera (mixed or non-predacious)	0.24	0.07	0.06
	Hemiptera (predacious)	0.01	0.31	0.31
	Coleoptera (mixed or non-predacious)	0.10	0.17	0.12
	Coleoptera (predacious)	0.01	0.09	0.28
	Odonata	0.16	0.01	0.00
Hydracarina		0.44	0.34	0.00
Crustacea	*Eubranchipus*	0.40	0.34	0.21
	Conchostraca	0.26	0.26	0.15
	Ostracoda	0.08	0.65	0.00
	Cladocera	0.06	0.74	0.12
	Copepoda	0.11	0.47	0.30
Mollusca	Pulmonata	0.47	0.14	0.13
	Sphaeriidae	0.00	0.00	0.32
Hirudinea		0.14	0.37	0.51

Wetland Function/Classification

An NMS ordination was also used to relate invertebrate community composition scores to hydrological pond function (recharge, flow-through and perched) (Figure 2.16). A final NMS model identified a 3-dimensional solution (Table 2.12) with three axes explaining approximately 26, 42, and 26% of the variance with a cumulative R^2 = 0.94. The stress value of the final NMS ordination was 9.06 which is near the recommended stress value of 10.0, indicating the model results are reliable (McCune and Grace 2002). Invertebrate community composition followed very similar trajectories particularly during 2008, however, the recharge and flow-through treatments contained invertebrate communities that were much more similar to each other than to the perched sites (Figure 2.16). This relationship is evident in both 2008 and 2009. The invertebrate communities of the perched treatment, while similar to each other between the two years, displays differences when compared to recharge and flow-through treatments. While there appear to be differences in invertebrate communities when comparing recharge, and flow-through to perched wetlands it is difficult to make assumptions due to having only two ponds in the perched treatment.

Table 2.12. Summary of final 3-dimensional solution for non-metric multidimensional scaling (NMS) using site invertebrate community composition scores of 20 aquatic invertebrate groups found in seasonal ponds comparing hydrological function during 2008 and 2009. Values indicate dissimilarity (stress) with site scores and results summarized for actual and randomized (Monte Carlo) data. P-values indicate improvement in actual data in comparison to randomized data. Dimensions of final solution were determined through preliminary test models with 6 axes (McCune and Grace 2002).

	Stress in source data						
	Actual data (250 runs)			Monte Carlo tests (250)			
Axes	Minimum	Mean	Maximum	Minimum	Mean	Maximum	P-value
1	30.33	46.99	56.437	38.172	51.334	56.44	0.004
2	15.638	17.981	40.125	22.578	26.695	40.128	0.004
3	9.056	9.058	9.058	15.659	18.258	20.199	0.004

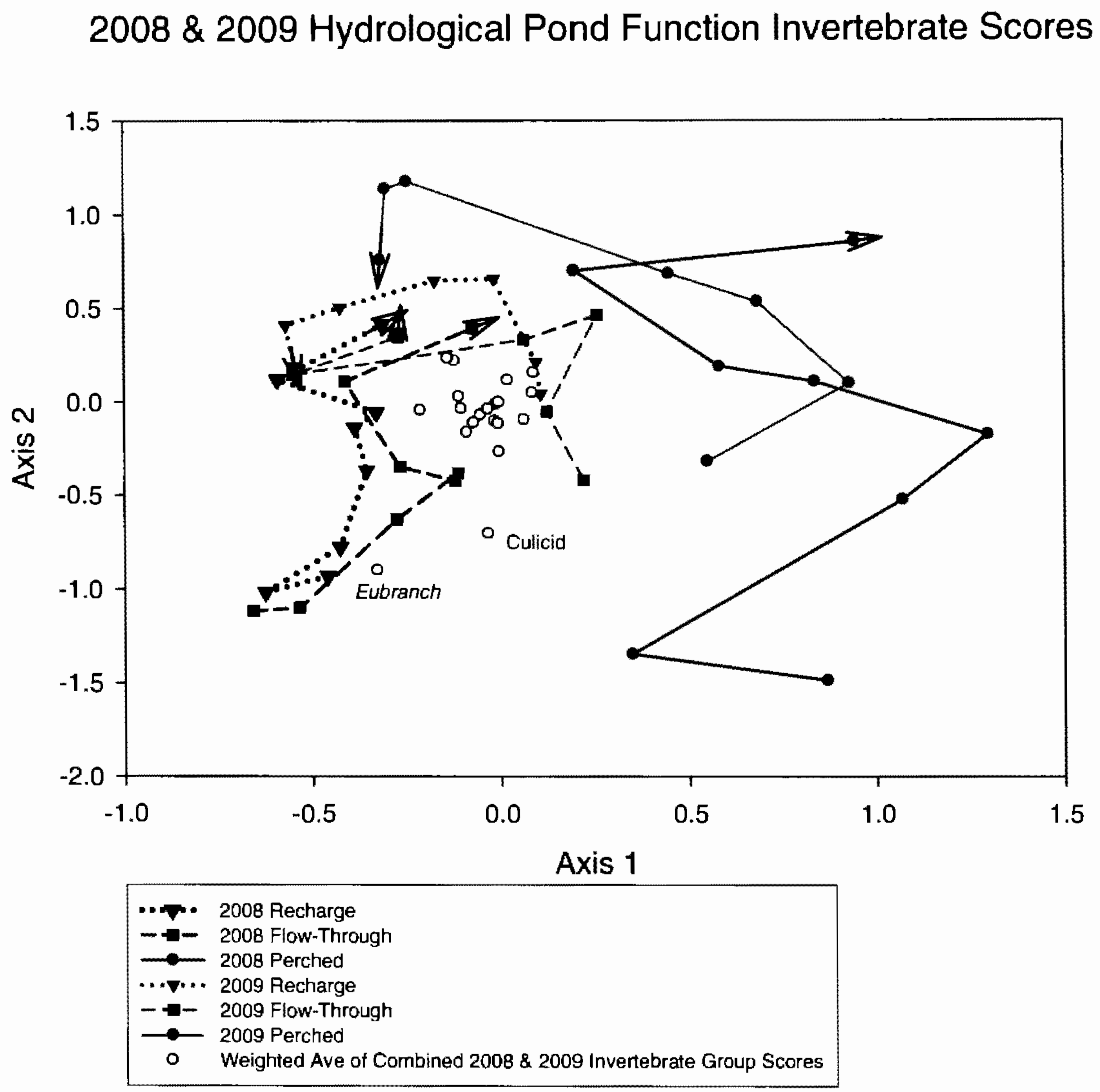

Figure 2.16. Hydrological function invertebrate community scores from non-metric multidimensional scaling (NMS) during 2008 (black lines) and 2009 (grey lines). Treatments include recharge ponds (light dash lines), flow-through ponds (heavy dash lines) and perched ponds (solid lines). Lines connecting sampling periods form a chronosequence for ponds within each treatment for each year. Arrows represent trajectory of shifts in invertebrate community composition through time. Grey circles represent weighted averages of the combined 2008 and 2009 invertebrate group scores (Eubranch: *Eubranchipus*, Culicid: Culicidae).

Several invertebrate groups showed a moderate (R^2 >0.30) to strong association with the NMS axes including, aquatic insects (Culicidae, Trichoptera, Hemiptera (predacious)), Hydracarina, crustaceans (Conchostraca, Ostracoda, Cladocera (other), Copepoda), and Hirudinea (Table 2.13). The invertebrate groups that likely had the most pronounced influence on the observed pattern on the final NMS model due to their high axes correlations include, Culicidae (R^2 = 0.784, axis 2), Trichoptera (R^2 = 0.527, axis 3), Hydracarina (R^2 = 0.505, axis 2), Conchostraca (R^2 = 0.831, axis 1), Ostracoda (R^2 = 0.505, axis 1), and Copepoda (R^2 = 0.549, axis 2).

Table 2.13. Summary of R^2 values displaying linear correlations between invertebrate groups ($\log_{10}$ (n+1)), and 3 axes identified in final non-metric multidimensional scaling (NMS) model for hydrological pond function.

Taxa		R^2 values		
		Axis 1	Axis 2	Axis 3
Insecta	Culicidae	0.00	0.78	0.33
	Chaoboridae	0.25	0.01	0.04
	Chironomidae	0.14	0.17	0.00
	Diptera (mixed or non predacious)	0.06	0.13	0.04
	Diptera (predacious)	0.00	0.00	0.23
	Trichoptera	0.00	0.13	0.53
	Hemiptera (mixed or non-predacious)	0.11	0.23	0.14
	Hemiptera (predacious)	0.05	0.01	0.48
	Coleoptera (mixed or non-predacious)	0.01	0.17	0.20
	Coleoptera (predacious)	0.00	0.00	0.30
	Odonata	0.05	0.08	0.02
Hydracarina		0.02	0.51	0.01
Crustacea	*Eubranchipus*	0.06	0.30	0.22
	Conchostraca	0.83	0.03	0.02
	Ostracoda	0.51	0.05	0.26
	Cladocera	0.22	0.36	0.26
	Copepoda	0.00	0.55	0.37
Mollusca	Pulmonata	0.08	0.08	0.18
	Sphaeriidae	0.10	0.22	0.20
Hirudinea		0.17	0.32	0.35

DISCUSSION

NMS and RDA models identified significant associations between invertebrate communities and environmental gradients in 16 seasonal ponds during 2008 -2009. However, despite intensive and simultaneous sampling of invertebrates, some associations between invertebrate communities and environmental gradients were still muted, as indicated by direct ordination (RDA). Using intensive sampling of invertebrates I hoped to overcome confounding effects of time, the main source of variability in invertebrate communities of past related studies (Miller 2008, and Hanson et al. 2009). Most muted relationships between invertebrate groups and environmental variables were also inconsistent from 2008 to 2009. Only 7 out of 20 invertebrate groups showed relationships with one of the three main environmental variables, these were predatory Hemiptera, non-predatory Hemiptera, Chironomidae, Hydracarina, Odonata, Conchostraca and Hirudinea. I identified 3 significant sources of variance in invertebrate community composition, which were maximum depth, percent canopy cover, and hydroperiod.

A unique finding in my study was that RDA models identified 3 sources of variance in the same relative order during both years of the study (2008, 2009). Maximum depth (Zmax), based on my direct ordination, had the largest influence on invertebrate community composition and explained 14% of variance in 2008 and 19% in 2009. The other two significant variables included % canopy cover, and hydroperiod, each explaining 12, and 11% respectively in 2008, and 11, and 9% respectively in 2009. These amounts of variance explained are high relative to past studies. For example, Hanson et al. 2009 reported that maximum depth and percent canopy openness explained 9.3 and 4.1% of the variance in these and other seasonal ponds during 1999-2005, values considerably lower than those reported here. These weaker invertebrate community associations (in comparison to my study) likely resulted from less intensive invertebrate sampling, with periods of several weeks between samples and non-simultaneous sampling of ponds, therefore obscuring sources of variance associated with shifts in community composition that my study was able to detect.

My NMS analyses indicated there were discernable differences among invertebrate communities associated with several environmental variables. However, as expected, within-year variability was more pronounced than variability contributed by other sources. There was an obvious shift in community composition in all seasonal ponds throughout each year. Early invertebrate communities were dominated by detritivores and herbivores such as *Eubranchipus*, Culicidae and Tricoptera, with invertebrate communities later in the season being represented by predacious migrating predators such as Hemiptera and Coleoptera (Wiggins et al. 1980). These shifts in community composition create high temporal variability which is a major source of variability in invertebrate communities in seasonal ponds (Miller et al. 2008). Miller et al. (2008) reported that Dipterans of the following families Culicidae, Chaoboridae, and Dixidae along with *Eubranchipus sp.*, Tichoptera and Hydracarina were associated with early collection dates in seasonal ponds near Remer, Minnesota. Seasonal ponds near Bemidji, Minnesota displayed similar trends with Culicidae, *Eubranchipus sp.*, Trichoptera, Copepoda, Ostracoda, and Hydracarina also associated with May sampling periods (Miller et al. 2008). Hanson et al. (2009) reported that the presence and abundance of several taxa including *Eubranchipus*, Hemiptera, and Hirudinea strongly influenced patterns observed in invertebrate communities among their seasonal ponds. *Eubranchipus* were closely associated with ponds having uncut adjacent stands. According to my results there was no relationship between *Eubranchipus* and stand-age, perhaps because tree harvest occurred 8 years before my study began.

NMS ordination models indicated that hydroperiod, percent canopy cover and hydrological pond function (recharge, discharge, flow-through, perched) showed strong associations with invertebrate communities. According to the NMS models invertebrate communities varied more by treatment than by year, particularly later in the season (June-early July). The maximum depth NMS ordination showed that invertebrate communities varied more by year than by treatment. Hydroperiod is widely considered to be the most influential environmental variable for invertebrate community composition in seasonal ponds (Batzer et al. 2004; Brooks 2000; Collinson et al. 1995; Williams 2005). The dynamic hydroperiod of seasonal ponds creates a fishless habitat, therefore low predation rates and relatively low rates of competition. These variable conditions promote the establishment of diverse and unique invertebrate communities when compared to invertebrate communities of permanent bodies of water, which are highly influenced by predation and competition. Seasonal ponds with extended hydroperiods sustain invertebrate communities showing increased influences of predation and competition when compared to invertebrate communities inhabiting seasonal ponds with relatively short hydroperiods (Schneider 1999). In my study sites the order Odonata was the only group of aquatic insects showing a consistent and positive association with extended hydroperiods. This association is likely due to the relatively longer life cycle of Odonata (1-6 years) when compared to other smaller invertebrates, particularly those inhabiting seasonal ponds with shorter hydroperiods (Thorp and Covich 2001). Odonata are also commonly one of the dominant predators in the invertebrate community. My invertebrate community composition data indicated that invertebrate communities of seasonal ponds with relatively long hydroperiods (110-157 days) differed from seasonal ponds with short (63-92 days) and medium (96-105 days) hydroperiods particularly starting during my mid season samples (beginning of June) (Figure 2.15).

A curious finding was that stand-age explained very little variance in invertebrate community composition in my sites. This may be because logging occurred in four of the sites during the winter of 1999-2000, eight years before my study began. Aust et al. (1997) studied tree harvesting techniques in the southeastern USA and found evidence of hydrologic responses to harvested sites with recovery to near pre-harvest conditions in as little as seven years. Hanson et al. (2009) did however observe a decrease in invertebrate taxon richness with increasing stand age, but their study occurred within 1 to 5 years after tree harvest. Age of adjacent stand explained 60% of their variance in canopy openness. They suggested the increase in invertebrate taxon richness was due to an increase in emergent macrophytes, particularly *Carex* spp. in ponds with relatively open canopies. Increases in emergent macrophytes increases habitat complexity as well as providing substrate for periphyton growth (Hanson et al. 2009). The negative association observed between Chironomidae and canopy cover in my study may also be due to an increase in periphyton growth following proliferation of emergent macrophytes, mainly *Carex* spp. Most Chironomidae are herbivores and detritivores (Thorp and Covich 2001), and thus would be expected to benefit from an increase in periphyton growth. Hanson et al. (2009) also reported a negative relationship between Chironomidae and canopy cover. Negative associations between predatory and non-predatory hemipterans and reduced canopy cover likely led to increased rates of aerial colonization by adult hemipterans (Hanson et al. 2010). A pond with less canopy cover is more visible to adult hemipterans, which disperse by flight in the spring after overwintering in permanent bodies of water (Williams 1996). Adult Hemiptera utilize seasonal ponds for their high food abundance where they lay their eggs and the young can grow quickly with relatively little competition (Williams 1996). Hanson et al. (2010) also observed an association between Hemiptera and ponds with decreased canopy cover. My data also indicated a difference (both within and between years) between invertebrate communities of seasonal ponds with low percent canopy cover compared to invertebrate communities inhabiting seasonal ponds with high percent canopy cover. The observed differences are likely due to increased colonization rates of Hemiptera (Hanson et al. 2010) and an increase in Chironomidae larvae resulting from increased periphyton growth (Hanson et al. 2009; Thorp and Covich 2001).

What sets my study apart from other similar accounts (in addition to intensive invertebrate sampling) is collection of hydrological pond function data and sampling intensity. There have been few studies looking at groundwater influences on seasonal ponds, and I am aware of no other research in which groundwater influences on invertebrate community composition has been studied. It is difficult to compare invertebrate communities in perched seasonal ponds with those in recharge and flow-through seasonal ponds because there were only two perched seasonal ponds out of the 16 sites in the study. Still, my data indicated that seasonal ponds with groundwater recharge or flow-through supported invertebrate communities that differed from perched seasonal ponds, based on invertebrate community composition. Generally, perched seasonal ponds exhibited much more variation in invertebrate community composition throughout the season than did recharge and flow-through seasonal ponds. There was little to no discernable differences in invertebrate community composition between recharge and flow-through seasonal ponds. My data suggests there is evidence that perched seasonal ponds may contain invertebrate communities that differ from other seasonal ponds (recharge and flow-through), however, further studies are needed to gain a better understanding of the influence of groundwater on invertebrate communities.

The likely reason for many of these muted associations is because many of these invertebrate taxa are able to tolerate a wide range of environmental gradients (Batzer et. al 2004, Hanson et. al 2009). Many of the past studies show weak and non-significant relationships between invertebrate communities inhabiting seasonal ponds and environmental gradients (Batzer et al. 2000, 2004; Hanson et al. 2009; Palik et al. 2001). Speculation suggests these weak and non-significant relationships between invertebrate communities in seasonal ponds and environmental gradients are due to high tolerance of the invertebrates to extreme and variable environmental conditions (Batzer et al. 2000, 2004; Hanson et al. 2009). This finding is not at all surprising due to the variation in environmental gradients (e.g. hydroperiod, maximum depth) that can occur at a single seasonal pond from one year to the next. For example, there was a personal observation that air-temperature during spring 2009 was much cooler than during the same period of 2008. The cold spring in 2009 may have been the reason for the observation of lower Culicidae (mosquito) densities and perhaps other differences in invertebrate community composition compared to 2008. Due to the relatively small size of seasonal ponds they are more likely to be influenced by changes in temperature when compared to bodies of water with a larger volume, such as, semi-permenant to permanent bodies of water. Therefore, invertebrate communities within seasonal ponds would be more exposed to temperature fluctuations. There was some unexplained variance in invertebrate communities in my RDA models which reflects responses to environmental variables that were unaccounted for. One specific environmental variable I did not model was temperature, and possibly accounted for some of the unexplained variance among invertebrate community composition.

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IMPLICATIONS

The broad objective of my research was to contribute to better understanding of ecological relationships between riparian communities and characteristics of adjacent upland forests. The hope in this research is to contribute to development of forest management practices to help maintain healthy, sustainable forests, and to protect the integrity of unique areas such as seasonal forest ponds within forested landscapes. Specifically, main objectives of the study were to assess the relationships between groundwater and seasonal forest ponds in the Bemidji, MN area and the influence of groundwater and other environmental gradients on aquatic invertebrate community composition.

I discovered there is high, but variable water exchange between seasonal ponds and groundwater in the Paul Bunyan and Buena Vista State Forests. Results suggest that patterns in aquatic invertebrate communities were related to hydrological function and hydroperiod, and appeared to be consistent between the 2 forest areas. Patterns in invertebrate communities also suggest that many aquatic invertebrates are generalist users of these seasonal ponds.

Invertebrate communities of semi-permanent to permanent bodies of water are typically influenced by fish predation, and/or predacious invertebrates, such as, Odonata, coleopterans and hemipterans (Schneider 1999; Wiggins et al. 1980). The Invertebrate community composition of seasonal ponds is typically a reflection of environmental gradients, rather than influences of predation or competition (Schneider 1999). Seasonal ponds with extended hydroperiods sustain invertebrate communities that show increased influences of predation and competition when compared to invertebrate communities inhabiting seasonal ponds with relatively shorter hydroperiods. My finding of Odonata, a common dominant predator in the invertebrate community, being associated with ponds having an extended hydroperiod, supports this. Also in my study, early invertebrate communities were dominated by detritivores and herbivores such as *Eubranchipus*, Culicidae and Tricoptera, and invertebrate communities later in the season being represented by predacious migrating predators such as Hemiptera and Coleoptera (Wiggins et al. 1980). These shifts in community composition create high temporal variability which is a major source of variability in invertebrate communities in seasonal ponds (Miller et al. 2008).

Canopy cover has been found to be associated with age of adjacent stands (Hanson et al. 2009), and this suggests canopy cover is influenced by tree harvest. Low canopy cover around seasonal ponds increases visibility of seasonal ponds to invertebrate taxa that disperse by flight such as adult Hemiptera, and Coleoptera (Williams 1996). In my study both predacious and non-predacious Hemiptera were associated with seasonal ponds having low percent canopy cover. Seasonal ponds are typically colonized by adult Hemiptera in the spring after overwintering in permanent bodies of water. Adult Hemiptera utilize seasonal ponds for their high food abundance where they lay their eggs and their young can grow quickly with relatively little competition. Predatory fish or even other predatory invertebrates can have strong negative impacts on seasonal pond fauna due to their adaptations toward environments with low predation pressures (Wiggins et al. 1980; Brooks 2005).

Seasonal ponds are important for maintaining regional biodiversity due to the unique aquatic invertebrate communities that inhabit these systems (Williams 2005). Maintaining densities of seasonal ponds across landscapes is also important given the very low dispersal rates specifically of non-flying aquatic invertebrate taxa, such as fairy shrimp (*Eubranchipus*), clam shrimp (Conchostraca), and Cladocerans. Studies in other parts of the world have linked the dispersal of fairy shrimp through their resting eggs with the movement and dispersal of salamanders (Bohonak, and Whiteman 1999). Salamanders that ingest fairy shrimp eggs, or egg-carrying female fairy shrimp, can transport the eggs and secrete viable resting fairy shrimp eggs into other ponds. Bohonk (1998) estimated over a 7-year period, an average of 35 viable fairy shrimp eggs were moved annually by salamanders between ponds. Rothermel (2004) suggests seasonal ponds that are suitable breeding sites for amphibians such as spotted salamanders and wood frogs, but are 50 meters or more from suitable undisturbed terrestrial habitat may isolate amphibian populations due to high mortality rate of juveniles during emigration. Therefore, even small seasonal ponds are important refugia for traveling juveniles.

My failure in identifying a relationship between invertebrate community composition and age of adjacent aspen stands was likely due to tree harvest adjacent to four of my seasonal ponds 8 years before the study began. However, I did detect an influence of percent canopy cover on invertebrate community composition. Hanson et al. (2009) reported a strong correlation between canopy cover and age of adjacent stand, suggesting tree harvest influences canopy cover

over seasonal ponds. Future researchers might benefit from including sites that have undergone harvest of adjacent stands within a year of the start of the study. This would improve the chances of identifying relationships between invertebrate communities of season ponds, the hydrology and age of adjacent stands that would develop immediately after tree harvest.

Another weakness in my study was that, although I did successfully identify relationships between seasonal ponds with groundwater, only two of my sites were classified as perched. Having only two perched ponds causes difficulty when trying to make comparisons between perched and recharge/flow-through ponds. Evidence from my study suggests there may be discernable differences between invertebrate communities that inhabit perched seasonal ponds when compared to recharge, or flow-through seasonal ponds. Further studies are needed to gain a better understanding of the influence of groundwater on invertebrate communities, and to allow better comparisons between characteristics of perched and recharge/flow-through seasonal ponds.

Another aspect of seasonal ponds needing further research is the chemical properties of the groundwater and relationship between ponds and geomorphic setting. Groundwater samples could be taken from the piezometers and tested for chemical constituents and these could be compared to the chemical properties of the pond water (Lee 1977; Sebestyen and Schneider 2004) as well as the invertebrate community. Hydraulic conductivity mapping could be conducted for each pond, in an attempt to identify major areas of groundwater discharge or recharge in the pond basins. Seepage meters (Lee 1977; Sebestyen and

Schneider 2004) could then be placed at the locations of these major groundwater discharge/recharge areas to measure the volume of water that is discharging/recharging from the sites.

My study has identified some of the strongest relationships between invertebrate communities in seasonal ponds and environmental gradients to date (Batzer et al. 2000, 2004; Hanson et al. 2009; Palik et al. 2001). My study suggests invertebrate communities of seasonal ponds can be influenced by harvest of adjacent stands, indirectly through changes that can occur specifically in the length of hydroperiod and canopy cover.

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APPENDIX

Appendix Table A.1. Paul Bunyan State Forest Raw Soil Data

Site	Location	Horizon	Depth	Clay %	Silt %	Sand %	Soil Texture	pH (H_2O)	Bray P1 (mg/kg)	Olsen P (mg/kg)	Total N (%)	Total C (%)
PBI-1	Pond Basin	O	0-28					5.07	95.15		2.01	32.93
		C	28-102+	17.7	34.6	47.7	Loam	5.41	175.97		0.7063	10.54
	Upland	A	0-13	13.8	29.8	56.4	Sandy Loam	4.60	15.12		0.6117	8.513
		E	13-30	9.9	30.3	59.8	Sandy Loam	5.02	7.70		0.0274	0.4954
		BW	30-45	10.4	31.8	57.8	Sandy Loam	5.30	14.46		0.015	0.1839
		C	45-55+	12.4	17.2	70.4	Sandy Loam	5.77	10.81		0.01	0.08
PBI-3	Pond Basin	A	0-45	17.7	37.6	44.7	Loam	4.97	103.65		1.254	15.25
		CG	45-80+	14.8	42.5	42.7	Loam	5.18	82.89		0.0904	0.9865
	Upland	O	2-0					4.79	34.00		1.853	30.48
		A	0-14	7.8	25.7	66.5	Sandy Loam	4.47	51.75		0.4803	5.91
		E/B	14-33	11.9	28.4	59.7	Sandy Loam	4.92	82.23		0.0903	1.354
		C	33-87+	4.9	7.8	87.3	Loamy Sand	5.25	38.38		0.0129	0.2901

Appendix Table A.1. (continued)

Site	Location	Horizon	Depth	Clay %	Silt %	Sand %	Soil Texture	pH (H_2O)	Bray P1 (mg/kg)	Olsen P (mg/kg)	Total N (%)	Total C (%)
PBII-1	Pond Basin	O	0-55								2.98	43.61
		A	55-64	16.8	25.8	57.4	Sandy Loam	4.95	252.01		0.3939	4.979
		B	64-83	16.8	27.6	55.6	Sandy Loam	5.08	324.32		0.1055	1.059
		C-G	83+	16.6	28.4	55.0	Sandy Loam	5.10	109.89		0.0275	0.313
		C-G	83+	5.7	37.0	57.3	Sandy Loam	5.13	119.42		0.0277	0.2948
	Upland	O	0-5								2.156	36.37
		A	5-15cm	3.4	19.5	77.1	Loamy Sand	4.47	8.96		0.766	12.12
		B	15-29	6.4	19.2	74.4	Sandy Loam	4.85	10.88		0.2274	1.739
		C	29-67.5+	5.4	12.4	82.2	Loamy Sand	5.09	39.60		0.087	0.9448

Appendix Table A.1. (continued)

Site	Location	Horizon	Depth	Clay %	Silt %	Sand %	Soil Texture	pH (H_2O)	Bray P1 (mg/kg)	Olsen P (mg/kg)	Total N (%)	Total C (%)
PBII-4	Pond Basin	O	0-60								2.84	39.52
		A	50-85	14.2	20.7	65.1	Sandy Loam	4.90	16.03		0.6681	9.263
		B	90-108	4.6	13.3	82.1	Loamy Sand	5.36	2454.16		0.046	0.5229
	Upland	A	0-8								0.81	17.96
		B_1	10-16.5	7.2	15.5	77.3	Loamy Sand	6.14		4.47	0.1643	1.87
		C	16.5-31	3.7	6.2	90.1	Sand	7.28		4.36	0.0224	0.2694
		O	45-60								2.09	29.72
		B_2	60-80	13.6	24.5	61.9	Sandy Loam	5.97	212.57		0.3568	5.84
		E	80-85	19.1	26.8	54.1	Sandy Loam	5.72	178.92		0.1425	1.956
		C	85-109	17.6	18.0	64.4	Sandy Loam	5.45	107.59		0.0886	1.056
		C	109-118+	10.6	14.3	75.1	Sandy Loam	5.65	219.14		0.0231	0.2031

Appendix Table A.1. (continued)

Site	Location	Horizon	Depth	Clay %	Silt %	Sand %	Soil Texture	pH (H_2O)	Bray P1 (mg/kg)	Olsen P (mg/kg)	Total N (%)	Total C (%)
PBIII-1	Pond Basin	O	0-5					5.16	36.72		1.942	29.09
		A	5-17.0	28.6	50.5	20.9	Clay Loam	5.23	115.69		0.2903	3.351
		C	17+	20.7	52.4	26.9	Silt Loam	5.68	31.48		0.0195	0.2453
	Upland	A	0-7	6.9	25.9	67.2	Sandy Loam	4.97	22.54		0.5347	8.32
		B	21	11.4	27.3	61.3	Sandy Loam	5.05	6.06		0.0323	0.4805
		C	21.-35.8+	10.4	28.3	61.3	Sandy Loam	5.15	3.53		0.0082	0.2302
PBIII-2	Pond Basin	O	0-28.5								2.82	39.89
		O	70-105+								2.36	45.29
	Upland	A	0-15	15.2	30.2	54.6	Sandy Loam	5.46	7.45		0.4759	6.805
		B (E)	15-28	12.6	26.3	61.1	Sandy Loam	5.64	3.24		0.0553	0.6811
		C	28-46+	7.6	20.6	71.8	Sandy Loam	6.08		3.42	0.0223	0.0753
PBIII-3	Pond Basin	NA										
	Upland	A	0-20	4.8	21.8	73.4	Sandy Loam	4.46	18.08		1.112	7.944
		B	20-30	7.7	23.4	68.9	Sandy Loam	4.89	2454.16		0.074	0.932
		C	30-64.5+	6.2	20.4	73.4	Sandy Loam	5.08	117.80		0.0366	0.3809

Appendix Table A.1. (continued)

Site	Location	Horizon	Depth	Clay %	Silt %	Sand %	Soil Texture	pH (H_2O)	Bray P1 (mg/kg)	Olsen P (mg/kg)	Total N (%)	Total C (%)
PBIII-3	Pond Basin	NA										
	Upland	A	0-20	4.8	21.8	73.4	Sandy Loam	4.46	18.08		1.112	7.944
		B	20-30	7.7	23.4	68.9	Sandy Loam	4.89	2454.16		0.074	0.932
		C	30-64.5+	6.2	20.4	73.4	Sandy Loam	5.08	117.80		0.0366	0.3809
PBIII-4	Pond Basin	NA										
	Upland	A	0-15	5.8	32.8	61.4	Sandy Loam	5.25	14.51		0.4499	5.986
		A-B	15-27	10.6	14.8	74.6	Sandy Loam	5.51	7.18		0.0524	0.5147
		C	27-35	5.6	14.8	79.6	Loamy Sand	5.65	9.82		0.0301	0.2405
		C	35-69.5	4.7	7.4	90.6	Sand	5.63	49.74		0.0067	0.1532
		C	69.5-106+	6.7	17.4	75.9	Loamy Sand	5.44	39.88		0.0332	0.2443

Appendix Table A.2. Buena Vista State Forest Raw Soil Data

Site	Location	Horizon	Depth	Clay %	Silt %	Sand %	Soil Texture	pH (H_2O)	Bray P1 (mg/kg)	Olsen P (mg/kg)	Total N (%)	Total C (%)
BVI-1	Pond Basin	A	0-15	16.2	30.9	52.9	Sandy Loam	6.51		47.68	0.3697	4.042
		A/B	15-21	13.2	24.2	62.6	Sandy Loam	7.19		19.83	0.0356	0.2712
		B	21-34	21.7	33.7	44.6	Loam	7.28		25.88	0.06	0.19
		C-G	34-69.5+	30.3	54.5	15.2	Silty Clay Loam	7.69		30.05	0.0138	0.8757
	Upland	A	0-20	6.8	27.7	65.5	Sandy Loam	6.28		8.26	0.99	13.63
		A-B	20-30	5.7	14.6	79.7	Loamy Sand	7.20		2.34	0.05	0.54
		B	30-72	5.7	15.7	78.6	Loamy Sand	8.04		2.47	0.0008	0.5009
		C-G	72-107+	5.3	18.5	76.2	Loamy Sand	8.38		2.20	0.0051	1.491
BVI-2	Pond Basin	O/ or A	0-28.5	8.5	40.6	50.9	Loam	5.19	10.13		1.384	14.9
	Upland	A	0-29	8.7	25.5	65.8	Sandy Loam	4.94	13.16		0.31	4.33
		AB	29-38	8.2	24.8	67.0	Sandy Loam	5.23	13.36		0.062	1.214
		B	38-61	7.2	13.8	79.0	Loamy Sand	5.24	22.44		0.0403	0.7479
		C	61-76+	16.2	22.0	61.8	Sandy Loam	5.28	1.64		0.0327	0.3237

Appendix Table A.2. (continued)

Site	Location	Horizon	Depth	Clay %	Silt %	Sand %	Soil Texture	pH (H_2O)	Bray P1 (mg/kg)	Olsen P (mg/kg)	Total N (%)	Total C (%)
BVII-3	Pond Basin	O	0-56								2.68	40.20
		C (clay)	56-83.5+	55.0	25.8	19.2	Clay	6.06		48.29	0.326	3.32
	Upland	A	0-10	13.6	13.9	72.5	Sandy Loam	6.62		22.78	0.65	10.38
		B	10-17.					6.25		5.25	0.12	1.51
		E	17-24	42.2	27.5	30.3	Clay	6.21		16.37	0.05	0.56
		C	24-70+	37.2	25.6	37.2	Clay Loam	7.72		29.10	0.066	1.233
BVII-4	Pond Basin	O	0-37	7.2	17.8	75.0	Sandy Loam	5.16	10.13		1.69	23.86
		C	37+	47.1	22.2	30.7	Clay	5.07	8.81		0.16	1.83
	Upland	A	0-7	5.8	14.8	79.4	Loamy Sand	4.83	6.97		0.40	6.93
		B	7-20.	16.6	29.3	54.1	Sandy Loam	5.05	1.39		0.03	0.62
		C	20-31	51.1	17.6	31.3	Clay	5.12	0.51		0.090	0.901
		C-G	34-65+	50.1	21.6	28.3	Clay	7.00		3.55	0.03	1.05
BVIII-1	Pond Basin	O	0-64								2.80	41.83
		C	64-94+	16.6	32.6	50.8	Loam	5.52	25.33		0.086	0.808
	Upland	A	0-14	9.2	20.4	70.4	Sandy Loam	4.82	3.61		0.206	2.847
		E	14-17	11.4	18.5	70.1		4.77	2.42		0.127	2.045
		B	17-27	12.2	18.4	69.4	Sandy Loam	5.02	3.55		0.064	0.691
		C	27-71+	10.7	8.7	80.6	Loamy Sand	5.29	1.92		0.028	0.131

Appendix Table A.2. (continued)

Site	Location	Horizon	Depth	Clay %	Silt %	Sand %	Soil Texture	pH (H_2O)	Bray P1 (mg/kg)	Olsen P (mg/kg)	Total N (%)	Total C (%)
BVIII-2	Pond Basin	O	0-69								2.95	39.77
		A	69-73	9.2	29.0	61.8	Sandy Loam	5.21	108.56		0.3077	4.628
		C-G	73-99.5+	8.7	37.4	53.9	Sandy Loam	5.45	114.49		0.0208	0.1332
	Upland	A	0-18	16.6	38.6	44.8	Loam	5.50	6.99		0.2741	3.932
		E	18-30	11.7	39.3	49.0	Loam	5.43	4.55		0.0067	0.1801
		C	30+	19.6	34.3	46.1	Loam	5.44	5.87		0.015	0.188
		C	37-73	23.6	30.4	46.0	Loam	5.89	4.82		0.0169	0.2552
BVIII-3	Pond Basin	A	0-8	14.4	40.6	45.0	Laom	5.89	78.34		0.5463	6.291
		B-E	25-Aug	24.4	40.6	35.0	Loam	6.29		33.90	0.04	0.15
		B-G	25-36.5	56.0	31.1	12.9	Clay	5.89	16.96		0.0526	0.314
		B-G	36.5-63	11.7	9.2	79.1	Sandy Loam	6.46		30.37	0.0192	0.1039
		C	63+	15.7	24.1	60.2	Sandy Loam	7.59		19.56	0.016	0.412
	Upland	A	0-6	14.4	51.1	34.5	Silt Loam	5.99	23.43		0.463	6.924
		E	6-19.	30.3	53.5	16.2	Silty Clay Loam	6.09		16.11	0.1164	1.149
		B-G	19-58	44.2	42.5	13.3	Silty Clay	6.45		9.04	0.0562	0.2994
		C	58-92+	10.7	15.3	74.0	Sandy Loam	8.01		3.96	0.028	0.558

Appendix Table A.2. (continued)

Site	Location	Horizon	Depth	Clay %	Silt %	Sand %	Soil Texture	pH (H_2O)	Bray P1 (mg/kg)	Olsen P (mg/kg)	Total N (%)	Total C (%)
BVIII-4	Pond Basin	NA	0-8	20.4	53.5	26.1	Silt Loam	5.71	94.20		0.7008	9.268
		NA	8-24.	29.6	51.5	18.9	Silty Clay Loam	6.07		45.18	0.04	0.2131
	Upland	A	0-10	20.7	56.4	22.9	Silt Loam	5.47	12.10		0.287	4.363
		E	10-17.	26.7	57.5	15.8	Silt Loam	5.62	33.50		0.0403	0.4152
		C	17-37	41.2	47.9	10.9	Silty Clay	5.60	40.78		0.061	0.303
		C	32-70	29.6	32.3	38.1	Clay Loam	5.54	23.56		0.020	0.149

Appendix Table A.3. 2008 Precipitation

2008 Weekly Precipitation (cm)

Pond Cluster	21-May	28-May	4-Jun	10-Jun	17-Jun	24-Jun	2-Jul	9-Jul
PB-I	1.2	0.4	2.6	5.45	3.54	0.13	2.06	0.56
PB-II		0.44	2.77	5.49	3.78	0.15	1.83	0.62
PB-III		0.43	2.71	4.9	3.84	0.1	1.62	0.8
BV-I	0.72	0.18	2.38	5.14	2.04	0.08	2.46	0.59
BV-II	0.6	0.5	2.7	4.075	1.8	0.13	2.19	0.55
BV-III		0.3	2.85	3.81	1.6		2.27	0.4

Pond Cluster	15-Jul	22-Jul	29-Jul	7-Aug	14-Agust	20-Aug	6-Sep	20-Sep
PB-I	2.7	0.6	3.15	0.02	1.05		2.24	
PB-II	2.48	0.63	3.24	0.01	1.04	0.01	2.74	
PB-III	2.01	0.62	3.18	0.02	0.72	0.01	3	
BV-I	2	1.39	3.16	0.4	0.6	0.01	4.38	7.16
BV-II	2.28	1.54	0.93	0.26	0.62		3.72	
BV-III	2.54	1.62	4.97	0.31	0.3		6.87	

Pond Cluster	21-Sep	5-Oct	11-Oct
PB-I	3.8	0.7	8.64
PB-II	3.94	0.73	8.56
PB-III	3.44	1.01	8.55
BV-I		0.96	5.68
BV-II	8.73	2.38	5.27
BV-III	7.03	0.86	6.62

2008 weekly precipitation volume measured at 3 locations within each state forest.

Appendix Table A.4. 2009 Precipitation

2009 Weekly Precipitation (cm)

Pond Cluster	13-May	27-May	2-Jun	10-Jun	16-Jun	24-Jun	1-Jul	9-Jul
PB-I	1.95	0.99	0.2	1.42	1.42	2.67	1.7	0.02
PB-II	1.95	1.08	0.15	1.46	1.54	2.72	1.76	0.02
PB-III	2	1.04	0.22	1.24	1.6	2.68	1.89	0.04
BV-I	2.42	1.96	1.04	2.26	0.8	1.86	1.34	
BV-II	2.57	2.12	1.02	1.99	0.41	2.28	1.4	
BV-III	2.17	2.02	1.13	1.92	0.59	2.3	1.32	
Pond Cluster	15-Jul	22-Jul	29-Jul	5-Aug	12-Aug	20-Aug	3-Sep	17-Sep
PB-I	1.64	1.52	2.09	2.16	1.66	3.24	0.22	0.67
PB-II	2.24	1.6	1.62	2.41	2.31	3.24	0.18	0.55
PB-III	1.54	1.02	2.23	1.8	1.78	3.06	0.28	0.7
BV-I	1.18	1.1	1.22	1.67	0.7	3.74	0.36	4.18
BV-II	0.93	0.62	1.78	1.78	1.14	3.98	0.34	
BV-III	1.18	1.61	1.95	1.78	0.76	2.39	0.45	3.21
Pond Cluster	3-Oct	15-Oct						
PB-I	4.15	1.98						
PB-II	4.37	1.79						
PB-III	3.8	1.95						
BV-I	3.54	1.61						
BV-II	3.36	1.52						
BV-III	2.76	1.41						

2009 weekly precipitation volume measured at 3 locations within each state forest.