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NOTE

Calcium and pH co-restrict abundance of *Drosera rotundifolia* (Droseraceae) in a *Sphagnum* bog in central British Columbia

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Abstract: The genus *Drosera* (sundews) is represented in British Columbia (BC), Canada, by *Drosera rotundifolia* (L.), *Drosera anglica* (Huds.), and their hybrid *Drosera* × *obovata* (Mert. & W.D.J. Koch). All three can be found in *Sphagnum* bogs of central BC, including those within the Aleza Lake Research Forest (ALRF) located 60 km east of Prince George. Vegetation patterns in bogs are known to be correlated with light, water, and nutrient gradients, and despite information being available on the influence of light and water on *Drosera* occurrence, little information is known about the role of nutrients. Here, we focused on a bog containing all three *Drosera* species, to determine whether nutrient levels are related to the abundance of the widespread species, *D. rotundifolia*. Univariate regression tree analysis between soil water chemistry and *D. rotundifolia* numbers indicates that *D. rotundifolia* is a calcifuge, preferring moderately acidic soil pH (>5.5) and relatively low calcium levels (<2.88 ppm). This study provides evidence that high soil water calcium and low pH limit the growth of *D. rotundifolia* in field populations. The physiology underlying this preference, how this is affected by hybridization between other sundew species, and how this mineralogical limitation interacts with other niche-defining factors to dictate the occurrence of *D. rotundifolia* are questions that remain to be answered.

Key words: Drosera rotundifolia, *Drosera anglica*, calcium, *Sphagnum* peatlands, carnivorous plants.

Résumé : Le genre *Drosera* (« sundews ») est représenté en Colombie-Britannique (CB), au Canada, par *Drosera rotundifolia* (L.), *Drosera anglica* (Huds.) et leur hybride *Drosera* × *obovata* (Mert. & W.D.J. Koch). Tous trois peuvent se trouver dans les tourbières du centre de la CB, incluant les tourbières de la forêt d'enseignement et de recherche d'Aleza Lake située à 60 km à l'est de Prince George. Les patrons de végétation des tourbières sont connus pour être corrélés avec les gradients de lumière, d'eau et de nutriments, et malgré le fait que l'information sur l'influence de la lumière et de l'eau sur la présence de *Drosera* soit disponible, le rôle des nutriments est peu connu. Les auteurs se concentrent ici sur une tourbière comportant les trois espèces de *Drosera* afin de déterminer si les niveaux de nutriments sont reliés à l'abondance de l'espèce répandue *D. rotundifolia*. L'analyse d'un arbre de régression multivariable entre la chimie de l'eau du sol et le nombre d'individus indique que *D. rotundifolia* est un calcifuge, préférant les sols à pH modérément acides (5,5) et à niveaux de calcium relativement faibles (<2,88 ppm). Cette étude fournit la preuve qu'un niveau élevé de calcium dans l'eau du sol et un pH faible limitent la croissance de *D. rotundifolia* dans les populations sur le terrain. La physiologie qui sous-tend cette préférence, comment elle est affectée par l'hybridation entre d'autres espèces de drosères et comment cette limitation minéralogique interagit avec d'autres facteurs définissant la niche afin de dicter l'établissement de *D. rotundifolia* sont des questions qui restent à examiner. [Traduit par la Rédaction]

Mots-clés : Drosera rotundifolia, *Drosera anglica*, calcium, tourbières, plantes carnivores.

Introduction

Members of the sundew genus *Drosera* represent a number of scientifically important species. Widely known for their carnivorous habit, sundews are key models for ecological processes such as plant population dynamics and plant responses to environmental change (Ellison et al. 2003). Although the genus has approximately 160 species worldwide (Barthlott et al. 2007), only the round-leaf sundew *D. rotundifolia* (L.), the English sundew *D. anglica* (Huds.), and their natural sterile hybrid *D.* × *obovata* (Mert. & W.D.J. Koch) are listed as occurring in British Columbia (BC), Canada (Schnell 2002). These species are typically restricted to *Sphagnum*-dominated peatland bogs, which are ecosystems defined by their

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waterlogged, acidic, and low-nutrient status (Van Breemen 1995; Mackenzie and Moran 2004). The low pH of these wetlands is thought to be the result of initial acidification by brown mosses followed by subsequent colonization by *Sphagnum* (Soudzilovskaia et al. 2010). The buildup of peat from *Sphagnum* growth isolates the rooting zone from pH-balancing groundwater and consequently the pH of the rooting environment in such habitats can be as low as 3.5 (Clymo 1963; Karlin and Bliss 1984).

Even though both *D. rotundifolia* and *D. anglica* can be found within the same bog, each of these species has a distinct ecological preference within the heterogeneous terrain of these wetlands. *Drosera rotundifolia* is tolerant of wide ranges of water and shade levels and is often found across different microhabitats such as hummocks and lawns (Crowder et al. 1990; Nordbakken 1996). Hummocks are mounds of living *Sphagnum* moss that rise from the surface of the bog to form small "hills" that are relatively isolated from the water table. As these hills are composed of *Sphagnum* plants actively taking up nutrients, their rooting zone is lower in nutrients and more acidic than that of their surroundings below (Karlin and Bliss 1984). Horizontal expanses of *Sphagnum* with little vertical variation are referred to as lawns, and can have similar chemical but not hydrological properties to hollows. Hollows are depressions in the *Sphagnum* layer with a higher water table than their surroundings, and are the preferred microhabitat of the more discriminating sundew, *D. anglica* (Crowder et al. 1990; Nordbakken 1996). The higher water table in hollows limits *Sphagnum* growth (Andrus et al. 1983; Rydin and Mcdonald 1985) and consequently the nutrient levels and pH are generally higher in hollows and lawns than in hummocks. It is important to note that although these generalizations may be made, bogs can be quite variable and microhabitat characteristics can be different from those mentioned above (e.g., Bragazza and Gerdol 2002).

The habitat differences noted for the BC sundews are consistent with the observation that overall bog plant vegetation patterns are primarily driven by light, water, and nutrient levels (Nordbakken 1996). Information regarding the influence of light and water table height is available for these BC species (e.g., Crowder et al. 1990), but the extent to which gradients in pore water chemistry might influence or correspond to the distribution of these two sundew species within these bog ecosystems is currently unknown. Therefore, our main objective was to gain a clearer understanding of the habitat requirements and ecology of the more abundant and common sundew (*D. rotundifolia*) in central BC, Canada, by testing the hypothesis that *D. rotundifolia* abundance is influenced by water chemistry.

Materials and methods

Study site

This study was carried out at the University of Northern British Columbia (UNBC) Aleza Lake Research Forest (ALRF) located ~60 km east of Prince George, BC. Forests on upland sites within the ALRF are generally wet and cool and consist of interior hybrid spruce (*Picea engelmannii* Parry ex Engelm. × *glauca* (Moench) Voss.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). However, lowland sites, especially those in basin depressional locations with perched water tables on clay subsoils develop wetland and wet forest communities. Wetlands in the ALRF range from eutrophic swamps and fens in areas with more active groundwater flow, to oligotrophic raised bogs in kettled depressions with restricted groundwater flow. Within these oligotrophic bogs are *Sphagnum* communities likely to contain *Drosera* species.

Of eight ALRF sites surveyed, one was chosen for in-depth analysis of sundew abundance, as it was easily accessible, surrounded by undisturbed primary forests, and harboured plentiful *D. rotundifolia* and *D. anglica*. The chosen site was classified as a Wb11 type peatland bog as per Mackenzie and Moran (2004); possessing minimal tree cover in the form of stunted black spruce (*Picea mariana* (Mill.)) and lodgepole pine (*Pinus contorta* var. *contorta* (Douglas)). The dominant herbaceous species included *Menyanthes trifoliata* (L.), *Vaccinium oxycoccos* (L.), and *Andromeda polifolia* (L.); major shrub species consisted of *Ledum groenlandicum* (Oeder; = Rhododendron groenlandicum, Hébert and Thiffault 2011), *Betula nana* (L.), and *Salix pedicellaris* (Pursh). *Sphagnum* lawns and hummocks were composed primarily of *S. magellanicum* (Brid.) and hollows of *S. teres* (Schimp.).

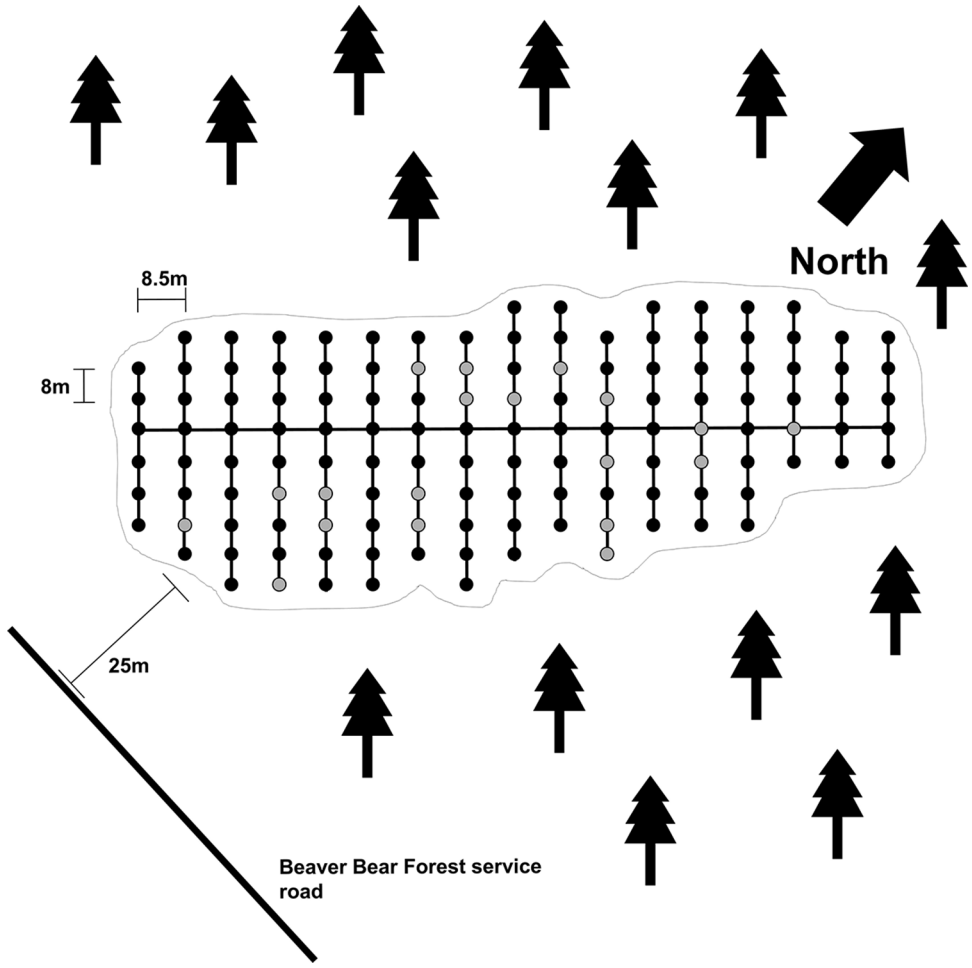
Data collection

Within the study site, a regular grid pattern was laid out and quadrats placed on grid intersection points for habitat analysis (Fig. 1). Each quadrat was a 30 cm × 30 cm square; quadrats were spaced 8 m apart vertically and 8.5 m apart horizontally for a total of 133 quadrats. Quadrat data were collected in July and August of 2012 and 2013. For each quadrat, the number, species and microhabitat location (hummock, lawn, hollow, or hollow edge) of any sundews were recorded, along with the percent cover of all non-*Drosera*, non-*Sphagnum* species. *Drosera* fitness was limited to the number of individuals present within a plot. Species were identified in the field, and representative samples of each species were deposited in the UNBC herbarium (Prince George, BC). Owing to the difficulty in identifying *Carex* spp. in the field, these were only identified to family (Cyperaceae). Similarly, *Equisetum* species were only considered at the genus level. Species identification of representative specimens was confirmed following the *Illustrated Flora of BC* (Douglas et al. 1998).

Water chemistry analysis

At each quadrat, a water sample of approximately 50 mL was taken for elemental analysis, in July 2013, using a nylon pipette, and was stored at 4 °C until analysed. When surface water was unavailable, a small hole

Fig. 1. Schematic representation of quadrat layout pattern used for sampling, with quadrat locations marked by circles at the grid intersection points. Each quadrat consisted of a 30 cm × 30 cm square separated from its neighbours by 8 m vertically and 8.5 m horizontally. Quadrat pattern was based on a horizontal middle line overlaid on the longest lengthwise portion of the bog, with vertical lines laid outwards in either direction to the start of forest cover (represented by the surrounding outline). Plots containing sundews (*D. rotundifolia*) are indicated by grey circles.



was incised into the peat and water released by compression of nearby *Sphagnum*. Elemental ion concentrations (Fl^-, Cl^-, SO_4^{2-}, Br^-, NO_3^-, PO_4^{2-}, Na^+, NH_4^+, K^+, Ca^{2+}, Mg^{2+}) were determined using a Dionex ICS-5000 ion chromatography system by the Northern Analytical Laboratory Services at UNBC. Water samples were centrifuged at 27 000*g* for 20 min prior to analysis. The pH and electrical conductivity (EC) were determined using an Orion 5 star meter with pH and electrical conductivity probes (Thermo Fisher Scientific, Burlington, Ontario, Canada). The EC values were corrected for conductivity of hydronium ions. In the overall analysis, the pH values were considered as is, and were not converted to or averaged as hydronium concentrations. Because most measured values for Fl^- were zero, Fl^- was not included in the statistical analyses.

Statistical analysis

Univariate regression tree (URT) analysis provides a statistical means by which explanatory environmental variables affecting the abundance of a given species can be estimated (De'ath 2002). Datasets in URT are clustered into groups where environmental variables consist of similar values. Groups are created by splitting the dataset along those variables, which give groups with the most intergroup similarity. By examining the splits and terminal nodes of a URT, variables relating to the number of a given species can be made clear. Using URT analysis software (R software suite, version 3.0.0; with the archived library packages mvpart and MVPARTwrap), predictive trees were constructed from the water chemistry data to identify possible mineral influences on *D. rotundifolia* abundance. Mantel tests were also conducted to determine possible spatial autocorrelation with the data (R software, version 3.2.1, with the library package ade4).

Results

Sundew distribution and habitat preference

Of the 133 quadrats analyzed, *D. rotundifolia* was present in 19 quadrats (Table 1; Fig. 1) with an average of 5.4 ±

Table 1. Abundances of plant species encountered at the study site.

Species name	Quadrats	Plant numbers
Drosera species		
Drosera rotundifolia[a]	19	5.4±1.2
Drosera anglica[b]	6†	10.7±2.6
Drosera × *obovata*[c]	N.A.	<20 total
Abundant species		
Cyperaceae	115	8.0±1.0
Menyanthes trifoliata	108	10.4±0.9
Andromeda polifolia	98	4.0±0.3
Ledum groenlandicum	94	9.3±1.0
Vaccinium oxycoccos	82	3.0±0.3
Salix pedicellaris	67	0.9±0.9
Betula nana	49	10.6±1.3
Equisetum spp.	20	4.9±0.8
Kalmia polifolia	18	2.6±0.6
Potentilla palustris	13	4.5±1.1
Rare species		
Gaultheria hispidula	4	13.8±6.0
Spiraea douglasii	2	18.5±6.5
Lysichiton americanus	1	60.0±0.0

Note: For *Drosera*, the average number of plants per quadrat is given ±SE, along with percentages for the total number of sundews occupying a given microhabitat. Microhabitats are edge (edge of a hollow), lawn, hummock, and hollow. Non-*Drosera* species are divided into abundant species (occupying 12 or more quadrats) and rare species (occupying less than 12 quadrats). For each plant type, the average percent cover per quadrat ± SE, as well as the number of occupied quadrats is given. A total of 133 quadrats were examined.

†Six areas not part of quadrat grid but of high plant abundance were chosen solely for the purpose of representative sampling.

[a]Microhabitat 58% Edge, 34% lawn, 8% hummock.

[b]Microhabitat 100% hollow.

[c]Microhabitat lawn, hollow.

1.2 plants per quadrat (±SE). *Drosera anglica* and *D.* × *obovata* were not found in any of the quadrats. Both of these species were highly localized to a specific portion of the bog or present in very low numbers, respectively. Therefore, further statistical analyses only considered *D. rotundifolia*. A total of 107 *D. rotundifolia* plants were counted within the 19 quadrats and, of these, 63 were present on the edges that joined two different microhabitats, 37 were present on *Sphagnum* lawns, and 7 were present on hummocks. Although found on the edges of hollows, no *D. rotundifolia* were ever found within the hollows proper.

Drosera rotundifolia is sensitive to calcium at high pH

All 133 quadrats were used to create a regression tree to determine the influence of water chemistry on *D. rotundifolia* abundance (average water chemistry across the entire bog is listed in Table 2). This initial regression tree explained 41.5% of the total variation and revealed four important variables: EC, NH_4^+, Cl^-, and Ca^{2+} levels (data not shown). However, only 19 quadrats out of the 133 total quadrats contained sundews, and consequently each leaf in this regression tree only contained between 2–6 quadrats with no more than six sundews total present in a given leaf. Therefore, a new regression tree analysis was performed using only quadrats containing sundews (Fig. 2A). The tree explained 53.7% of the total data variation, splitting once at a water pH of 5.46, and a second time at a Ca concentration of 2.88 ppm. The leaves of this regression tree contained 17 (pH < 5.46) and 90 (pH ≥ 5.46) individual *D. rotundifolia* plants, but the majority of sundews (73 plants in 7 quadrats) in the bog were found at higher pH (≥5.46) and lower Ca^{2+} (<2.88 ppm). This provides evidence confirming the initial hypothesis that *D. rotundifolia* abundance is linked negatively to pore water nutrient concentrations. However, because only about 50% of the variation in *Drosera* numbers was explained by water chemistry, additional trees were constructed to explore the possible effects of plant cover on *D. rotundifolia* abundance.

Drosera rotundifolia is associated with several bog plant species that do not share its calcium sensitivity

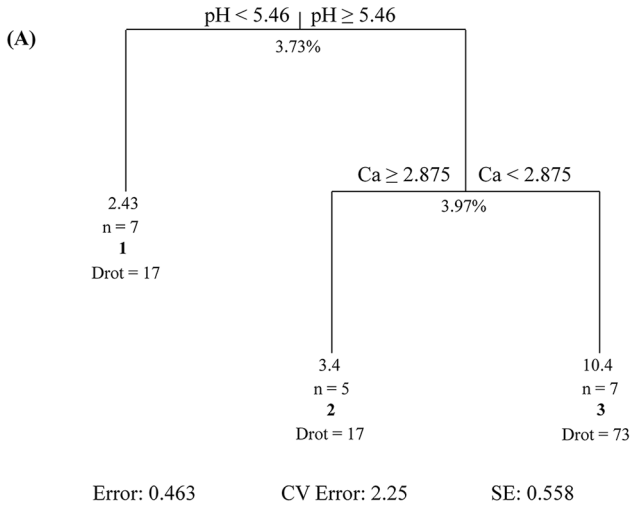
Based on the reported poor competitive ability of carnivorous plants, it was hypothesized that the percent cover of other plant species would be a negative indicator of *D. rotundifolia* abundance. The regression tree for this analysis was constructed using all quadrats and included the percent cover data as possible explanatory variable. This tree split twice, once at an *V. oxycoccos* percent cover of 4.5%, and a second time at a *K. polifolia* percent cover of 1.5%. The number of sundews segregated into each leaf were 29 (*V. oxycoccos* < 4.5%, $n = 114$ quadrats), 23 (*V. oxycoccos* ≥ 4.5%, *K. polifolia* < 1.5, $N = 14$ quadrats) and 36 (*K. polifolia* ≥ 1.5, $n = 4$ quadrats). As with the initial water chemistry tree, this tree also suffered from the low number of sundew quadrats, and explained only 29.4% of the variation in *Drosera* number. Therefore, an additional tree was constructed from only the quadrats containing sundews ($n = 19$), which explained 60% of the variation in sundew numbers, and split only once at a *S. pedicellaris* percent cover of 9%. Based on the interpretation of this tree, however, it was decided that it did not accurately represent the data, as only 2 quadrats (representing 34 sundews) were included in the >9% percent cover leaf. Therefore, *S. pedicellaris* was excluded from the explanatory variables, and the tree reconstructed. The resulting regression tree explained 70.6% of the variation in sundew number (Fig. 3). The data were split first at pH 5.46 and second at a *L. groenlandicum* percent cover of 4.5%. Similar to the tree presented in Fig. 2, the number of quadrats was evenly spread along each of the three leaves (7, 6, and 6, respectively), and each leaf contained nearly the same number of sundews (17, 19, and 71, respectively) as the leaves in the regression tree presented in Fig. 2.

Table 2. Water chemistry variables measured at the study site.

Water chemistry		Cations (ppm)		Anions (ppm)	
pH	5.62±0.02 (5.47–5.81)	Na^{+}	0.551±0.021 (0.408–0.681)	Fl^{-}	0.039±0.014 (0.004–0.0103)
EC ($\mu S \cdot cm^{-1}$)	31.58±0.65 (26.82–35.75)	NH_4^{+}	0.267±0.028 (0.036–0.404)	Cl^{-}	0.358±0.035 (0.063–0.441)
		K^{+}	1.460±0.088 (0.708–1.665)	SO_4^{-2}	0.029±0.004 (0.002–0.023)
		Mg^{+2}	2.000±0.103 (1.198–2.483)	Br^{-}	0.034±0.005 (0.019–0.036)
		Ca^{+2}	3.820±0.152 (2.071–4.071)	NO_3^{-}	0.009±0.002 (0.000–0.010)
				PO_4^{-3}	0.014±0.002 (0.000–0.019)

Note: Average water pH, electrical conductivity (EC), and measured cations and anions are given ±SE, with ranges (first and third quartiles) of these variables included after the means. Water data were collected from each quadrat present at the grid intersection points (n = 133). EC values were corrected for pH.

Fig. 2. (A) Regression tree constructed from only quadrats containing one or more *Drosera rotundifolia* (Drot) to determine important variables affecting sundew abundance. Above each split is the water chemistry variable and associated quantity used for that split. The number of each leaf in the regression tree is given along with the total number of quadrats segregating into the leaves (n) and the total number of sundews found in those quadrats (±SE). Under each split is the percent variation explained by that split. (B) Average (±SE) number of *D. rotundifolia* plants in each leaf's quadrats, along with pH/Ca values and the average number of *D. rotundifolia* across all sundew-containing quadrats. Both the total number and the per-quadrat average of sundews in leaf 3 are distinctly larger than those in the other leaves or across the bog respectively.

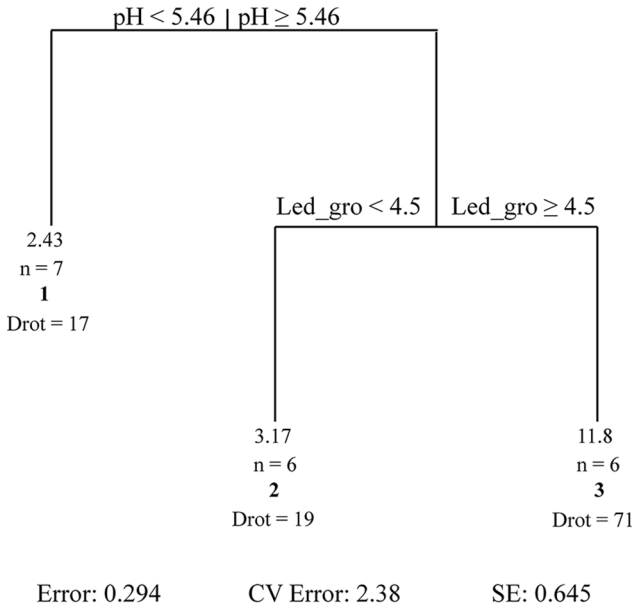


(B)

	D. rotundifolia	Ca (ppm)	pH
Leaf 1	2.4 ± 0.7	1.708 ± 0.223	5.36 ± 0.04
Leaf 2	3.4 ± 0.9	5.484 ± 1.001	5.67 ± 0.05
Leaf 3	10.4 ± 2.1	2.338 ± 0.116	5.61 ± 0.04
Across bog	5.4 ± 1.2	3.820 ± 0.152	5.62 ± 0.02

Because of the unusual observation that *D. rotundifolia* abundance appeared positively-linked with the percent cover of *V. oxycoccos*, *K. polifolia*, and *L. groenlandicum*, the hypothesis that these associates, like *D. rotundifolia*, are also negatively influenced by water chemistry was tested. Because of the weak quadrat separation in the *Salix* tree, *Salix* was not included. A regression tree was

Fig. 3. Univariate regression tree constructed from all plots to predict influences of both water chemistry and percent plant cover on the abundance of *Drosera rotundifolia*, excluding *Salix pedicellaris*. This regression tree explained a total of 70.6% of the variation in *D. rotundifolia* abundance. Under each leaf, the leaf number along with the number of plots (n) and the total number of sundews (Drot) in those plots is included. The second split in the tree, Led_gro ≥ 4.5, refers to a percent cover value of 4.5% for the species *Ledum groenlandicum*.



constructed for each species using all quadrats with the water nutrients as explanatory variables as per the *D. rotundifolia* analysis. Similar to *D. rotundifolia*, *K. polifolia* was present in only a small number of quadrats (n = 18), and so the tree for this species was constructed with only plots containing that species. Of these three trees, only *V. oxycoccos* shared a similar water chemistry influence to *D. rotundifolia*, with the highest percent cover of this species being found in quadrats where the Ca^{+2} levels were below 2.80 ppm. The average percent cover of *V. oxycoccos* when this condition was met was 2.84% (n = 63), whereas otherwise the average percent cover was 0.96% (n = 69). The tree explained only 15% of the variation in percent cover for this species, indicating a minor influence of calcium on this species. In contrast, *L. groenlandicum* was weakly and positively influenced (15.5% variation ex-

plained) by phosphate levels higher than 0.089 ppm (data not shown). The regression tree for *K. polifolia* indicated this species was strongly and negatively influenced by bromine levels greater than 0.02 ppm, and positively by pH greater than 5.53 (data not shown). The low quadrat number, however, limits the applicability of the *K. polifolia* regression tree, and two of the three leaves of this tree contained three or fewer quadrats.

Discussion

The objective of this study was to determine whether the local abundance of the common *Drosera* species (*D. rotundifolia*) was influenced by surface water chemistry within a populated central BC bog habitat using univariate regression tree analysis. Abundance of *D. rotundifolia* was positively related to a combination of more alkaline pH (>5.46) and lower Ca^{2+} (<2.88 ppm), suggesting that the ecological niche of this species may be restricted by Ca^{+2} levels at higher pH, although pH varied little within the examined bog. These results, however, are limited by the examination of water chemistry at only one time point and by the small number of quadrats where *Drosera* were found. Following Vitt et al. (1995), the study site here falls between a bog and poor-fen in terms of pH and Ca values. In their 1995 study, Vitt et al. showed that some water chemistry variables (e.g., pH) varied little seasonally in bogs and poor-fens, whereas other variables (e.g., K levels) varied across the year, owing to water input patterns. Importantly, calcium was found to be highest in bogs during the spring, with a drop in early summer and gradual increase over the remaining summer months. Therefore, the Ca^{+2} concentrations measured here are not necessarily representative of the Ca^{+2} concentration during the entire growing season, although the values measured here likely serve as an adequate approximation. In further studies seeking to clarify ecologically relevant water-chemistry values for *D. rotundifolia*, there are two recommendations based on the results presented here. First, if possible, measurements of water chemistry and *Drosera* populations should be made across the growing season, and ideally include a measure of *Drosera* plant fitness. Second, although underlying vegetation gradients may not be known a priori, sampling should be comparative and focus on areas of high *Drosera* abundance, low *Drosera* abundance, and no *Drosera*. Even with the most common species examined here, *D. rotundifolia*, it was difficult to properly examine abundance values because the sundews were not widely distributed across the studied habitat, and seemed to be constrained to "pocket populations" on favourable microhabitats.

The sensitivity of *D. rotundifolia* to calcium at higher pH (>5.46) found here is quite similar to the results of Rychnovska-Soudkova (1953), who found that *D. rotundifolia* tolerated low levels of calcium up to pH 6.7, but suffered when calcium levels were increased and pH was greater than 3. The sensitivity of *D. rotundifolia* to calcium is in keeping with previous work describing this species as a calcifuge during examination of fens in the UK (Wheeler 1980). Calcifuge plants are defined by being unable to grow on calcareous substrates, and this has been linked to an inability to acquire sufficient phosphorus and iron for growth (Tyler and Ström 1995). Phosphorus (Stewart and Nilsen 1992) and nitrogen (Ellison 2006; Millet et al. 2015) have been found to limit or co-limit carnivorous plant growth, and so the lack of sufficient phosphorus for growth is an appealing explanation for the seeming inability of *D. rotundifolia* to tolerate increased calcium levels. Two things provide evidence to contradict this, however. First, the *D. rotundifolia*/water chemistry tree indicated only a nutrient excess influencing *D. rotundifolia* numbers in the study site, not a nutrient deficiency. Second, all carnivorous plants have access to an alternative source of phosphorus that is unaffected by calcium-mediated soil solubility: insect prey. Sundews have been shown to successfully utilize phosphorus derived from prey sources (Adamec 2002). Thus, it may be that the ability of calcium-sensitive carnivorous plant species such as *D. rotundifolia* to tolerate calcium is not only based on the pH of the soil medium, but also the amount of prey. Another explanation may be that, living in a nutrient-poor environment, *D. rotundifolia* is simply unable to adequately respond to cytotoxic levels of calcium in the soil, as has been observed with other herbaceous calcifuges species (Zohlen and Tyler 2004), and this seems to confirm previous hypotheses regarding some carnivorous plants (Juniper et al 1989).

It is worth mentioning that many published cultivation guides on growing carnivorous plants report the intolerance of a majority of these plants to waters containing greater than 40–100 ppm of minerals (e.g., D'Amato 1998; Schnell 2002; Barthlott et al. 2007). Calcium or a combination of other salts (e.g., magnesium bicarbonate; Schnell 2002) may be to blame; however the critical concentration determined here is one to two orders of magnitude smaller than that given for cultivated plants. It is possible that the degree of sensitivity changes throughout the life stages of the plant; a dynamic that could be easily missed in cultivation. Sensitivity also likely depends on other factors such as macronutrient (e.g., phosphorus) availability, pH, the type of carnivorous plant, and interactions with other plant species. For example, another carnivorous plant species, *Sarracenia purpurea* L., does not appear to follow the calcium sensitivity found here, as specimens have been reported to grow in North Michigan fens with pH values exceeding 5.46 and Ca^{+2} levels over 2.9 ppm (Schwintzer 1978). Although examined as a primary determinant of *D. rotundifolia*'s ecological niche, calcium likely acts in combination with other factors to restrict *Drosera* growth (e.g., competition, with *Sphagnum* [Svensson 1995]). As carnivorous plants in general are poor compet-

itors (Ellison 2006), the additional nutrient stress could indirectly limit their distribution by affecting their ability to compete with other plant species for similar habitats. Furthermore, we were only able to establish a critical value for one of the two sundew species we observed. Although not as widespread as *D. rotundifolia*, *D. anglica* has previously been reported to be quite tolerant to increased Ca^{+2} levels and has been found growing in calcareous soil conditions (Crowder et al. 1990). Why *D. anglica* is able to cope with higher Ca^{+2} levels while *D. rotundifolia* is not, what factors determine *D. anglica* abundance, and how potential mineral sensitivity is altered when these two species hybridize to give *D.* × *obovata* are questions that remain to be answered.

Unexpectedly, the abundance of several other bog plant species was found to be positively linked with larger numbers of *D. rotundifolia*; this is at odds with the deduction that carnivorous plants are poor competitors (Ellison 2006). The bog cranberry *V. oxycoccos* has previously been recorded as occurring alongside this species of sundew on hummock habitats (Crowder et al. 1990), but *L. groenlandicum* and *K. polifolia* appear to simply share the same open bog microhabitat (e.g., Fontaine et al. 2007). The percent cover of each of these three associated species was not above 10% within the quadrats they were present in, and we thus assume competitive interactions with *Drosera* were minimal. One explanation for the association between *L. groenlandicum* and *D. rotundifolia* is that *L. groendlandicum* negatively affects the presence of other plant species by competing with them for soil nitrogen and phosphorus (Hébert and Thiffault 2011). The ability of *Drosera* spp. to acquire both nitrogen and phosphorus from prey items (Adamec 2002) may allow these carnivorous plants to live in the midst of otherwise nutrient-competitive neighbours. The hypothesis that these associated species share a similar habitat to *D. rotundifolia*, owing to a shared nutrient sensitivity, is rejected based on the results obtained here, although the limited sampling methodology makes this rejection tentative and requiring further confirmation.

Based on our study, the ecology of the two species in central BC can be clarified and expanded. The round-leaf sundew, *D. rotundifolia,* is a widespread wetland species often found associated with *Sphagnum* and the nutrient-poor, waterlogged conditions (Crowder et al. 1990; Nordbakken 1996; Nordbakken et al. 2004) that these mosses provide. It is capable of tolerating some degree of shade, but is not completely shade-tolerant (Crowder et al. 1990; Hoyo and Tsuyuzaki 2014). It is found most often in wetter areas of *Sphagnum* peatlands such as on *Sphagnum* lawns and the edge of hollows, but is unable to grow in hollows where plants are frequently inundated (Fontaine et al. 2007). It displays varying degrees of sensitivity to soil nutrient levels (Stewart and Nilsen 1992; Thorén et al. 2003), but seems especially intolerant of Ca^{+2} levels when the soil pH is less acidic (>5.46). It was found to positively associate with *L. groenlandicum* at the surveyed site, possibly due to *L. groenlandicum*'s ability to outcompete other plant species for nutrients.

The English sundew *D. anglica* is more restricted in its ecological distribution; being less tolerant of shading than *D. rotundifolia* and requiring a higher water table (Crowder et al. 1990; Nordbakken 1996; Nordbakken et al. 2004; Hoyo and Tsuyuzaki 2014). Although carnivorous plants in general are poor competitors for light and space (Ellison et al. 2003), *D. anglica* is restricted to the wettest portions of *Sphagnum* bogs (Crowder et al. 1990; Fontaine et al. 2007; Hoyo and Tsuyuzaki 2014), which helps to minimize interspecific competition (Hoyo and Tsuyuzaki 2014). It appears to be much more tolerant of soil nutrients, and can be found on calcareous wetland soils (Crowder et al. 1990). However, its scattered distribution in bogs of central BC makes it more challenging to study and limited our ability to further clarify its ecological requirements during this project.

Conclusion

Although knowledge of the ecological requirements of *D. rotundifolia* has been expanded in this study to include the pH-dependant sensitivity to calcium, more questions remain. The physiological mechanisms that give rise to this sensitivity are still unknown, as are the means by which the co-occurring *D. anglica* is able to cope with higher calcium levels and how the sensitivity is altered when these two species hybridize. The interactions of *Drosera* with other plant species such as *L. groenlandicum*, as well as the cumulative effect of calcium/high pH and other abiotic factors that were not measured here (e.g., shade and water level) remain to be clarified. Further explorations, such as lab-grown sundews given varying calcium/pH treatments to determine specific tolerances, and expanded field studies measuring additional abiotic factors are clearly necessary to fully understand these fascinating denizens of the northern sub-boreal *Spagnum* wetlands of Western Canada.

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