

# Environmental predictors of shrubby cinquefoil (*Dasiphora fruticosa*) habitat and quality as host for Maine's endangered Clayton's copper butterfly (*Lycaena dorcas claytoni*)

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Received: 21 November 2014 / Accepted: 30 April 2015  
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**Abstract** Population size of habitat-specialized butterflies is limited in part by host plant distribution and abundance. Effective conservation for host-specialist species requires knowledge of host-plant habitat conditions and relationships with the specialist species. Clayton's copper butterfly (*Lycaena dorcas claytoni*) is a Maine state-endangered species that relies exclusively on shrubby cinquefoil (*Dasiphora fruticosa*) as its host. *Dasiphora fruticosa* occurs in 28 wetlands in Maine, ten of which are occupied by *L. d. claytoni*. Little is known about environmental conditions that support large, persistent stands of *D. fruticosa* in Maine. We evaluated the environment (hydrology, pore water and peat nutrients) associated

with *D. fruticosa* distribution, age, and condition in Maine wetlands supporting robust stands of *D. fruticosa* to compare with *L. d. claytoni* occurrence. Although dominant water source in *D. fruticosa*—containing wetlands included both groundwater discharge and surface-flow, *D. fruticosa* coverage was greater in wetlands with consistent growing season water levels that dropped into or below the root zone by late season, and its distributions within wetlands reflected pore water hydrogen ion and conductivity gradients. Flooding magnitude and duration were greatest during the *L. d. claytoni* larval feeding period, whereas, mean depth to water table and upwelling increased and were most variable following the *L. d. claytoni* egg-laying period that precedes *D. fruticosa* senescence. Oldest sampled shrubs were 37 years, and older shrubs were larger and slower-growing. Encounter rates of *L. d. claytoni* were greater in wetlands with larger *D. fruticosa* plants of intermediate age and greater bloom density. Wetland management that combines conditions associated with *D. fruticosa* abundance (e.g., non-forested, seasonally consistent water levels with high conductivity) and *L. d. claytoni* occurrence (e.g., drawdown below the root zone following egg-laying, abundant blooms on intermediate-aged *D. fruticosa*, nearby *D. fruticosa*-containing wetlands) will aid *L. d. claytoni* conservation.

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Judith Rhymer: Retired.

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**Electronic supplementary material** The online version of this article (doi:10.1007/s11273-015-9427-1) contains supplementary material, which is available to authorized users.

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**Keywords** *Dasiphora fruticosa* · *Lycaena dorcas claytoni* · Maine · Wetland · Endangered · Butterfly

## Introduction

Habitat loss, fragmentation, and degradation are primary causes of decline and extinction of many insect species (Fahrig 2003). Monophagous insect species with limited dispersal ability and short flight periods may be particularly vulnerable to extinction when habitats are isolated (Hughes et al. 2000; Kotze et al. 2003; Kotiaho et al. 2005). While habitat spatial characteristics such as patch arrangement, size, connectivity, and dynamics affect the occurrence and persistence of butterfly populations (Hanski 1998), local host plant patch quality and quantity also are important (Thomas et al. 2001; León-Cortés et al. 2003; Krauss et al. 2005). Host plant density is a key determinate of population size for habitat-specialized butterflies (Schultz and Dlugosch 1999; León-Cortés et al. 2003; Ehrlich and Hanski 2004; Krauss et al. 2005), because their distribution is limited by the occurrence of their host plant. Successful conservation of rare and endangered butterflies, particularly host-specialist species, necessitates knowledge of host plant habitat requirements and consideration of within-site host plant quality for all life history stages.

Host plant populations may inhabit a range of environmental conditions that are more variable than is suitable for host-specific or habitat-specialized butterflies. Hydrological conditions are a primary driver of wetland plant community development, structure and persistence. Wetland water depth, duration and flood frequency, and water source directly affect nutrient availability and peat and pore water pH (Mitsch and Gosselink 2007) and thus also may influence host plant establishment and persistence in wetlands (Vitt 1990; Vitt et al. 1995; Anderson and Davis 1997; Bedford et al. 1999; Bragazza and Gerdol 2002; Mitsch and Gosselink 2007). Environmental conditions tolerated by the host plant may not be suitable for butterfly survival and persistence. For example, environmental factors that alter a plant's physiology and biochemistry potentially change its nutritional value to herbivores (Bryant et al. 1983; Mattson and Haack 1987; Herms and Mattson 1992). Nectar plant availability and quality can influence an individual adult butterfly's dispersal (Wiklund 1977; Britten and Riley 1994; Dover 1997; Schneider et al. 2003; Auckland et al. 2004) and oviposition site selection (García-Barros and Fartmann 2009), and

host plant foliar chemistry can affect egg and larval survival (e.g., Ehrlich and Raven 1964; Barros and Zucoloto 1999) and herbivore population size and persistence (Awmack and Leather 2002).

Suitability of a butterfly host plant also may be affected by host plant age. As perennials age, resource allocation shifts from growth and leaf expansion to reproduction (Bond 2000). Plant age may affect bloom production and vigor (Oñate and Munné-Bosch 2010) and nectar quality and availability (Búrquez and Corbet 1998). Age-dependent nectar quality and quantity potentially can affect butterfly population persistence particularly for those reliant on few or isolated host plant species.

Clayton's copper butterfly (*Lycaena dorcas claytoni*) is a Maine state-endangered species that relies exclusively on shrubby cinquefoil (*Dasiphora fruticosa*) as its host plant (Webster and Swartz 2006). Although *D. fruticosa* is not considered rare, only 10 of 28 Maine wetlands with *D. fruticosa* support large, persistent stands of the species (McCollough et al. 2001), and the environmental conditions in these wetlands are not well-defined. Wetlands with *D. fruticosa* in Maine are classified as circumneutral fens and streamside shrublands and meadows (McCollough et al. 2001). Fens are groundwater-fed systems (Bedford and Godwin 2003), and the plant rooting zone is supplied with nutrients from groundwater that has been in contact with mineral substrate (Wassan et al. 1990). Most fens are relatively nutrient-poor, and vegetation community establishment is affected by nutrient availability (Keddy 2000).

Recent extinction of an *L. d. claytoni* population in one of eight historically occupied wetlands lends urgency to an environmental assessment of *D. fruticosa* habitat in Maine. The objectives of our study were to describe and compare the hydrological environment, pore water and peat chemistry and *D. fruticosa* distribution and condition (size, coverage, age, bloom density, leaf and nectar quality) in wetlands inhabited (7) or uninhabited (3) by *L. d. claytoni*. We compared *D. fruticosa* leaf quality (i.e., foliar nitrogen, moisture), nectar quality (i.e., chemistry), and shrub size, age structure, and growth rate among and within these wetlands. Our overarching goal was to increase knowledge about environmental conditions in wetlands supporting robust stands of *D. fruticosa*, as well as the condition of *D. fruticosa* in

these wetlands, to inform wetland habitat conservation for *L. d. claytoni*.

## Methods

### Study species and area

Much of what is known about the life history of *L. d. claytoni* is reported by McCollough et al. (2001). Similar to the nominate species, *L. dorcas* (Scott 1986), Clayton's copper eggs are deposited singularly on the underside of cinquefoil leaves in July–August and drop with the leaves in the autumn to overwinter on the substrate. Larvae emerge in the spring to feed on cinquefoil leaves, completing five instars from larva to pupa. Adults nectar on *D. fruticosa* during late July–August when shrubby cinquefoil is flowering, and they remain near cinquefoil stands throughout the flight season. Timing of butterfly larval emergence and egg-laying, as well as host-plant flowering, may vary with seasonal temperatures and moisture conditions. Adults also nectar on *Solidago uliginosa*, although the species is unlikely to be a primary nectar source given its infrequent occurrence in wetlands hosting *L. d. claytoni* (Drahovzal per. obs.).

Clayton's copper butterflies occupy nine wetlands in central (Dwinal Pond Wildlife Management Area, Mattagodus Meadows, Holt Pond, Pickle Ridge), western (Pillsbury Pond, Soper Pond, Little Round Pond), and northern (Woodland Bog and a nearby wetland documented in 2010) Maine (Fig. 1). Encounter surveys conducted in 2007–2008 estimated butterfly densities ranging from abundant in Soper (1107 adults/ha) and Dwinal (882 adults/ha), to moderate densities in Mattagodus (323 adults/ha), Holt (388/ha), and Pillsbury (450 adults/ha), to few *L. d. claytoni* in Woodland Bog (170 adults/ha) and Pickle Ridge (77/ha) (Knurek 2010). Crystal Fen previously was occupied with “medium-sized populations” (McCollough et al. 2001), however, Clayton's copper butterflies have not been observed at this site since 2008 (Knurek 2010), and the wetland currently is considered unoccupied. In addition to Crystal Fen, two other unoccupied wetlands (Portage Lake, Salmon Stream) were selected for comparison to occupied wetlands, given the abundance of robust shrubby cinquefoil plants found in these wetlands as well as their proximity to occupied sites.

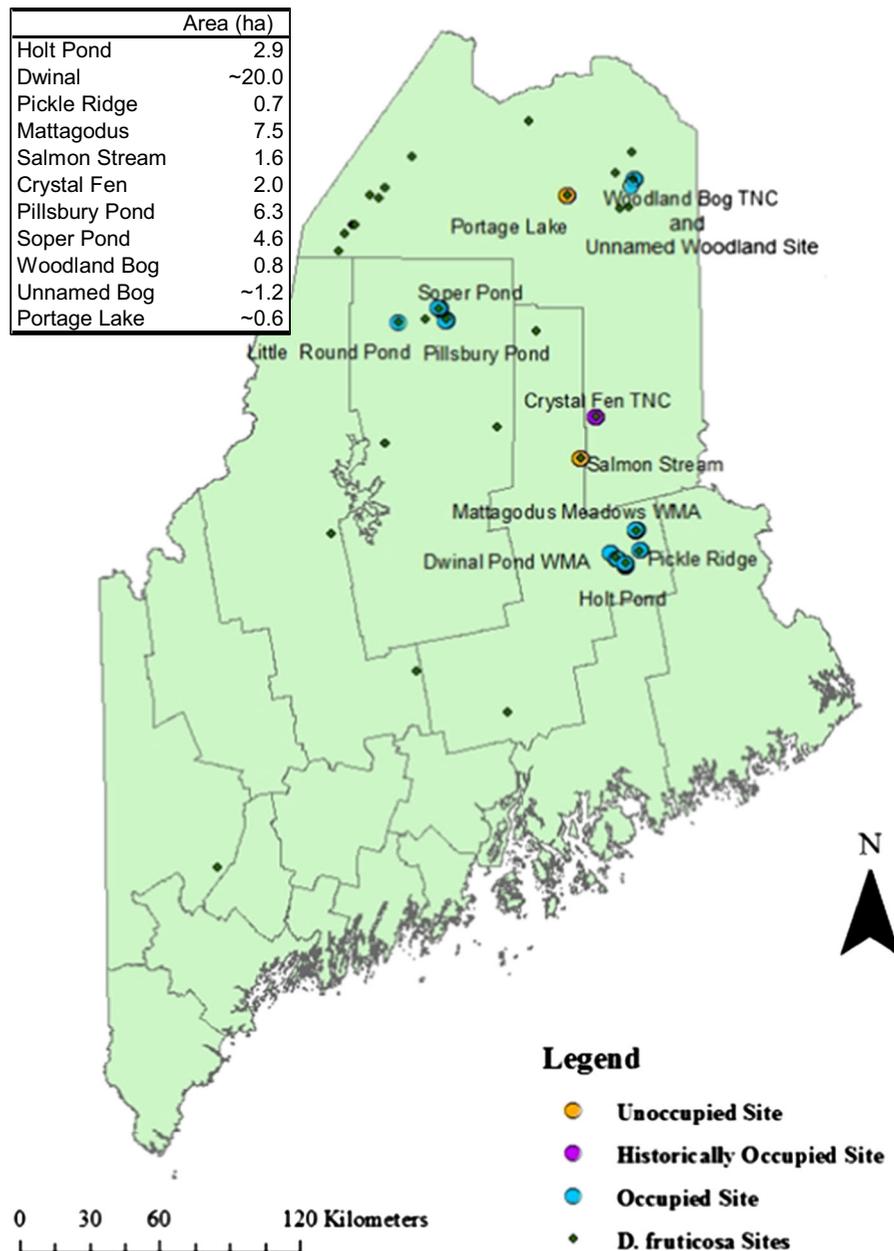
## Data collection

### Hydrologic sampling

We recorded the hydraulic head every 30 min during May–October 2010 in hydrologic monitoring wells (2.5 cm diameter polyvinyl chloride tubes slotted at the lower end) equipped with continuous recording, non-vented pressure transducers (Solinst Model 3001 level logger, Georgetown, Ontario, Canada) in seven wetlands (Dwinal, Holt Pond, Pickle Ridge, Mattagodus, Pillsbury, Soper, Woodland) hosting *L. d. claytoni* and three wetlands (Salmon Stream, Portage Lake, Crystal Fen) with *D. fruticosa* but without the butterfly (Fig. 1). We installed two wells vertically into the peat with one end open to the atmosphere in dense *D. fruticosa* distant from open water and forested wetland edge. One transducer monitored the water table position and measured the vertical hydraulic gradient in the near surface substrate, while the other transducer monitored groundwater upwelling at the peat-mineral substrate interface in the second well (Fig. 2). We corrected water levels for barometric pressure with Model 3001 Barologgers (Solinst, Georgetown, Ontario, Canada) recording every 30 min. We measured water depths periodically by hand to assess transducer accuracy. Water depth measurement error was  $\pm 0.1$  cm per meter of water above the logger.

### Pore water sampling

We collected pore water samples during 24 May–3 June ( $n = 102$ ), 12–23 July ( $n = 102$ ), and 17–25 August ( $n = 65$ ) 2010 to determine if pore water analytes reflected wetland hydrology and *D. fruticosa* quality and quantity. We collected the samples along previously established transects that traversed the most dense stands of *D. fruticosa* in seven wetlands surveyed by Knurek (2010) for a taxonomic and population status assessment of Clayton's copper, and we established additional transects in three unoccupied wetlands (Supplementary Material; Drahovzal 2013). Transects spanned each wetland's vegetation and topographic variation delineated in three zones (near open water sedge, non-forested shrub-sedge interior, forested wetland), with length and number of transects per wetland determined by wetland area (Supplementary Material). We collected pore water

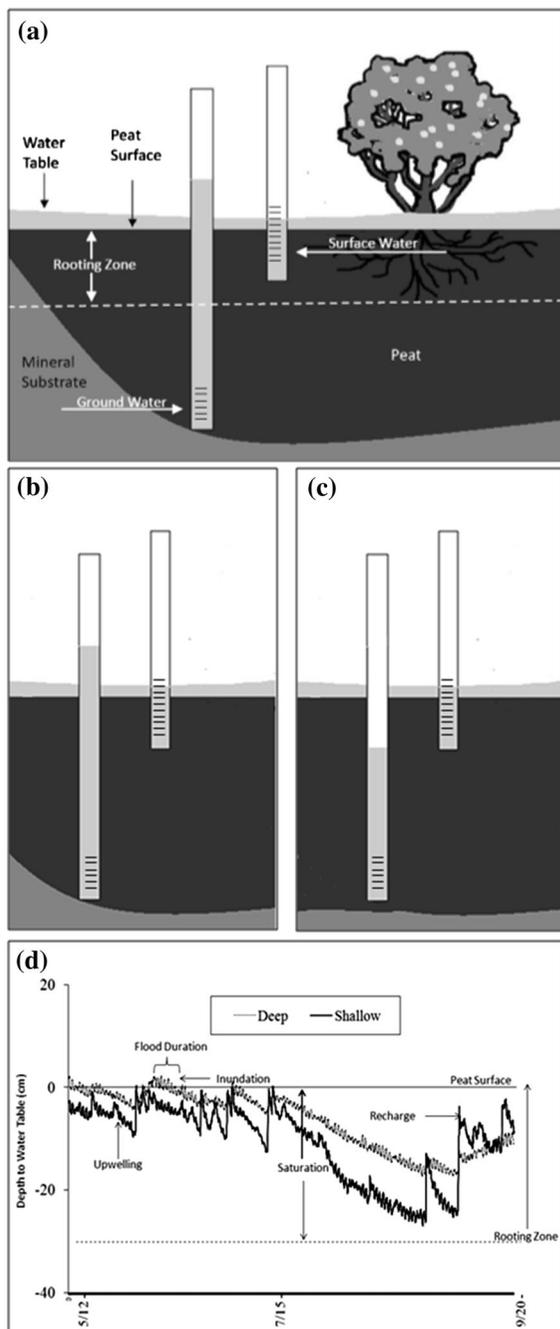


**Fig. 1** Locations of wetlands with shrubby cinquefoil and Clayton's copper butterfly in Maine. *Small dots (green)* indicate sites with *D. fruticosa*. Occupied sites (*blue circles*) currently host *L. d. claytoni* and *D. fruticosa*. Historically occupied sites

(*purple circles*) contain *D. fruticosa* but no longer host *L. d. claytoni*. Unoccupied sites (*orange circles*) contain *D. fruticosa* but not *L. d. claytoni*

samples with a hand vacuum pump attached to a flexible plastic tube placed into a slotted 2.5 cm diameter PVC pipe inserted 10–15 cm below the peat surface into the root zone of randomly selected *D. fruticosa* along each transect in each vegetation zone.

We stored water samples at 4 °C in 120 cc glass amber bottles and filtered them within 2 h of collection. Samples were analyzed for nutrients [ $\text{NH}_4\text{-N}$ ,  $\text{NO}_3\text{-N}$ , phosphorus ( $\text{PO}_4\text{-P}$ )], pH, and organic conductivity by the University of Maine Soil Testing Service



**Fig. 2** Example of **a** hydrological monitoring well set-up for 10 wetlands in Maine, **b** groundwater upwelling, **c** groundwater recharge, and **d** hydrograph illustrating periods of upwelling, saturation, and flood duration

Laboratory (AMSTS). Water sample  $\text{NH}_4/\text{NO}_3\text{-N}$  was determined colorimetrically by an autoanalyzer. The cadmium reduction/sulfanilamide method measured

$\text{NO}_3\text{-N}$ , and the hypochlorite/salicylate method measured  $\text{NH}_4\text{-N}$ . Phosphorus was determined with the automated ascorbic acid reduction method (APHA 1995). Water pH was determined potentiometrically with an electronic pH meter. Conductivity was measured with a Fisher Scientific Digital Conductivity Meter.

#### Peat sampling

We collected peat samples ( $n = 102$ ) within the top 30 cm of the ground surface (root zone) at pore water collection sites in May 2010 to compare peat nutrient and mineral composition to wetland hydrological conditions and *D. fruticosa* quality and quantity. We stored peat samples in cardboard boxes at 4 °C until they were analyzed at the UMaine AMSTS. Samples were air-dried, ground, and sieved (2 mm mesh). Peat pH was determined with a pH meter inserted into a peat and deionized water slurry (McLean 1982). Calcium (Ca), potassium (K), magnesium (Mg), phosphorus (P), aluminum (Al), boron (B), copper (Cu), iron (Fe), manganese (Mn), sodium (Na), lead (Pb), sulfur (S), and zinc (Zn) were analyzed by Inductively Coupled Plasma (ICP) emission spectrophotometry after acidifying the peat samples with pH 4.8 ammonium acetate (Modified Morgan) solution. Extractable ammonium ( $\text{NH}_4\text{-N}$ ) and nitrate ( $\text{NO}_3\text{-N}$ ) in peat were determined in a 1 M KCl extract. Solution analysis was done colorimetrically by an autoanalyzer. The cadmium reduction/sulfanilamide method measured  $\text{NO}_3\text{-N}$ , and the hypochlorite/salicylate method measured  $\text{NH}_4\text{-N}$ . Organic content of oven dried samples was determined by measuring loss on ignition (LOI) after combustion at 375 °C for 2 h.

#### Shrubby cinquefoil sampling

##### *Shrub community and D. fruticosa* stature, foliar moisture and nitrogen

During May–August 2010 we categorized shape (cone, cube, sphere) and measured the height, width, and length of intersection of each shrub species along a line placed 5 m left of the transect centerline to avoid previously disturbed shrubs (Mitchell and Hughes

1995). We collected leaves ( $n = 119$ ) during the *L. d. claytoni* larval growth period (29 May–14 July) from top branches on randomly selected *D. fruticosa* plants in each transect zone to evaluate leaf nitrogen content. Pre-weighed whirl-pack bags containing the collected leaves were stored on ice at 4 °C and weighed within 6 h of collection to determine initial leaf sample weight. We dried leaves in a drying oven at 105 °C until consecutive weight measurements were consistent, indicating the sample was no longer losing moisture to evaporation. The ratio of the difference between the initial and final and the initial weight is the proportion of the leaf that was water (leaf moisture). We ground dried leaves with a mortar and pestle and burned away the sample organic material in a muffle furnace at 550 °C for 5 h at the AMSTS. The AMSTS determined total leaf nitrogen (N) with plasma emission spectrophotometric analysis.

#### *Bloom surveys and nectar analysis*

We counted open blooms during the adult *L. d. claytoni* flight period (15 July–19 August) on each *D. fruticosa* shrub intersecting the transect center line and collected blooms ( $n = 503$ ) from randomly selected *D. fruticosa* ( $n = 83$ ) in the transect zones to measure nectar sugar concentrations. We excluded Portage Lake (unoccupied) from nectar collection, given the travel time required to access this wetland, which prohibited sampling on the same day as occurred at the other wetlands. We selected six, newly-opened blooms on each plant, enclosed three of these blooms in fine-meshed (250- $\mu$ m), nylon tulle to exclude nectivores, and left three blooms un-enclosed but marked. After 24 h, we placed the individual blooms in a vial with 2 mL of distilled water, agitated the vial for 1 min (Marrant et al. 2009), removed the bloom, and stored the remaining liquid on dry ice during transport within 6 h to storage in a freezer (−15 °C). We quantified sucrose, fructose, and glucose in 100  $\mu$ L samples with high performance liquid chromatography and compared these concentrations to sugar concentrations in standards.

#### *Age structure and growth rate*

We randomly selected and harvested entire *D. fruticosa* ( $n = 145$ ) from the three zones of each transect

during mid-September to mid-October 2010 to examine *D. fruticosa* age structure. We collected all stems, attached branches, and roots of individual shrubs; shrubs with a prostrate growth form were extracted from the peat where adventitious roots originated on the main stem.

We dried the main stem (i.e., largest, central stem) and attached branches (i.e., secondary stems) to a consistent weight (i.e., repeated, consecutive weights over several days were the same) to estimate above ground stem biomass (AGB). We removed a 2–4 cm section from the main stem at the root collar and from four secondary stems to measure stem growth. We sanded sections, counted annual rings (designating time zero at the 2010 ring), and measured ring width along four radii (WINDENDRO<sup>TM</sup>; Guay et al. 1992). We calculated the area of each growth ring to eliminate the geometric decrease of ring width as stem diameter increases. This method can be used to determine age only on woody plants >7 years old; thus, our minimum detectable age was seven.

#### **Data analysis**

We determined mean difference between the water table and deep well depths, mean depth to water table, groundwater upwelling (proportion of water level measurements with upwelling; %), saturation (proportion of water depth measurements in the rooting zone; %), inundation (proportion of water depth measurements above the peat surface; %), and flood duration (days; %) for each wetland and interval corresponding to *D. fruticosa* (leaf out, bloom, senescence) and *L. d. claytoni* (egg, larval, flight periods) life stages from hydrographs we constructed from each wetland's well data (Fig. 2). We categorized water flow direction as downward (shallow well water level above deep well water level), neutral (shallow minus deep well water level  $\leq 0.1$  cm), or upward (deep well water level above shallow well water level (Fig. 2a). We described daily water level fluctuations with a running average of wetland inundation depth for each wetland and season.

We estimated shrubby cinquefoil volume and percent linear coverage from shape categories and height and width measurements. We converted peat and pore water pH to H<sup>+</sup> ion concentration and

compared pore water, peat analytes, and vegetation volume among wetlands with principal components analysis (PCA; SYSTAT 12; SYSTAT Soft Inc, Chicago, IL) and scatter plots of the principal component score centroids.

We compared mean N concentration and foliar moisture of leaf samples among wetlands with a one-way ANOVA and post hoc Tukey's test (N concentration) or a Kruskal–Wallis test (foliar moisture) and evaluated pair-wise differences among the wetlands with follow-up Mann–Whitney U tests. We assessed correlations between foliar N and moisture with Pearson correlation coefficients. We compared log-transformed fructose and glucose concentrations with a paired *t* test, and enclosed and unclosed bloom sugar concentrations with two-sample *t*-tests. We calculated bloom density as the number of blooms per transect meter intersected by individual *D. fruticosa*.

We aggregated growth rate and age data for comparisons of individual *D. fruticosa* within a wetland, within zones, and between upright and prostrate growth forms. We compared mean age of ramets among wetlands with Kruskal–Wallis owing to non-normality in ages, and we evaluated pairwise differences among wetlands with post hoc Mann–Whitney U tests. We examined Pearson correlations between age and height (primary stem length), age and AGB and age and the diameter of the main ramet among individuals in the wetlands, among the three different zones, and among the two growth forms. We normalized growth rate data with a square root transformation and compared average growth rate among wetlands and among zones with a one-way ANOVA and post hoc Tukey's test with significance for  $P < 0.05$ . We created growth curves with the average growth rate by year and age of the shrub, and we compared growth rates among wetlands and zones within wetlands with Gleichläufigkeit (GLK) values (Eckstein and Bauch 1969). The GLK score is based on sign tests (+ indicates shrubs grow similarly between years;—indicates one shrub grows more and one shrub grows less than in previous year) and is calculated with a classical agreement test. A pair-wise GLK score is calculated from the sum of the points divided by the number of years compared. We visually compared age structure and number of secondary branches within age classes with histograms.

## Results

### Wetland hydrology

We identified five wetland hydrological types (HT) based on primary water source and inundation variation (Table 1; Fig. 2). Groundwater discharge and constant, minimum inundation characterized Type 1 (HT1), where *L. d. claytoni* was absent (Crystal), uncommon (Woodland), or moderately abundant (Holt) (Knurek 2010). Constant growing season surface water inundation with late season below root-zone drawdown dominated Type 2 (HT2), where *L. d. claytoni* was moderately abundant (Mattagodus, Pillsbury) to abundant (Soper) (Knurek 2010). Early growing season surface water inundation and rapidly declining end-of-growing season water level were representative of Type 3 (HT3), where *L. d. claytoni* was abundant (Dwinal) or absent (Salmon) (Knurek 2010). Prolonged root zone saturation with surface water throughout the late season drawdown dominated Type 4 (HT4), and *L. d. claytoni* was uncommon (Pickle) (Knurek 2010). Fluctuation between root zone saturation and draining with groundwater discharge and recharge characterized Type 5 (HT5; Portage), which was not occupied by *L. d. claytoni*. In all wetlands, flooding magnitude and duration generally were greatest during the mid-summer larval feeding period (Fig. 3), whereas, mean depth to water table and upwelling generally increased during shrubby cinquefoil senescence in early autumn (Table 1).

### Wetland pore water and peat chemistry

Wetland pore water and peat chemistry were loosely grouped by hydrological types. Wetland pore water separated along the electrical conductivity (EC) and hydrogen ion concentration (H<sup>+</sup>) gradients (63.8–77.6 %) of the variation explained by the first two PCA dimensions; Fig. 4), while 56 % of the variation in peat nutrient and mineral composition was explained by the first three principal components (Fig. 5). During larval emergence (24 May–3 June) pore water in HT1 wetlands (where *L. d. claytoni* are uncommon to moderately abundant) contained less H<sup>+</sup> and greater EC, and peat contained greater concentrations of base cations indicating upwelling, whereas, HT5 (unoccupied by *L. d. claytoni*) pore

**Table 1** Hydrological type (HT), upwelling (%), difference (cm) between water table and deep well (mean  $\pm$  standard deviation, SD), saturation (%), depth (cm) to water table (mean  $\pm$  SD), and flood duration (%) for 10 wetlands monitored May–September 2010

	HT <sup>a</sup>	Upwelling <sup>b</sup> (%)	Difference (cm) ( $\pm$ SD)		Saturation <sup>c</sup> (%)	Depth to water table (cm) ( $\pm$ SD)		Flood duration <sup>d</sup> (%)
<i>SC leaf out/CC egg</i>								
Holt pond	1	100	-3.86	0.81	100	-0.71	1.01	25.3
Crystal fen	1	0	0.99	0.21	100	-9.1	1.62	0
Woodland bog	1	97.9	-0.96	0.23	100	-10.4	1.08	0
Mattagodus	2	0	4.82	1.55	100	-13.5	1.89	0
Pillsbury pond	2	0	3.58	0.79	100	-7.8	2.55	0
Soper pond	2	0	14.79	1.16	100	-5.4	1.31	0
Dwinal	3	0	8.2	0.71	100	1.4	1.75	78.2
Salmon stream	3	0	15.21	1.96	100	-11.8	1.69	0
Pickle ridge	4	0	n/a	-	100	4.9	2.17	100
Portage lake	5	71.1	-1.06	1.44	100	1.1	4.29	65.8
<i>CC larval feeding</i>								
Holt pond	1	95.7	-3.59	1.61	100	-5.3	2.53	16.8
Crystal fen	1	0.3	0.92	0.31	100	-8.1	2.02	0
Woodland bog	1	92.8	-0.87	0.57	100	-12.5	2.78	0
Mattagodus	2	0	5.11	1.8	100	-11.9	2.8	0
Pillsbury pond	2	5.6	4.48	2.53	100	-8.8	4.59	0
Soper pond	2	0	13.94	2.48	100	-7.4	3.56	0
Dwinal	3	0	7.7	1.57	100	0.5	3.95	61.6
Salmon stream	3	0	12.04	1.65	100	-10.4	3.19	0
Pickle ridge	4	0	n/a	-	100	7.2	4.05	97.9
Portage lake	5	34.4	-0.04	4.01	100	-0.9	5.28	58.7
<i>SC bloom/CC adult nectaring</i>								
Holt Pond	1	100	-7.14	2.53	100	-16	6.09	0
Crystal fen	1	1.2	0.77	0.44	100	-15.3	2.81	0
Woodland bog	1	9.08	0.37	0.59	100	-15.8	5.46	0
Mattagodus	2	42.3	0.28	2.32	71.2	-26.3	6.73	0
Pillsbury pond	2	9.9	2.85	2.03	100	-9.1	4.42	0
Soper pond	2	0	9.59	5.64	100	-7.1	2.68	1.45
Dwinal	3	0	5.25	1.42	61.6	-24.8	14.36	1.79
Salmon stream	3	29.9	3.32	7.58	73.1	-23.8	10.71	0
Pickle ridge	4	24.2	0.63	1.99	100	-7.9	5.36	7.18
Portage lake	5	73.4	4.79	5.37	99.2	-9.2	9.04	25.8
<i>SC senescence</i>								
Holt pond	1	49.5	-1.81	5.78	100	-15.8	7.41	0
Crystal fen	1	0	1.5	0.43	100	-16	5.79	0
Woodland bog	1	0	7.62	7.9	56.8	-23.4	11.94	0
Mattagodus	2	61.2	-0.54	7.91	24.2	-37	7.5	0
Pillsbury pond	2	37.4	1.68	5.41	100	-16.8	10.97	0
Soper pond	2	0	4.44	2.06	100	-9.4	4.62	0
Dwinal	3	0	8.18	5.5	48.8	-27.1	22.04	2.4
Salmon stream	3	50.1	-0.05	17.4	48.9	-37.1	18.49	0

**Table 1** continued

	HT <sup>a</sup>	Upwelling <sup>b</sup> (%)	Difference		Saturation <sup>c</sup> (%)	Depth to water table		Flood duration <sup>d</sup> (%)
			(cm)	(± SD)		(cm)	(± SD)	
Pickle ridge	<i>4</i>	41.1	−0.48	4.59	100	−15.4	5.25	0
Portage lake	<i>5</i>	22	1.81	1.33	80.8	−15.9	14.74	16.2
<i>Growing season</i>								
Holt pond	<b>1</b>	86.7	−4.2	3.8	100	−10.65	7.4	9
Crystal fen	<i>1</i>	0.4	1	0.45	100	−12.11	4.98	0
Woodland bog	<i>1</i>	48.5	0.1	1.35	90	−15.66	8.09	0
Mattagodus	<b>2</b>	26	2.4	4.92	74.3	−21.97	11.49	0
Pillsbury pond	<b>2</b>	13.5	3.3	3.4	100	−10.62	7.31	0
Soper pond	<b>2</b>	0	9	5.56	100	−7.51	3.64	0.4
Dwinal	<b>3</b>	0	7.2	3.17	77.4	−12.84	18.8	33
Salmon stream	<i>3</i>	19.9	7.2	11	78.8	−21.27	15.27	0
Pickle ridge	<i>4</i>	21.5	3.7	9.04	100	−2.51	10.42	50
Portage lake	<i>5</i>	47	0.3	6.97	95.3	−6.42	11.23	41

Data are reported for periods corresponding to shrubby cinquefoil (SC) leaf out and Clayton's copper (CC) egg (12 May–28 May), CC larval feeding (29 May–14 July), SC bloom and CC adult nectaring (15 July–19 August), and SC senescence (20 August–mid-September) in Maine

The values in column 2 indicates relative abundance of Clayton's copper butterflies as absent (the value without emphasis), uncommon (italicized values), moderately abundant (bold-faced values), abundant (bold and italicized values)

<sup>a</sup> Hydrological type: HT1 = groundwater discharge, constant water levels, little to no inundation; HT2 = surface water input dominant, constant water levels, little to no inundation; HT3 = surface water input dominant, inundation at beginning of season, drawdown below rooting zone at end of season; HT4 = surface water input dominant, inundation at beginning of season, no drawdown below rooting zone; HT5 = fluctuated between groundwater discharge and surface water inputs, inundation and drained root zone several times during season

<sup>b</sup> Proportion of deep water level measurements above water table well

<sup>c</sup> Proportion of water level measurements within SC rooting zone ( $\leq 30$  cm below peat surface)

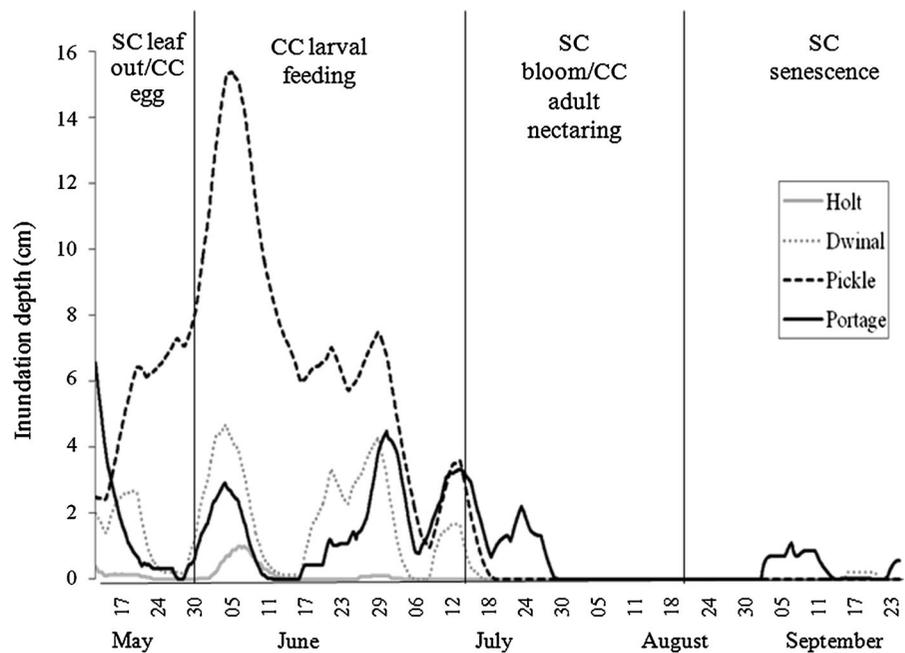
<sup>d</sup> Proportion of water level measurements above peat surface

water and peat showed reversed trends (Figs. 4, 5). Pore water and peat from HT2 and HT3 wetlands (where *L. d. claytoni* are moderately abundant to abundant; Knurek 2010) exhibited intermediate component scores along both axes suggesting prolonged surface water inundation, whereas, HT4 (low abundance of *L. d. claytoni*; Knurek 2010) showed intermediate pore water component scores (but greater concentrations of Mn, Zn and Na (Figs. 4, 5). During *D. fruticosa* bloom and *L. d. claytoni* nectaring (12 July–23 July 2010) and *D. fruticosa* senescence (17–25 August 2010; Fig. 3), pore water analytes generally were similar among hydrological types, except HT5 ( $P < 0.001$ ,  $T = -6.85$  to  $-15.23$ ,  $A = 0.316$  to  $0.805$ ) (Fig. 4). During senescence (late August–September) pore water analytes did not reflect hydrological type (Figs. 4, 5).

Shrubby cinquefoil foliar moisture, nitrogen, bloom number, and nectar chemistry

Percent foliar N ( $F_{9,86} = 15.4$ ,  $P < 0.001$ ) and proportion of leaf moisture (Kruskal–Wallis  $X^2 = 63.6$   $df = 9$ ,  $P < 0.001$ ) differed among wetlands, however, foliar N did not differ with wetland zone ( $F_{2,93} = 1.9$ ,  $P = 0.144$ ) (Table 2). Foliar N was correlated with leaf moisture only in Holt and Soper. *Dasiphora fruticosa* bloom density ranged 0 (Pickle)–1.5 (Salmon) blooms/transect m. During the *L. d. claytoni* flight period, 91 % of 349 *D. fruticosa* plants contained 0–10 blooms, and  $< 1$  % had  $> 30$  blooms. *Dasiphora fruticosa* produces hexose-dominant nectar (sucrose/[glucose + fructose]  $< 0.1$ ) with only trace amounts of sucrose measured in  $< 3$  % of the samples (Fig. 6) and fructose:glucose ratio of 1:1.

**Fig. 3** Running mean inundation depth (cm) during Clayton's copper (CC) life history stages in representative wetland hydrological types during the 2010 Shrubby Cinquefoil (SC) growing season in Maine



Glucose and fructose concentrations were greater in enclosed than unenclosed blooms (two sample t-test, fructose  $t = 15.5$ ,  $P < 0.001$ ,  $df = 444$ , glucose  $t = 16.7$ ,  $P < 0.001$ ,  $df = 444$ ).

#### Shrubby cinquefoil age structure and growth rate

*Dasiphora fruticosa* was the dominant shrub along all transects except those in Pickle Ridge and Portage Lake, which were dominated by *Myrica gale*. Average *D. fruticosa* volume (Fig. 7) and linear coverage generally were greater in wetlands with more consistent water levels (HT1, HT2). Shrubby cinquefoil main stem age ranged 7 – 37 years, and average age differed among wetlands (Kruskal–Wallis  $X^2 = 57.4$ ,  $df = 9$ ,  $P < 0.01$ , Fig. 8), with oldest stems collected from Pillsbury ( $\mu = 22.4$  years,  $SE = 1.4$ ), where *L. d. claytoni* are moderately abundant and Portage ( $\mu = 22$  years,  $SE = 0.4$ ), where *L. d. claytoni* are absent, and youngest from Pickle ( $\mu = 7.4$  years,  $SE = 0.5$ ), with few *L. d. claytoni*. Age structure was similar among wetlands, with most *D. fruticosa* ranging 15–20 years.

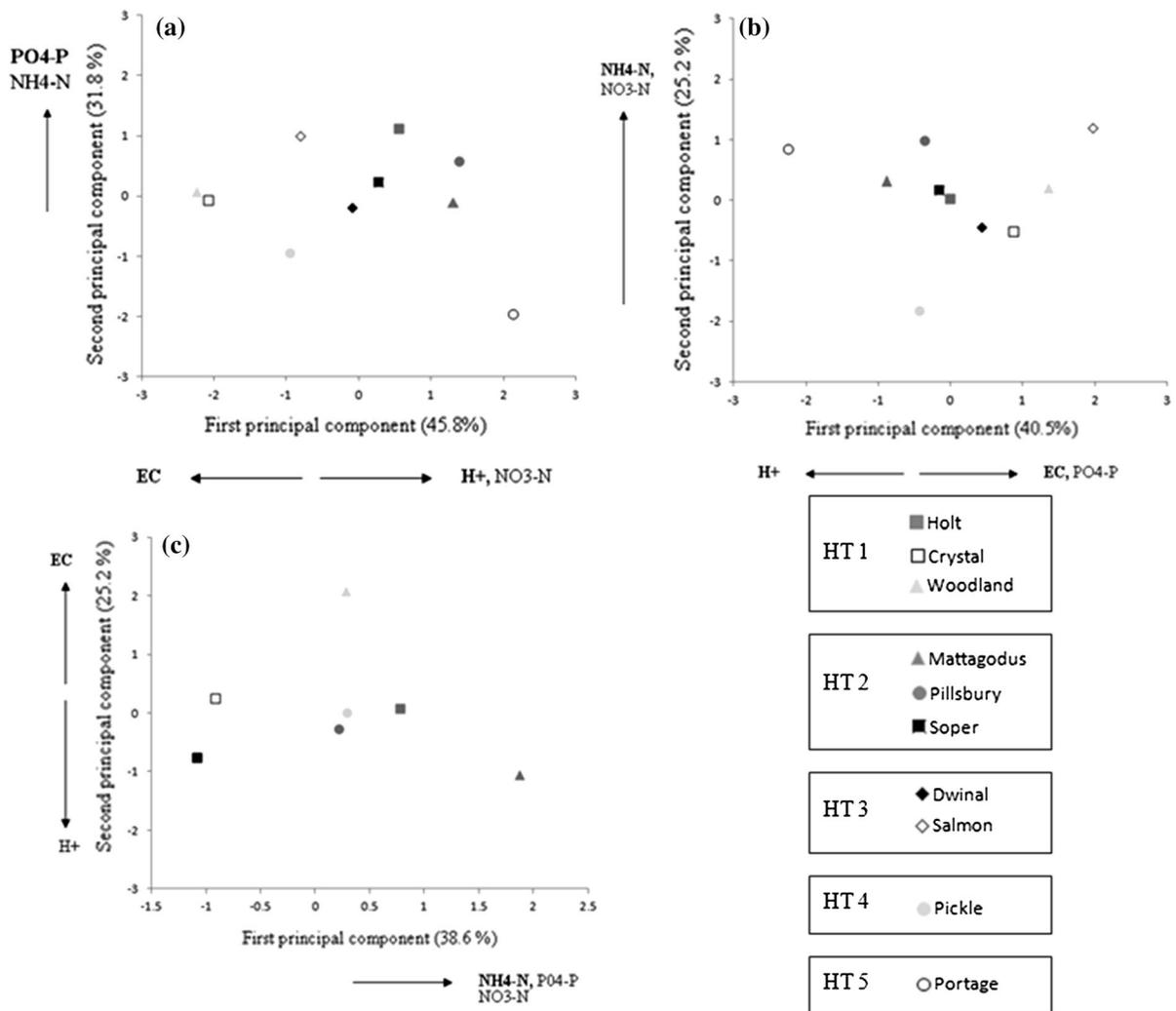
Although average annual growth rates differed among wetlands ( $F_{9,253} = 8.4$ ,  $P < 0.001$ ), periods of increasing and decreasing growth were similar among

wetlands (global GLK = 0.47); growth rate declined as shrubs aged and generally increased in the recent decade (Fig. 9). Growth curve shapes were similar among wetland zones (global GLK = 0.57), however, shrubby cinquefoil growth in the non-forested zone ( $\mu = 2.05$ ,  $SE = 0.20$ ) was slower than that near the water's edge ( $\mu = 3.23$ ,  $SE = 0.34$ ; Tukey's post hoc  $P = 0.03$ ).

## Discussion

### Chemical and hydrological environments of *Dasiphora fruticosa*

Wetland structure and function are determined in part by the hydrological environment (Rydin and Jeglum 2006), and relationships between hydrological conditions, a primary driver of wetland plant community establishment and persistence, and wetland plant community composition and structure are complex (Carter 1986; LaBaugh 1986; Mitsch and Gosselink 2007). Fluctuations in the water table can affect availability of nutrients in peat and pore water (Carter 1986; Boyer and Wheeler 1989; Smolders et al. 2006;

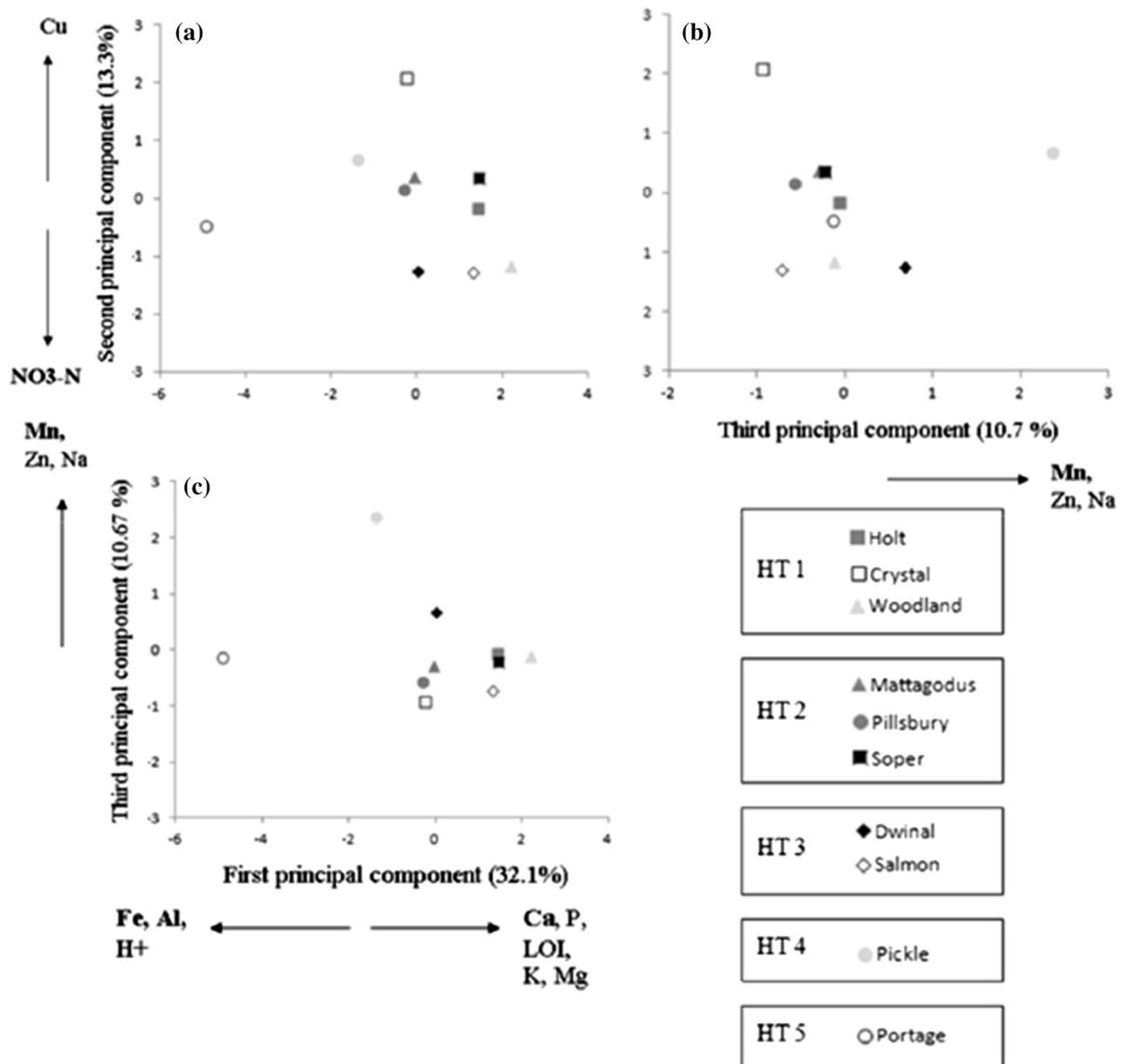


**Fig. 4** Principal component biplots of centroids of pore water analytes from samples collected in 2010 from Maine wetlands during **a** *L. d. claytoni* larval emergence (24 May–3 June), **b** nectaring (12–23 July), and **c** *D. fruticosa* senescence (17–25 August). Analytes exhibiting heavy loadings ( $|\text{loading}| > 0.5$ )

are listed on appropriate axes with the dominant analyte loading on each axis in **bold**. Shading of plot symbol indicates relative abundance of Clayton's copper butterflies as absent (*white*), uncommon (*light*), moderately abundant (*medium*), abundant (*dark*). HT hydrological type, defined in Table 1

Boomer and Bedford 2008) and mineral and oxygen concentrations (Wassan et al. 1990), which may affect wetland vegetation composition and productivity (Mitsch and Gosselink 2007). In Maine wetlands, pore water chemistry in the *D. fruticosa* rooting zone generally reflected the wetland's water source, whereas, peat chemistry was only weakly related to water source and hydrological types. Wetlands dominated by groundwater discharge had greater pore water pH and conductivity owing to mineral nutrients transported in groundwater (Wassan et al. 1990), while

wetlands dominated by surface water runoff generally had a lower pH reflecting a reduction in ion concentration in surface water that dilutes or leaches nutrients from the peat (Mitsch and Gosselink 2007). Peat in all of the study wetlands was saturated for most of the growing season, and nutrient availability may have been reduced by the anoxic conditions. Minerals and nutrients in peat generally are bound in organic forms and may not be available for plant uptake (Mitsch and Gosselink 2007). Similar to conditions where *D. fruticosa* occurs in Britain (Elkington and Woodell



**Fig. 5** Principal component biplots of centroids of peat analytes from samples collected in 2010 from Maine wetlands. Analytes exhibiting heavy loadings ( $|\text{loading}| > 0.4$ ) are listed on appropriate axes with the dominant analyte loading on each

axis in *bold*. Shading of plot symbol indicates relative abundance of Clayton's copper butterflies as absent (*white*), uncommon (*light*), moderately abundant (*medium*), abundant (*dark*). HT hydrological type, defined in Table 1

1963), calcium was the dominant cation in the peat nutrient profiles, while phosphate concentrations varied within and across wetlands, with no indication of phosphate or micro mineral limitations. Morphological differences in *D. fruticosa* plants among the wetlands did not correspond to peat and pore water nutrient availability, however, and may instead reflect physiological and metabolic responses to both the

chemical and physical environment created by water level variation.

Environment of *Dasiphora fruticosa* as habitat for immature *Lycaena dorcas claytoni*

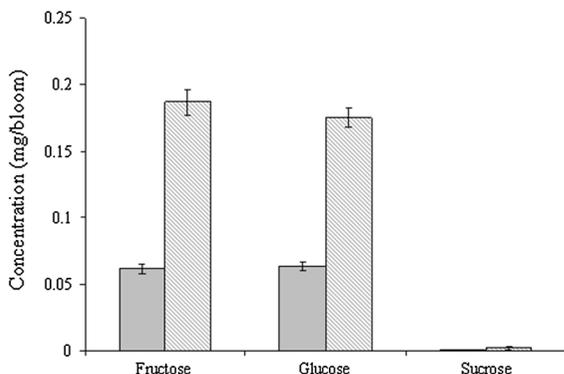
*Dasiphora fruticosa* abundance and coverage were greater in Maine wetlands with consistent water tables

**Table 2** Mean foliar nitrogen (%) and moisture (%) for 10 wetlands

	HT*	Mean foliar N		Mean foliar moisture	
		(%)	(± SD)	(%)	(± SD)
Holt pond	<b>1</b>	1.80 <sup>b</sup>	0.14	59.30 <sup>a</sup>	0.02
Crystal fen	1	1.57 <sup>b</sup>	0.10	73.22 <sup>b</sup>	0.02
Woodland bog	<i>1</i>	2.02 <sup>c</sup>	0.15	67.83 <sup>ab</sup>	0.05
Mattagodus	<b>2</b>	1.69 <sup>b</sup>	0.12	56.80 <sup>a</sup>	0.01
Pillsbury pond	<b>2</b>	1.85 <sup>c</sup>	0.15	57.08 <sup>a</sup>	0.02
Soper pond	<b>2</b>	1.88 <sup>c</sup>	0.14	57.08 <sup>a</sup>	0.02
Dwinal	<b>3</b>	1.70 <sup>b</sup>	0.15	61.79 <sup>ab</sup>	0.03
Salmon stream	3	1.90 <sup>c</sup>	0.22	73.41 <sup>b</sup>	0.02
Pickle ridge	4	1.24 <sup>a</sup>	0.19	56.21 <sup>a</sup>	0.01
Portage lake	5	2.05 <sup>c</sup>	0.16	67.37 <sup>b</sup>	0.01

Means with the same letters do not differ significantly (foliar nitrogen: Tukey's HSD post hoc comparison after one-way ANOVA; foliar moisture: Mann-Whitney U tests post hoc pairwise comparisons after one-way ANOVA; threshold for significance  $P < 0.05$ )

\* Hydrological type (HT). The values in column 2 indicates relative abundance of Clayton's copper butterflies as absent (the value without emphasis), uncommon (italicized values), moderately abundant (bold-faced values), abundant (bold and italicized values)



**Fig. 6** Average concentration (mg/bloom) of fructose, glucose and sucrose for unenclosed (solid bars) and enclosed *Dasiphora fruticosa* blooms (hatched bars) in wetlands in Maine. Error bars represent  $\pm 1$  SE

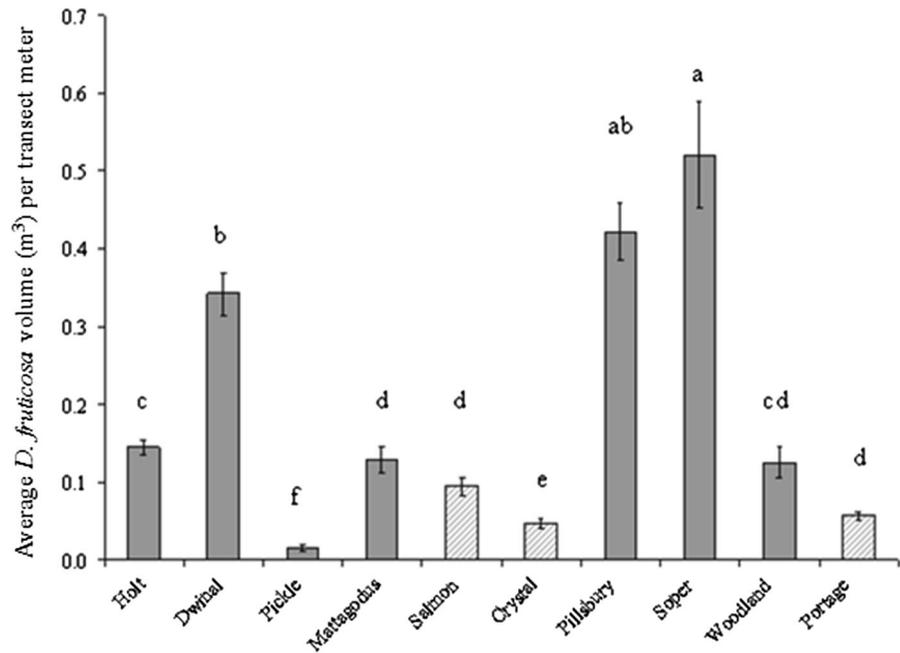
that saturated the root zone with minimal surface flooding (e.g., HT 2, 3) during the growing season, when *L. d. claytoni* larval and stages are attached to leaves in the shrub canopy. Inundation following leaf drop in early autumn (such as that recorded at Pickle and Portage where *L. d. claytoni* are uncommon or

absent, respectively) may drown the eggs, which remain attached to fallen leaves until larvae hatch in spring. Widely fluctuating water levels may not be suitable for butterfly eggs and larvae that are intolerant of submergence (Webb and Pullin 1998; Nicholls and Pullin 2003; Severns et al. 2006). Eggs of *Lycaena xanthoides* on inundated plants were seven times less likely to survive compared with eggs on non-flooded plants (Severns et al. 2006). Larvae of *Lycaena dispar batavus* submerged for 28 days experienced increased mortality (Nicholls and Pullin 2003). Similarly, *L. d. claytoni* larvae have limited mobility and may drown if the host plant is submerged during the early- to mid-summer. In addition to drowning mortality, flooding that makes leaves inaccessible to feeding also may cause larval mortality (Joy and Pullin 1999). Microtopographic variation that maintains exposed substrate below the branches of *D. fruticosa* plants during early spring when the wetland is inundated may enhance survival of *L. d. claytoni* eggs overwintering in fallen litter that does not become submerged.

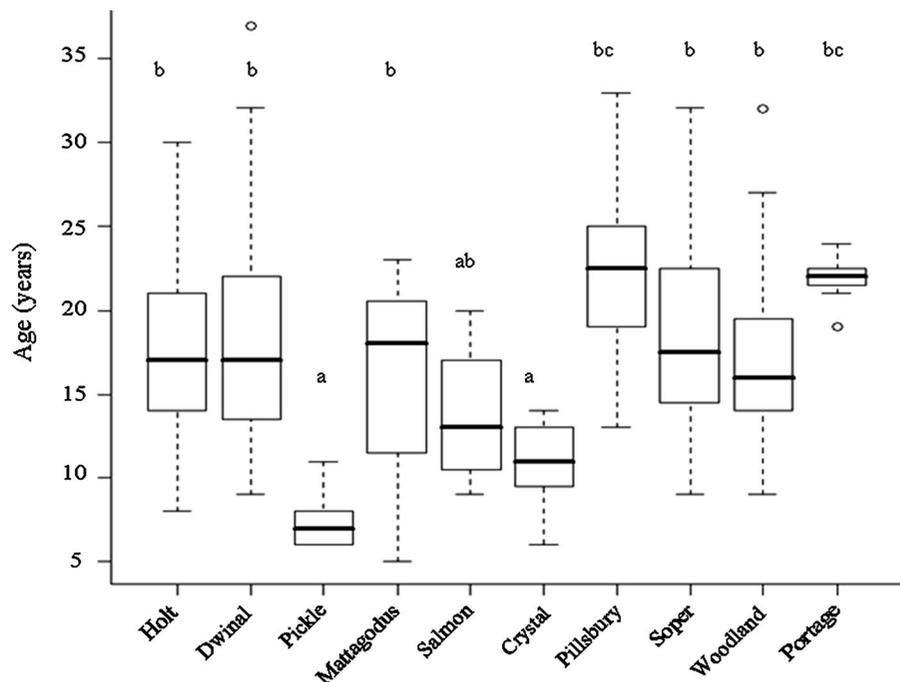
#### Resource conditions for *Lycaena dorcas claytoni*: *Dasiphora fruticosa* age and stature

Age-related differences in the quality of shrubs as a food resource may affect butterfly abundance. Juvenile shrubs typically do not flower or produce seeds (Bond 2000), and bloom vigor may decrease in older shrubs (Oñate and Munné-Bosch 2010), potentially limiting resources for nectaring butterflies. *Dasiphora fruticosa* regenerates clonally as well as through recruitment of seedlings (Elkington and Woodell 1963; Lent and Reier 1999). Our samples did not include shrubs  $< 7$  years old, however, so seedling recruitment in these wetlands is unknown. Most sampled shrubs were 15–20 years old. Wetlands with the greatest *L. d. claytoni* encounter rates in 2008 contained primarily intermediate-aged shrubs and the greatest range in shrub age. Despite differences in size and coverage among wetlands, *D. fruticosa* age structure and side stem production were similar among wetlands, and growth rates declined with stem age in all the wetlands. Age-dependent patterns of growth have been observed in other woody plants (White 1980). As multi-stemmed shrubs age, productivity and growth rates decline (Yoda and Suzuki 1993; Ishii and Takeda 1997; Aikawa and Hori 2006), and more growth is allocated to below than above ground

**Fig. 7** Average *Dasiphora fruticosa* volume ( $\text{m}^3$ ) per transect meter in Maine wetlands. Hatched bars indicate unoccupied wetlands. Error bars represent 1 SE. Bars with the same lowercase letter are not significantly different ( $P \geq 0.05$ )

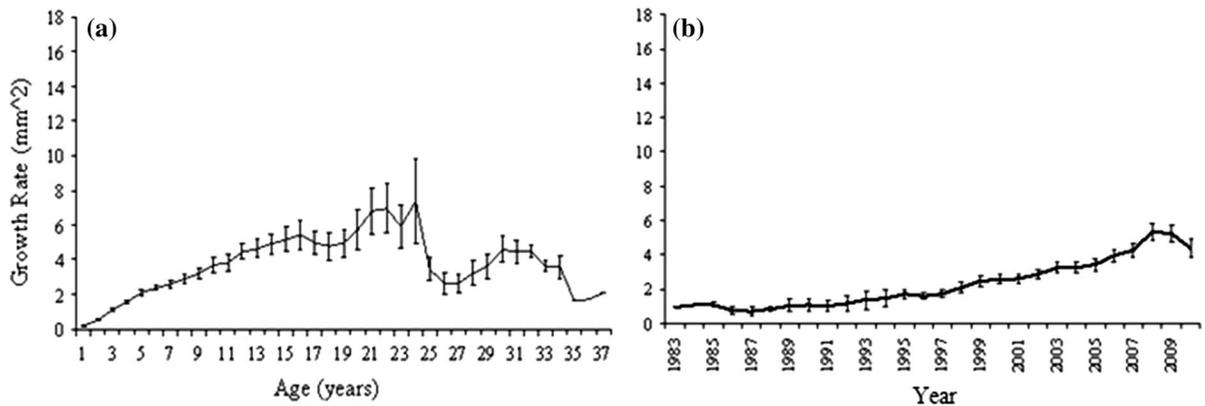


**Fig. 8** Age of *Dasiphora fruticosa* shrubs sampled in Maine wetlands. In each box plot, the top bar is the maximum, and bottom bar is the minimum observation. The third and first quartiles are indicated by the top and bottom of the box, respectively. The mean value is indicated by the middle bar, and the circles are outliers. Mann–Whitney U tests post hoc pairwise comparisons after one-way ANOVA, with significance threshold  $P < 0.05$



(Kawamura and Takeda 2008). *Dasiphora fruticosa* growth rate was greater in the wetland perimeter (near water and forested zones) than the wetland center (non-forested shrub-sedge), and shrub age was correlated with shrub above ground growth and height within wetland zones. Areas with *D. fruticosa* near

open water are not shaded and experience more dynamic hydrological conditions, whereas, the forested zone is more consistently dry and shaded. Shrubby cinquefoil in the non-forested shrub-sedge zone at the wetland center is embedded in dense sedge that is more scattered in the adjacent forested and near water zones.



**Fig. 9** Growth rate curves derived from average *Dasiphora fruticosa* stem ( $n = 145$ ) cross-section increments by age (a) and year (b) for stems collected in Maine wetlands. Bars represent standard error

The variation in phenotypic response to inundation, shading, and crowding may provide insight into this species' potentially broad tolerance of management actions affecting wetland vegetation or water.

Given that *Lycaena dorcas claytoni* spend the majority of their lifetime in juvenile life stages, availability and quality of larval resources are particularly important for their survival. Lepidopteron larvae prefer young, emerging leaves, which may be in response to decreasing leaf N and moisture concentrations as leaves age (Mattson 1980; Meyer and Montgomery 1987). Although differing among wetlands, foliar N and moisture concentrations were not correlated in our study nor did they reflect wetland hydrological and chemical environments. *Lycaena dorcas claytoni* larvae were observed on new leaves of *D. fruticosa* at branch tips (C. Michaud, pers. comm., University of Maine), where they may find refuge from flooding in addition to a quality food source. Feeding behavior of *L. d. claytoni* larvae, as well as relationships among *L. d. claytoni* life stage, *D. fruticosa* plant age and leaf and nectar quality and volume, and changes in foliar N with site environmental conditions need additional study.

Flower density may affect butterfly foraging efficiency (May 1985). *Lycaena dorcas claytoni* nectar on *D. fruticosa* during the mid-July to mid-August egg-laying period. Shrubby cinquefoil bloom density varied among wetlands, and wetlands with greater bloom densities during 2010 (e.g., Soper and Pillsbury) also had greater *L. d. claytoni* encounter rates during 2008. Conditions that promote bloom

abundance are unclear; late growing season below surface drawdown characterizes hydrological conditions at three of four Maine wetlands with greatest bloom density. Availability of abundant *D. fruticosa* blooms may affect wetland site suitability for *L. d. claytoni*, however, two of these wetlands (Salmon, Portage) with robust blooming *D. fruticosa* currently are unoccupied by *L. d. claytoni*.

Adult Lepidopteran flight is an energetically expensive activity that may be limited by carbohydrate availability (O'Brien 1999), which also can significantly affect longevity and fecundity (Hill 1989; Hill and Pierce 1989). Butterflies are able to differentiate between glucose, fructose and sucrose in nectar, and some species demonstrate a preference of sucrose over hexose (fructose and glucose; Erhardt 1991, 1992; Rusterholtz and Erhardt 1997), although these sugars contain roughly the same energetic content per unit gram ( $16.48 \times 10^3$  J/g; Weast 1980). *Dasiphora fruticosa* produces hexose-dominant nectar, and sucrose was absent in all but a few of the nectar samples. We also observed *L. d. claytoni* nectaring on *Solidago uliginosa*, a member of Asteraceae that was sparsely distributed in the study wetlands. Asters typically produce hexose dominant nectar (Percival 1961), suggesting that *L. d. claytoni* may be able to use other hexose-dominant nectar sources in addition to *D. fruticosa*. Resource quantity is a key predictor of densities of monophagous butterflies (Krauss et al. 2003, 2005; León-Cortés et al. 2003), and adult densities may be driven by host plant quantity regardless of plant quality (Krauss et al. 2005). Adult Clayton's copper butterflies do not fly far from their

host plant (Layberry et al. 1998), which may reflect *D. fruticosa*'s patchy distribution, the small amount of nectar it produces and the limitations of this energy source (VanOverbeke et al. 2007), as well as flight limitations of the butterfly. It is not known if *L. d. claytoni* can disperse to unoccupied wetlands with *D. fruticosa* without assistance, given the lack of contiguous wetland habitat separating these wetlands. It is possible that *L. d. claytoni* eggs may be carried in leaf litter transported among hydrologically connected wetlands in flooding events, however, survival of flooded eggs is unknown, and Maine's wetlands containing *D. fruticosa* are disparate. Gene flow is limited among regions of Maine with populations of *L. d. claytoni* (C. Michaud, University of Maine, unpubl. data), however, relatedness among wetlands within these regions is unknown. Understanding the dispersal ability of *L. d. claytoni* is key to identifying additional, accessible wetlands with quality *D. fruticosa* to enhance *L. d. claytoni* conservation without creating a potential ecological trap (Severns 2011).

### Conservation implications

Although abundance of larval food plants may be a critical factor for the persistence of food plant specialists (Krauss et al. 2005), access to these resources also is important (e.g., Fahrig and Merriam 1985). *Lycaena d. claytoni* conservation will be enhanced by management strategies that maintain wetlands with extensive *D. fruticosa* coverage that are connected with suitable dispersal habitat and ensuring that occupied sites do not become further isolated (Severns 2011). *Dasiphora fruticosa* can tolerate a range of hydrological conditions (Elkington and Woodell 1963), however, we found the most robust plants with greatest bloom density in wetlands with a saturated root zone in the growing season and late growing season drawdown into or below the root zone. These wetlands also contain moderately abundant to abundant populations of Clayton's copper butterflies. The three unoccupied wetlands have a variety of dominant water sources, chemical environments, and water level variability representing three hydrological types. Although an unoccupied wetland, the hydrological and chemical environment of Salmon is similar to wetlands with moderately abundant to abundant Clayton's copper butterflies, and shrubby cinquefoil is robust and widely distributed across this wetland.

Water level fluctuation with nearly continuous saturation of the peat surface (Portage) and sparsely distributed, small-statured shrubby cinquefoil (Crystal) may inhibit butterfly population establishment and persistence in these wetlands.

Wetland management strategies that permit a seasonally dynamic water level, in addition to reduced hydrological disturbances in the surrounding watersheds, may be critical for maintaining inundation conditions and timing suitable for *D. fruticosa* leaf-out and bloom while also meeting the changing needs of *L. d. claytoni* life stages. More information is needed about spring flooding effects on early life stages of *L. d. claytoni*, nutrient uptake of *D. fruticosa* during leaf out, and relationships between wetland environmental conditions and *D. fruticosa* quality as larval and adult food. Little is known about what limits *L. d. claytoni* dispersal and the degree of dispersal occurring among occupied wetlands. Robust stands of *D. fruticosa* currently are restricted to the ten isolated wetlands surveyed in this study. Long-term *L. d. claytoni* population persistence may require conserving and enhancing *D. fruticosa* stands along waterways that connect the scattered occupied sites to facilitate *L. d. claytoni* dispersal among these sites while minimizing potential subsequent isolation.

**Acknowledgments** Funding was provided by the Maine Agricultural and Forest Experiment Station (MAFES), U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit, Maine Department of Inland Fisheries and Wildlife (MDIFW), Maine Outdoor Heritage Fund, The Nature Conservancy (TNC), U.S. Fish and Wildlife Service (USFWS), and the University of Maine Wildlife, Fisheries, and Conservation Biology Department. We are especially grateful to B. Swartz, N. Sferra, M. McCollough, W. Halteman, A. Reeves, F. Drummond, M. Day, L.B. Perkins, B. Libby, D. Anderson, A.T. Fessenden, and K. Chenard. We thank the landowners for their generosity in allowing access to their land. The manuscript was improved with a review provided by A. Calhoun and 2 anonymous reviewers. Mention of trade names and commercial parts does not constitute endorsement or recommendation for use by the U.S. Government. This is Maine Agricultural and Forest Experiment Station Publication Number H-6-00531-13.

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