Observations of Pitcher Plant (*Sarracenia purpurea* L.) Phytotelm Conditions from Two Populations in Jackson Bog, Stark County, OH

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Abstract. The physical and chemical characteristics of pitcher plant leaf fluid, or phytotelm, influence the phytotelm inhabitants, which in turn affect plant fitness. Phytotelm conditions vary between seasons yet few studies sample in multiple seasons or during the winter in portions of the plant's range where winter freezing normally occurs. Phytotelm conditions were characterized in two populations of *Sarracenia purpurea* L. in Jackson Bog State Nature Preserve, Jackson Township, Stark County, OH. Twenty leaves were arbitrarily sampled from each population once every ten days from November 2008 to September 2009. Phytotelm characteristics were compared between populations and with bog water adjacent to each population. Temperatures significantly differed between seasons, between pitcher plant populations and between the phytotelm and adjacent bog water. pH significantly differed between seasons and between pitcher plant populations, but not between the phytotelm and the adjacent bog water. Phytotelm volume and the number of frozen and dry leaves differed between populations. Results suggest that the presence and duration of non-frozen fluid could be an important source of selection on phytotelm inhabitants. Differences in phytotelm conditions between populations suggest that sampling regimes in sites with multiple populations or one very large population should account for microhabitat variations.

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INTRODUCTION

The purple pitcher plant, *Sarracenia purpurea* L., is a carnivorous plant with funnel-shaped, fluid-filled leaves. *Sarracenia purpurea* L. is geographically widespread and found in wetlands stretching from the Gulf coast of the United States through the southern tier of Canada. The southern portion of its range includes the Atlantic and eastern Gulf coastal plains, with a disjunct population in the mountains of western North Carolina, South Carolina, and Georgia. The middle and northern portions of its range includes all or part of the Middle Atlantic and Great Lakes states, Iowa, Ontario, Quebec, Newfoundland, and west into British Columbia (McPherson 2007). Introduced populations of *Sarracenia purpurea* L. also grow in Europe (Gebühr and others 2006).

Purple pitcher plants are found in nutrient-poor wetland soils, containing low amounts of nitrogen and phosphorus for the plants' roots to acquire. Pitcher plants use carnivory to supplement their nutrient supplies (Gray and others 2006). Each pitcher plant produces about ten modified leaves, which collect rainwater and act as insect traps. Insects are attracted by bright coloration and nectaries, and drown in the pitcher liquid (Juniper and others 1989). Dead insects are processed by a relatively simple food web, composed of detritivores (midges, mites, flesh flies, fungi and bacteria), bacterivores (protozoans and rotifers) and an omnivorous top predator, the larva of the pitcher plant mosquito, *Wyeomyia smithii* (Coquillet). As prey is decomposed, nitrogen, phosphorus, and other nutrients are released and assimilated by specialized gland cells in the pitcher wall (Buckley and others 2003; Miller and Kneitel 2005). *Sarracenia purpurea* pitchers have been used to test ecological theories such as cascade effects in food webs (Kneitel and Miller 2002), cost-benefit analyses (Adlassnig and others 2009; Ellison and Gotelli 2009; Karagatzides and Ellison 2009), and effects of resource availability on food web structure and dynamics (Bergland and others 2005; Trzcinski and others 2005; Gotelli and Ellison 2006).

Phytotelm temperature, pH, and volume have been identified as important factors that can affect the inhabitants, and potentially the overall fitness of the pitcher plant. Temperature affects the leaf environment in several different ways. During the summer and winter, temperature extremes can affect development times of the mosquito and mortality of it and other leaf inhabitants through desiccation or freezing respectively (Paterson 1971; Kingsolver 1979; Bradshaw and others 2000; Ragland and Kingsolver 2007; Adlassnig and others 2011). Temperature determines the oxygen carrying capacity of the fluid, and it affects the rate of decomposition of the plant's prey (Kitching 2009). High temperatures can also decrease phytotelm volume and cause hydric stress on leaf inhabitants (Bradshaw and others 2000). pH can affect the presence and abundance of the inhabitants. Extreme pH values can cause physiological stress (Kitching 2009). Phytotelm volume plays a role in determining the number and types of leaf inhabitants. It also affects prey capture and breakdown rates. Volume has been positively correlated to the presence of the midge and mosquito, two key leaf residents (Rango 1999; Buckley and others 2004; Hoekman and others 2007). Phytotelm volume can also affect pH due to its dilution capability (Kitching 2009).

Previous studies offer only a limited understanding of seasonal variation in the pitcher plant phytotelm environment. Most of the studies have limited scope - short duration and/or limited number of pitcher plants and very few for which pitchers were sampled in multiple seasons (Bledzki and Ellison 1998; Buckley and others 2004). Several generalizations about pitcher plant leaf conditions have been made based on meta-analyses (Kneitel and Miller 2003). Other previous studies have focused solely on the effects of winter temperatures on overwintering mosquito larvae (Heard 1994; Bradshaw and others 2000). The northern portion of the pitcher plant range has lower mean summer and winter temperatures, wider temperature extremes, shorter growing season, and summer day lengths are longer than middle and southern portions of the range (Buckley and others 2003; Hoekman and others 2007). In addition, most *S. purpurea* populations in the southern portion of the range grow in acidic substrates (McPherson 2007), whereas some populations in the Great Lakes Region, Quebec, the Maritime Provinces, and northern Maine, grow in alkaline substrates (Schnell 2002).

The goal of this study was to investigate seasonal variation of phytotelm conditions using two pitcher plant populations

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located in the same bog. I asked three questions: (1) What is the seasonal variation in phytotelm temperature, pH and volume? (2) Are there differences in phytotelm conditions between the two populations? and (3) Are phytotelm conditions similar to the bog water adjacent to the plants? In order to address these questions I sampled phytotelm temperature, pH, and volume and bog surface water temperature and pH adjacent to the pitcher plant populations over a ten month period.

MATERIALS AND METHODS

Study area

Two *Sarracenia purpurea* L. populations within Jackson Bog State Nature Preserve, Jackson Township, Stark County, OH (N 40° 51.563′ W 81° 29.897′) were sampled. The site is a 23.5 hectare preserve adjacent to residential homes, baseball and soccer fields, and a high school (Fig. 1). Jackson Bog is a fen, or alkaline bog, carved from glacial scouring (Ohio Department of Natural Resources n.d.; Witt 2005). One *S. purpurea* population referred to as the Overlook Site contains approximately 60 widely dispersed rosettes, near several groundwater seeps, and located adjacent to a viewing platform. The other population, the Historic Site, contains approximately 25 rosettes, mostly clustered in close proximity to a seep. Both populations exhibit hummock-hollow topography and contained mats of *Sphagnum* spp. moss. The populations were accessed from a two-km-long boardwalk trail with interpretive signing.

Collection of environmental data and analyses

The populations were sampled at approximately 1100 hrs. once every 10 days from November 2008 to September 2009. Twenty leaves were arbitrarily sampled at each site during each sampling event. Temperature and pH were measured by placing the electrode of a Fischer Scientific® meter into the leaves. Phytotelm levels were recorded as present, dry or frozen. Temperature and pH measurements were taken from the bog water adjacent to the sampled leaves. Temperature values were square-root transformed and statistical outliers were excluded to approximate normality. pH values were temperature corrected and log transformed prior to inclusion in statistical analyses. Temperature and pH data were compared between leaves and adjacent bog water within and between sites with repeated measures analyses of variance (ANOVAs) and paired T-tests using SPSS v. 14 (SPSS Inc., Chicago, IL).

RESULTS

Phytotelm temperature significantly differed ($p < 0.05$) between populations, populations and bog water and between seasons (Fig. 2A, Table 1). Seasonal phytotelm and bog water temperatures significantly differed ($p < 0.05$) between winter 2008 and spring 2009, but not spring and summer 2009 (Table 1). Phytotelm temperatures differed significantly ($p < 0.05$) between pitcher plant populations. Historic Site mean phytotelm temperatures were higher than the Overlook Site during spring and summer

FIGURE 1. Aerial photo of Jackson Bog State Nature Preserve and surrounding areas. Approximate locations of the pitcher plant populations are designated OLPL (Overlook Site) and HSPL (Historic Site). Source: USDA, 2004

2009 (Table 1). Historic Site phytotelm temperatures were more variable than the Overlook Site during all three sampling seasons (Fig. 2A). Phytotelm temperatures significantly differed ($p < 0.05$) from the adjacent bog water at both populations (Table 1). Mean phytotelm temperatures were higher and more variable than adjacent bog water during spring and summer 2009, and lower and more variable during winter 2008 (Fig. 2A). Temperatures of bog water adjacent to the pitcher plant populations significantly differed ($p < 0.05$) from each other (Table 1).

Phytotelm pH differed significantly ($p < 0.05$) between populations and seasons, but not between the phytotelm and the adjacent bog water (Fig. 2B, Table 1). Mean phytotelm pH decreased from winter 2008 through summer 2009 but most fluid remained alkaline. Summer 2009 phytotelm pH was highly variable in both populations (Fig. 2B). The pH of bog water adjacent to the pitchers did not significantly differ from their respective phytotelm, but did significantly differ ($p < 0.05$) from each other (Table 1). Bog water pH decreased from winter 2008 to spring 2009, but increased from spring 2009 to summer 2009.

Both populations showed similar trends with phytotelm freezing and drying. Winter 2008 had the highest percentage of frozen phytotelm. Spring 2009 had the highest percentage of dry pitchers, followed by summer 2009, then winter 2008 (Fig. 3). Almost 70 percent of Historic Site pitchers and 45 percent of Overlook Site pitchers were dry during spring 2009. A significantly ($p < 0.05$) greater percentage of Historic Site pitchers were dry than Overlook Site pitchers during all three sampling seasons (Fig. 3). Historic Site phytotelm froze slightly, but not significantly ($p > 0.05$) more frequently than Overlook Site phytotelm. Only a few pitchers at the Overlook Site contained frozen phytotelm during spring 2009. Neither population had frozen phytotelm during summer 2009 (Fig. 3). Bog water adjacent to both populations was never completely dry or frozen during this study.

DISCUSSION

It is not surprising that temperature differed between the phtytotelm and adjacent bog water. This is likely from the difference in volume between the leaves and bog, with the much larger volume of bog water taking longer to heat up and cool down. The difference in temperature between the two populations is more difficult to explain. Factors that affect phytotelm retention include wind velocities, soil temperature, degree of burial in *Sphagnum*

Table 1

Summary of paired t-Tests on temperature ane pH data

Grouping	n	paired means	significance
HSPL vs HSAdj - temperature	177	19.5, 13.0	p<0.05
HSPL vs HSAdj - pH	145	7.62, 7.78	NS
OLPL vs OLAdj - temperature	347	16.9, 14.0	p<0.05
OLPL vs OLAdj - pH	281	7.44, 7.54	NS
HSPL vs OLPL - temperature	196	15.5, 14.1	p<0.05
HSPL vs OLPL - pH	172	7.76, 7.41	p<0.05
HSAdj vs OLAdj - temperature	344	13.2, 14.5	p<0.05
HSAdj vs OLAdj - pH	276	7.76, 7.55	p<0.05

HSPL = Historic Site, pitcher plant leaves
HSAdj = Historic Site, adjacent surface waters
OLPL = Overlook Site, pitcher plant leaves
OLAdj = Overlook Site, adjacent surface waters

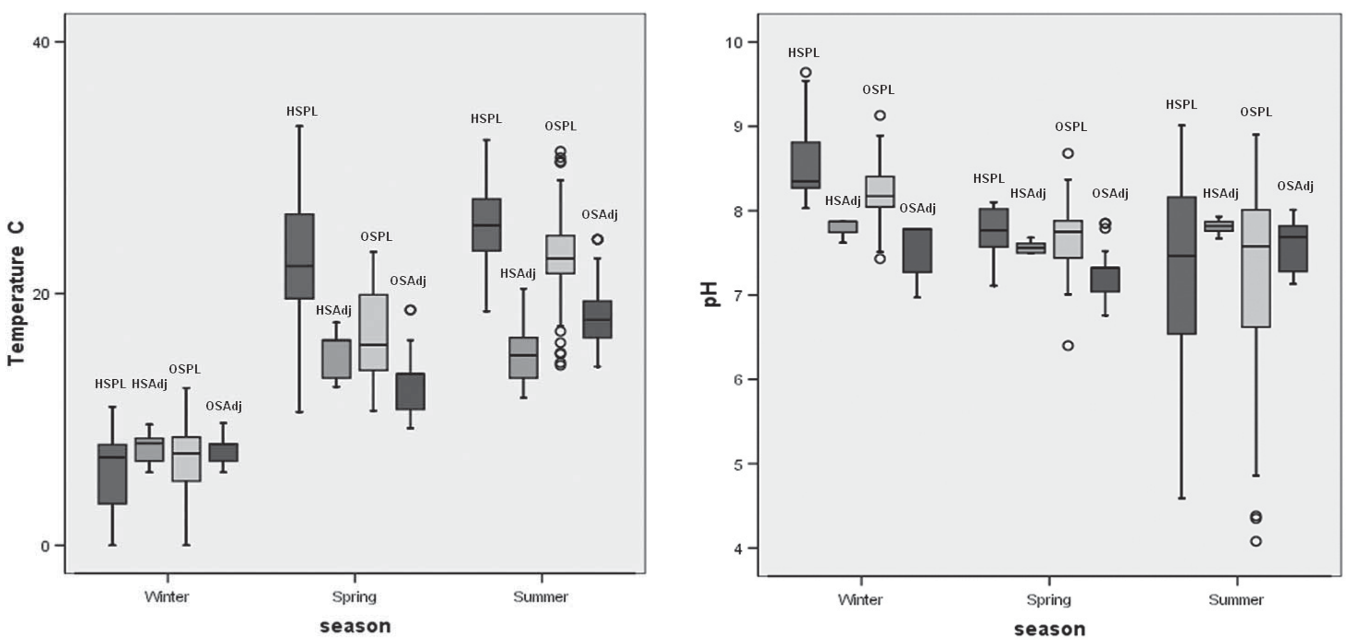

Figure 2a and b. Seasonal variation in temperature (a) and pH (b) in pitcher plant leaves and adjacent surface waters. Boxplots show upper and lower quartiles and median values. Error bars show 1.5x the interquartile range. Circles indicate outliers, or values between 1.5x – 3x the interquartile range.
HSPL = Historic Site, pitcher plant leaves
HSAdj = Historic Site, adjacent surface waters
OLPL = Overlook Site, pitcher plant leaves
OLAdj = Overlook Site, adjacent surface waters

moss, and the degree to which pitchers are exposed to sunlight or shade (Kingsolver 1979). Both populations lack overarching vegetation and are likely exposed to the similar amounts of sunlight and wind velocities, although neither factor was quantified. This difference in temperature may suggest that thermal impacts on a wetland do not equally affect all populations within the wetland. Each population could be a unique microhabitat with respect to environmental conditions. Kingsolver (1979) found differences in microclimates within pitcher plants bogs based on whether plants were located in open water, on floating *Sphagnum* mats, or in sedge-covered portions of fens. Bog hydrology may also create these microhabitats as surface and ground water inputs meet and disperse through the bog. Further study of Jackson Bog's hydrology would provide more insight into this possibility. Further study is also required to determine if the phytotelm temperature differences between the populations affect the leaves' ability to capture prey or attract inhabitants. In addition, the solubility of oxygen has an inverse relationship to temperature, but it is not know if the differences reported in this study are significant enough to have a measurable impact on phytotelm inhabitants.

Phytotelm pH differed between populations, but not between the populations and the bog water adjacent to them. Both phytotelm pH and bog water pH were consistently significantly more alkaline than the average pH of 4.8 of local precipitation (NADP, 2010). The similarity of phytotelm with adjacent bog water and the significant divergence from precipitation pH suggests that bog hydrology is likely the primary influence on pH for both. Consequently, population difference between phytotelm pH would be the result of microhabitat conditions within the bog. This supposition also suggests that any impacts that would affect the pH of the bog water could affect the phytotelm in populations adjacent to the impacted area. Common urban pollutants reported in waters near Jackson Bog include fuels, engine and transmission oil, grease, brake fluid, and antifreeze (Witt 2005).

Known influences on phytotelm pH are presence of prey and microbial degradation of prey. Differential prey capture by individual leaves may partially explain the large variance observed in phytotelm pH in both populations during summer 2009. In both Jackson Bog populations and acidic populations reported in the literature phytotelm becomes more acidic as the leaves age. However, pH here ranged between 7.11(HSPL), 6.70(OLPL) to 8.10(HSPL), 9.23(OLPL) as opposed to values reported by Fish and Hall (1978) (3.5-6.5), Ellison and others (2002) (3.5-5.5), and Kneitel and Miller (2002) (5.63-6.76). The ramifications of this difference, if any, are not known. Little has been previously reported about the seasonal variations in leaf conditions and

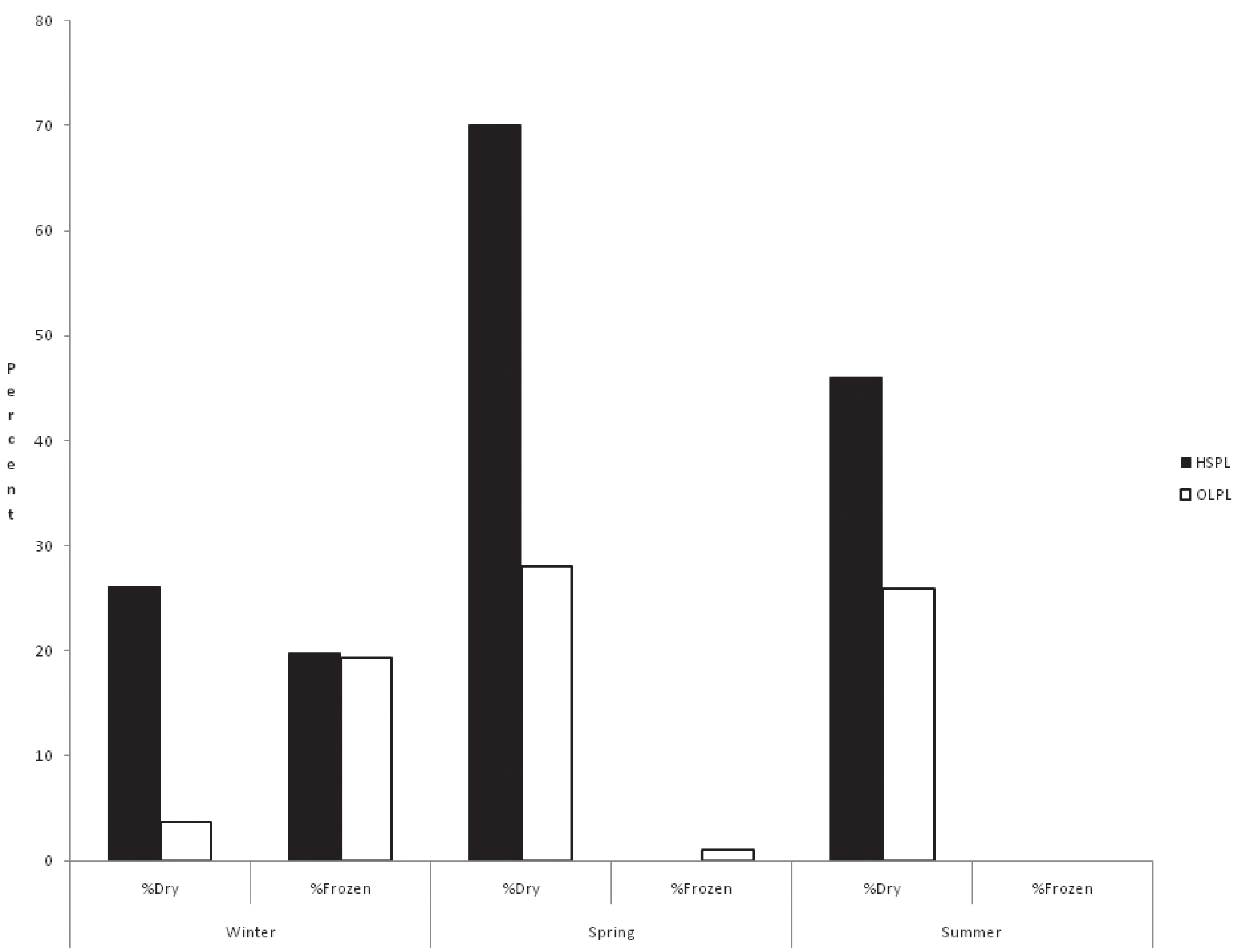

Figure 3. Seasonal variation of pitcher plan leaf fluid volume in the Historic Site population (HSPL) and Overlook Site population (OLPL). (Winter 2008: November 2008 – February 2009; Spring 2009: March 2009 – May 2009; Summer 2009: June 2009 – August 2009)

inhabitants in alkaline populations. Adlassnig and others (2011) reported phytotelm pH in greenhouse-reared plants to range between five and seven, but found outliers and extreme outliers within the range of this study.

Since pitchers are filled primarily by rainfall, the frequency and amount of precipitation would have a significant impact on phytotelm volumes. According to the National Oceanic and Atmospheric Administration (NOAA), precipitation levels were below average during spring 2009, but average or above during summer 2009. August 2009 had the largest amount of precipitation (111 mm) during 2009 (NOAA, 2009). This likely explains the decrease of dry pitchers from spring to summer of 2009. Bergland and others (2005) reported that in one Wisconsin pitcher plant population mosquitoes that laid eggs later in the summer had higher larval survivorship than ones early in the summer. That approach may also work in Jackson Bog. It is not known why leaves in the Historic Site population were more consistently lacking phytotelm than the Overlook Site population. Possibilities include less capability to acquire rainwater, less capability to retain rainwater, or a combination of the two. Fish and Hall (1978) suggested that leaf aspect may influence acquisition of rainwater. Leaf size may explain some of the observed patterns of phytotelm retention. Kingsolver (1981) reported that most pitchers are devoid of phytotelm one to three times a year, but smaller leaves may be dry up to eight times a year. Neither leaf aspect or size was quantified in this study but they may partially explain the pattern of phytotelm retention that was observed. Dry leaves can have a significant impact on phytotelm inhabitants and prey retention. When empty, pitchers have a reduced ability to retain prey and reduced larval inhabitant survivorship (Bradshaw and others 2000; Bergland and others 2005; Adlassnig and others 2011). Phytotelm volume has been positively correlated to abundance of the midge and mosquito, so fifty percent or more of the leaves being dry during the spring and summer in the Historic Site would not be beneficial for their populations.

Winter 2008 temperatures resulted in the phytotelm being completely frozen approximately 20 percent of the time in both populations. Bradshaw and others (1998) found that simulated winter conditions with a phytotelm temperature of 0°C for just two weeks caused significant mortality to the overwintering mosquito larvae. Bradshaw and others (2004) found significant mortality when phytotelm temperatures fell below -3° C for four or more consecutive days. Kingsolver (1979) observed 100% mortality in mosquito larvae when phytotelm completely froze. Phytotelm conditions at both Jackson Bog sites exceeded the conditions observed by Bradshaw and others (1998, 2004), potentially causing higher mosquito mortality. Average ambient air temperatures for Jackson Bog in December 2008 through February 2009 were -1.0, -7.5, and -1.4° C respectively (NOAA 2008, 2009). Despite the low temperatures, the bog water never froze.

In summary, this study provides quantitative data of the seasonal phytotelm dynamics of two populations in a region and under environmental conditions that have been rarely quantified. Further study of pitcher plant sites within this physiographic region and/or alkaline sites is necessary to increase our understanding of these systems. These data also suggest that in sites with multiple pitcher plant populations or one very large population one should collect data in a manner to account for microhabitat variations.

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