

Assessment of differences in microhabitat preferences between *Drosera rotundifolia* and *Drosera intermedia* in a northern Michigan bog

Mark Bradley

University of Michigan Biological Station
EEB 381 General Ecology
19 August 2010
Professor Cathy Bach

Abstract

The purpose of this study was to compare microhabitat distributions of two species of sundew, *Drosera rotundifolia* and *Drosera intermedia*, in a northern Michigan bog. I examined height distribution of *D. rotundifolia* and *D. intermedia* above the low point of the bog, noted the color of *Sphagnum* on which each individual sundew occurred, and collected measurements of pH, conductivity, and dissolved oxygen to attempt to explain any microhabitat differences I found.

D. rotundifolia density did not vary significantly with any abiotic factors, while *D. intermedia* density increased significantly with decreasing pH and with increasing conductivity, but did not vary with dissolved oxygen. The number of total sundews present did not vary as a function of species, but did decrease significantly with greater height above the quadrat low point; a significant interaction was found between these two factors, indicating that *D. rotundifolia* and *D. intermedia* occur at different heights above the low point of the bog. Additionally, *D. rotundifolia* was significantly associated with a red *Sphagnum* background, while *D. intermedia* was significantly associated with a green *Sphagnum* background. I conclude that, within Mud Lake Bog, *D. intermedia* has microhabitat preferences based on pH and conductivity. Further, I conclude that *D. rotundifolia* tends to occur along with red *Sphagnum spp.* on hummocks, while *D. intermedia* tends to occur along with green *Sphagnum spp.* in hollows, probably because each responds to similar microhabitat differences such as level of desiccation.

I grant the Regents of the University of Michigan the non-exclusive right to retain, reproduce, and distribute my paper, titled in electronic formats and at no cost throughout the world.

The University of Michigan may make and keep more than one copy of the Paper for purposes of security, backup, preservation and access, and may migrate the Paper to any medium or format for the purpose of preservation and access in the future.

Signed,

INTRODUCTION

Bogs, mostly continuous growths of *Sphagnum* moss (*Sphagnum spp.*) underlain by a layer of peat of appreciable thickness and which has exercised a selective influence on the community of plants growing in it, are common in southern Canada and the northern United States (Rigg 1940; McQueen 1990). The bog surface is covered by formations called hummocks, where *Sphagnum* moss rises as small hills above the lower levels of the bog; the areas between the hummocks are called hollows, and the flatter areas without hummocks or hollows are commonly referred to as *Sphagnum* lawns (van Breemen 1995). Below this, peat forms the bog subsurface; peat is a soil high in organic content which develops in water-logged, anaerobic conditions (which inhibit decomposition, contributing to peat formation) such as those found in bogs (McQueen 1990); in North American bogs, these underlying peat areas may be a few feet to more than fifty feet deep (McQueen 1990). Bogs occur in areas of poor or no drainage (Rigg 1940), and create an environment low in nutrients, pH, and dissolved oxygen (DO) (McQueen 1990).

Peat mosses such as *Sphagnum* are widely distributed around the world, occurring in nutrient-poor and poorly drained wetlands on all continents except Antarctica (McQueen 1990). *Sphagnum spp.* are gametophytes with branches arranged in fascicles along an erect stem containing at least two spreading branches and at least one hanging branch, with newer branches concentrated near the top in a capitulum (McQueen 1990). The specific numbers of each branch type are important to species identification, as is the shape of the capitulum (McQueen 1990). Leaves and branches contain large, empty hyaline cells which aid in retaining water; hanging branches conduct water upwards externally, maintaining wet conditions for the upper levels of the plant (McQueen 1990).

Sphagnum species ranges vary within their habitats based on several factors, prominent among which is water level (McQueen 1990; Thum 1986; Rydin 1985). This variation in microhabitat also leads to morphological variation between species. Species occurring near the water level (such as *Sphagnum cuspidatum*) tend to be weak-stemmed and limp, with widely-spaced fascicles and less developed capitula, while species occurring above the water level (such as *Sphagnum magellanicum* and *Sphagnum fuscum*) tend to have more rigid stems, closer fascicles and more developed capitula (McQueen 1990). Species living above the water level also tend to be colors other than green; one species which occupies the hollows is *Sphagnum cuspidatum*, which is often green; *Sphagnum magellanicum*, a red species, tends to form hummocks, while *Sphagnum fuscum*, a reddish-brown species either forms its own compact hummocks or caps the hummocks of other species (McQueen 1990; Crum 2004).

Another factor affecting distribution of *Sphagnum* is nutrient gradient (McQueen 1990); *Sphagnum* makes its habitat more acidic via cation exchange as it releases hydrogen ions (lowers pH) and takes in other cationic nutrients like potassium, sodium, calcium, and magnesium (lowering conductivity) (McQueen 1990; van Breemen 1995). The capacity for cation exchange varies with species, so different species release more hydrogen ions and take in more other nutrients than others (McQueen 1990; van Breemen 1995); this establishes a gradient in both pH and nutrient levels coinciding with species ranges within a bog (McQueen 1990). More acidic conditions tend to exclude other plants, reducing competition for the *Sphagnum spp.* (McQueen 1990; van Breemen 1995).

Looking at pH, nutrient, and water level gradients together gives a useful way to compare hummocks and hollows; the drier environments on top of hummocks tend to be more acidic, while the wetter environments in hollows tend to be more neutral (McQueen 1990). Since bogs

are low-oxygen environments (McQueen 1990), dissolved oxygen levels may also play an important role in comparisons between hummocks and hollows.

Hummock- and hollow-inhabiting species of *Sphagnum* (including *Sphagnum fuscum*) have been shown to engage in interspecific competition at the boundaries between their vertical and horizontal distribution ranges within bogs (Rydin 1993; van Breemen 1995). This competition is not surprising, as the species exhibit considerable overlap in habitat preferences (McQueen 1990; Crum 2004). Additionally, succession of bogs toward drier and more acidic conditions is largely controlled by *Sphagnum spp.*, with different species having greater influence at different stages (Crum 2004). *Sphagnum spp.* are significant ecosystem engineers in bog environments, establishing a mat on which other plant types can grow, altering the pH of the environment, and sequestering nutrients away from other plant types (McQueen 1990; Svensson 1995; Crum 2004; van Breemen 1995); differential capacities between *Sphagnum spp.* for altering the environment may allow different species to coexist with the *Sphagnum* (van Breemen 1995; McQueen 1990; Rydin 1985; Rydin 1993). Svensson (1995) found in a selective fertilization experiment that *Sphagnum fuscum* captured mineral nutrients and sequestered them within the plant before they could reach the roots of *Drosera rotundifolia*, a bog plant which grows on the *Sphagnum* mats, for uptake. Interestingly, *D. rotundifolia* responded to fertilization in ways which minimized its negative impact on its surrounding *Sphagnum*; *D. rotundifolia* grew more leaves, but did not increase the surface area of its leaves, avoiding excessively shading its supporting *Sphagnum* (Svensson 1995).

An interesting plant adaptation to bog environments not exhibited in *Sphagnum* is plant carnivory, which has long been a topic of interest in the field of ecology, likely because it is a unique adaptation vastly different from nutrient acquisition by photosynthesis and absorption via

roots which allows certain species of plants to occupy habitats so deficient in nutrients that survival would otherwise be impossible. The ability to catch and digest insects allows for nutrients to be acquired from sources other than soil, so when conditions are especially poor, particularly when soil (or other substrate) is deficient in nitrogen, these plant species can still survive (Ellison and Gotelli 2001). Carnivorous plants occur in highest numbers and diversity in low-nutrient and bright environments such as bogs (Ellison and Gotelli 2001) because these adaptations for carnivory are energy intensive; there is a tradeoff between carnivory and photosynthesis. Plants investing in carnivory tend to have low maximal photosynthetic rates compared to plants that do not make this investment (Ellison and Gotelli 2001), which explains the tendency to find them in areas with high light levels. Carnivorous plants are better able to compete with nutrient-sequestering *Sphagnum* than are non-carnivorous plants because of their alternate strategy for obtaining nutrients in nutrient-poor environments where sunlight is not a limiting resource (Svensson 1995; Ellison and Gotelli 2001). In bog environments, conditions favor carnivory in the tradeoff between carnivory and photosynthesis (Ellison and Gotelli 2001).

One carnivorous plant type found in the bogs of northern Michigan is the sundew (*Drosera spp.*). The minute individuals of this genus produce basal rosettes of diminutive leaves, sometimes modified to be active traps for insects or more frequently equipped with irritable, mucilage-tipped tentacle-hairs called trichomes, and cymes of delicate white florets which grow well above its leaves to avoid trapping potential pollinators (Gleason and Cronquist 1991). Past studies on individual species within *Drosera* have observed that sundews are frequently found in unshaded areas where their photosynthetic rates can be maximized to lower their necessary energy investment in carnivory (Thorén et al. 2003; Steven and Dickson 1990). They also tend to occur in fairly low densities because high rates of intraspecific competition for insects occur

when the plants are in dense clusters (Gibson 1991). Further, a feeding experiment performed on sundews showed positive correlations between increased insect feeding and growth and reproduction rates of the plants, but no positive correlation between feeding via increased soil fertility and either growth or reproduction rates (Krafft and Handel 1991). This study in particular demonstrates the consequences of carnivory within *Drosera*; these plants are so specialized to obtain nutrients via carnivory that advantageous soil conditions do not improve their fitness.

Significantly, an experiment comparing two sundew species (*Drosera rotundifolia* and *Drosera intermedia*) in a bog environment in Germany showed both species survived with about equal fitness levels based on their nearly equivalent biomasses, but occupied different microhabitats within the bog (Thum 1986). It was observed that *D. rotundifolia* generally lived in drier areas of the bog, above the saturation point on *Sphagnum* hummocks, whereas *D. intermedia* lived in the more water-logged hollows between the hummocks (Thum 1986). Finally, *D. rotundifolia* and *D. intermedia* are generally associated with different bog plant communities (Thum 1986), further indicating that they may have different microhabitat preferences.

D. rotundifolia and *D. intermedia* exhibit interesting morphological differences, most prominent among which are leaf shape and leaf orientation (Gleason and Cronquist 1991). *D. rotundifolia* has leaves which are fairly circular, whereas *D. intermedia* has leaves which are more elongate (Gleason and Cronquist 1991). The basal rosette of *D. rotundifolia* lies roughly horizontally along the ground, while the basal rosette of *D. intermedia* is angled upwards, resulting in leaves that are oriented somewhere between horizontal and vertical (Gleason and Cronquist 1991).

These same two species of sundew (*Drosera rotundifolia* and *Drosera intermedia*), both native to the bogs of northern Michigan, were the subjects of a study in which I investigated the vertical distribution of both species. Citing general tendencies of *D. rotundifolia* and *D. intermedia* (Thum 1986), I expected to find both species in different microhabitats, with the *D. rotundifolia* showing a preference for hummocks (drier, lower pH, lower conductivity), and *D. intermedia* for hollows (wetter, higher pH, higher conductivity). I further expected to find *D. rotundifolia* growing sympatrically with red *Sphagnum* (assumed to be *S. magellanicum* and *S. fuscum*, both determined to occur at this site [Crum 2004]), and *D. intermedia* growing on green *Sphagnum* (primarily assumed to be *S. cuspidatum*, also shown to grow at this site [Crum 2004]), because of red *Sphagnum*'s tendency to form hummocks, green *Sphagnum*'s tendency to form hollows (Crum 2004; McQueen 1990), and *D. rotundifolia*'s and *D. intermedia*'s respective tendencies to occur on hummocks and in hollows and to occur with different plant communities (Thum 1986). I also expected that dissolved oxygen levels would be an important factor in microhabitat preferences between *D. rotundifolia* and *D. intermedia*, based on the importance of low dissolved oxygen levels in bogs (McQueen 1990).

METHODS

I examined microhabitat differences between *D. rotundifolia* and *D. intermedia* at the southern end of Inverness Mud Lake Bog, which is owned by the Little Traverse Conservancy in northern Michigan's Cheboygan County. Mud Lake Bog is a quaking bog with an extensive *Sphagnum* mat containing both red and green *Sphagnum*. A tree line separates the most extensive portion of the mat from a newer, thinner portion closer to the open water of Mud Lake not yet covered with *Sphagnum*. On the south side of this tree line, I selected 12 hummocks of various sizes, 6 in areas of predominantly red *Sphagnum* and 6 in areas of predominantly green

Sphagnum, all away from major foot traffic to avoid disturbance. At each hummock, I established a quadrat with a corner based on the center of the hummock. Each quadrat's size was made to be double the diameter of the hummock in a direction parallel to the corresponding side; the area and percent cover of both red and green *Sphagnum* (adding up to 100%) of each quadrat was noted. Within each quadrat, I counted the number of sundews and noted each individual's species, height above the lowest point in the quadrat (to the nearest centimeter), and on which color of *Sphagnum* (red or green) each individual occurred. In order to explain in more detail factors which may influence microhabitat differences between *D. rotundifolia* and *D. intermedia*, I also measured conductivity, dissolved oxygen (DO), and pH in the hollow of each quadrat. Because submersion of the meters' probes was not possible on the dry tops of the hummocks, measurements could not be taken there; it will be assumed that pH, conductivity, and DO gradients will be similar between hummocks and hollows across the bog.

I performed linear regression analyses to compare the density of each species in each quadrat to pH, conductivity, and dissolved oxygen. After grouping height above the bog low-point into four categories (0 cm, 1- 10 cm, 11-20 cm, 21+ cm), I used a 2-way ANOVA to analyze whether the number of sundews was affected by species, height category, and an interaction between species and height category. A χ^2 test was used to determine association between *Drosera* species and *Sphagnum spp.* color, and a linear regression analysis was used to further examine the correlation between sundew density and *Sphagnum* color for each species.

RESULTS

D. intermedia density per quadrat was significantly inversely related to pH ($r^2 = 0.286$, $N = 11$, $p = 0.005$; Fig. 1) and significantly positively related to conductivity ($r^2 = 0.386$, $N = 11$, p

= 0.018; Fig. 2), but not significantly related to dissolved oxygen (DO) ($r^2 = 0.184$, $N = 11$, $p = 0.188$). *D. rotundifolia* density per quadrat was not significantly related to pH ($r^2 = 0.153$, $N = 11$, $p = 0.235$; Fig. 1), conductivity ($r^2 = 0.266$, $N = 11$, $p = 0.104$; Fig. 2), or dissolved oxygen ($r^2 = 0.003$, $N = 11$, $p = 0.864$; Fig. 3).

The number of sundews present was not significantly related to species but was significantly inversely related to height, with significant interaction between these two factors (Table 1). Both species were found to decrease in number with greater height above the quadrat low point, but *D. intermedia* density decreased with height at a significantly faster rate than did *D. rotundifolia* (Fig. 4).

The number of each species present was significantly associated with the background *Sphagnum* color on which they occurred (about 94.5% of *D. rotundifolia* individuals observed occurred on red *Sphagnum*, and about 83.5% of *D. intermedia* individuals observed occurred on green *Sphagnum*) ($\chi^2 = 726$, $df = 1$, $p < 0.001$; Fig. 5). Within any one quadrat, the number of *D. intermedia* was significantly inversely related to percentage of red background *Sphagnum* color ($r^2 = 0.750$, $N = 12$, $p < 0.001$; Fig. 6), whereas the number of *D. rotundifolia* was significantly positively related to percentage of red background *Sphagnum* color ($r^2 = 0.446$, $N = 12$, $p = 0.018$; Fig. 6).

DISCUSSION

My results showing that *D. intermedia* density is inversely related to pH and positively related to conductivity indicate that *D. intermedia* has specific microhabitat requirements within Mud Lake Bog related to these factors. Occurrence of higher densities of *D. intermedia* in more acidic quadrats does not appear to support my hypothesis that *D. intermedia* would occur in

hollows. Previous literature indicates that hollows tend to be more neutral than hummocks (McQueen 1990); my findings contradict this, and also do not correspond with the higher pH expected to be associated with higher conductivity due to cation exchange capacities (McQueen 1990; van Breemen 1995). This may have been because pH was measured only in hollows and not on hummocks, assuming that pH gradient is similar in magnitude for each quadrat; thus pH essentially is being compared between quadrats and not between hollows and hummocks. However, this assumption that higher hollow pH indicated higher hummock pH may not be correct.

On the other hand, my result may not contradict previous literature at all. Finding higher densities of *D. intermedia* in areas with lower pH may mean that the areas of Mud Lake Bog sampled are in the lower end of the pH tolerance range of *D. intermedia*; this might indicate that the pH range Mud Lake Bog as a whole is shifted toward the lower end (and may not even include some of the higher end) of *D. intermedia*'s range of pH tolerance. If this were the case, then *D. intermedia* would tend to occur in higher densities in areas which lie closer to the optimal pH for *D. intermedia* and I might see results similar to the ones of this study. An alternative explanation supporting my results in the context of relevant literature is that multiple factors contribute to the determination of microhabitat distributions (Rydin 1985; Thum 1986; McQueen 1990; Svensson 1995; Rydin 1993; van Breemen 1995), and in Mud Lake Bog factors other than pH are more important for *D. intermedia*.

Higher densities of *D. intermedia* in quadrats with higher conductivity support my hypothesis that *D. intermedia* would occur in hollows, as hollows tend to be higher in nutrients than hummocks (McQueen 1990). However, because conductivity was measured in the same manner as pH, only once per quadrat in a hollow, this finding is subject to a similar potential

error as the pH finding. Like for pH, conductivity measurements were made according to this assumption of similar conductivity gradients between all quadrats. Future studies should use modified methods to compare measurements of pH and conductivity between hollows and hummocks for more conclusive results.

That no relationship between *D. intermedia* density and dissolved oxygen (DO) was found indicates this factor does not limit the microhabitat preferences *D. intermedia* in Mud Lake Bog. This is contrary to my hypothesis that DO would be an important factor in microhabitat preferences of *D. intermedia*. This may explain why past literature seems to discuss low DO as a characteristic of bogs (McQueen 1990), but not as a factor in microhabitat preference for *D. intermedia*.

My results showing no relationship between *D. rotundifolia* density and any of pH, conductivity, or DO suggest that none of these factors influence *D. rotundifolia* microhabitat preferences within Mud Lake Bog. These findings do not support my hypotheses that *D. rotundifolia* would tend to occur on hummocks. Also, the lack of a relationship between *D. rotundifolia* density and DO is contrary to my expectation of the importance of DO in microhabitat preferences of *D. rotundifolia*. This may mean that other factors are more important in determining *D. rotundifolia* microhabitat, such as competitive ability of *D. rotundifolia* with its co-occurring *Sphagnum* (van Breemen 1995; Rydin 1993; McQueen 1990) or ability to benefit from water retention capacities of surrounding *Sphagnum* (Rydin 1985). Here again, conclusions based on measurements of pH, conductivity, and dissolved oxygen are subject to error because of the way they were measured, and should be re-evaluated in future studies in terms of my hummock-hollow hypothesis because they were measured in hollows only.

My results show no significant relationship between the number of sundews present and their species, indicating neither species is more prevalent at Mud Lake Bog. This finding aligns with Thum (1986), who found that *D. intermedia* and *D. rotundifolia* were roughly equally successful. However, the total number of sundews (*Drosera rotundifolia* and *Drosera intermedia* together) was different at different heights above the bog low point, with more occurring at lower heights; this indicates that individuals of *Drosera* (as represented by these two species) can only survive so far above water level. Survival ability at different heights above water level (desiccation tolerance) has been found to be an important factor for bog plants, *Drosera* (Rydin 1985; Thum 1986).

Most importantly, the interaction between species and height suggests that *D. rotundifolia* and *D. intermedia* occur at different heights above the lowest level within Mud Lake Bog, even within short horizontal the distances covered by my quadrats. The interaction between species and height supports my hypothesis that *D. rotundifolia* will occur on hummocks, and that *D. intermedia* will occur in hollows. This indicates that height above water level is a factor in different microhabitat preferences between species. Water content of surrounding *Sphagnum* and desiccation tolerance (McQueen 1990; Thum 1986; Rydin 1985) may be additional factors in microhabitat preferences of *D. intermedia* and *D. rotundifolia*. *D. intermedia* would thus be less tolerant of desiccation than *D. rotundifolia*, and must inhabit the wetter hollow regions of the bog, while *D. rotundifolia* is better able to colonize the drier hummocks. Gradients of pH and conductivity may also contribute to these differences; past studies have found pH and conductivity are lower on the tops of hummocks, and each gradually increases moving towards the bottoms of hollows (van Breemen 1995; McQueen 1990), though my findings for pH differ.

In addition to the possibilities discussed above, and related to desiccation tolerance and height above water level, *D. rotundifolia* may be able to benefit from the higher water retention capacity of hummock species of *Sphagnum* in a way that *D. intermedia* cannot. A similar idea has been demonstrated in *Sphagnum*, with plants of hollow-inhabiting species which happen to occur on hummocks sometimes being able to survive because they can benefit from the higher water retention capabilities of surrounding hummock-inhabiting species (Rydin 1985). It seems this idea of benefit from the water retention abilities of another species could be reasonably extended to interactions between *Sphagnum* and non-*Sphagnum* species to explain *Drosera* vertical distribution occurrence. If this is so, *D. rotundifolia*'s increased ability relative to *D. intermedia* to benefit from water retention properties of surrounding *Sphagnum* suggests that *D. rotundifolia* will occur at greater heights above the water level than will *D. intermedia*. This probably acts in concert with higher desiccation tolerance of *D. rotundifolia*, but could act independently.

My results indicating association between *D. rotundifolia* and red *Sphagnum* spp. (94.5% of *D. rotundifolia* individuals red *Sphagnum*) signify that they share common microhabitat preferences within Mud Lake Bog (Thum 1986; McQueen 1990); my data indicating association between *D. intermedia* and green *Sphagnum* spp. (about 83.5% of *D. intermedia* individuals observed occurred on green *Sphagnum*) signify they also share common microhabitat preferences (Thum 1986; McQueen 1990). This evidence strongly supports my hypothesis that *D. rotundifolia* would grow sympatrically with red *Sphagnum* and that *D. intermedia* would grow sympatrically with green *Sphagnum*. These two strong associations indicate that the *D. rotundifolia*-red *Sphagnum* spp. group and the *D. intermedia*-green *Sphagnum* spp. group each

have differing microhabitat preferences (Thum 1986; Crum 2004; McQueen 1990; Rydin 1993), and the boundary between the microhabitats is rather distinct.

My findings discussed earlier indicate that this boundary may be established by pH differences (McQueen 1990), differences in conductivity (McQueen 1990), desiccation tolerance and height above water level (Thum 1986; Crum 2004), or a combination of these factors. In the context of my findings associating *D. intermedia* with green *Sphagnum*, it makes sense that *D. intermedia* may require higher conductivity than *D. rotundifolia*. Rydin (1993) found that green *Sphagnum* tends to occur in areas of higher conductivity and to have a higher growth rate than red *Sphagnum*. I have found that *D. intermedia* also tends to occur in areas of high conductivity, and that it tends to occur in association with green *Sphagnum*, supporting Rydin's (1993) findings. These findings help to explain the morphological and growth strategy differences between *D. intermedia* and *D. rotundifolia* (Gleason and Cronquist 1991). Since *D. intermedia* tends to occur on green *Sphagnum*, which has a faster growth rate, it must compensate by having its leaves grow more upwards (Gleason and Cronquist 1991); *D. rotundifolia*, on the other hand, in association with slower-growing red *Sphagnum*, can then grow with leaves closer to the ground (Gleason and Cronquist 1991; Rydin 1993).

Additionally, it has been suggested that species of *Sphagnum* tend to occur not where the conditions are most optimal for their growth and development, but rather where they best outcompete other species of *Sphagnum* (van Breemen 1995; Rydin 1993). This concept may apply not just between *Sphagnum* species, but also between *Drosera* species and between *Sphagnum* and *Drosera* species. Any bog-occurring species (*Sphagnum* or not, including *Drosera*) which can better compete with *Sphagnum* will be more successful than one which cannot compete as well. Though any competition with *Sphagnum* is likely to be asymmetrical

(Svensson 1995), *D. rotundifolia* can probably compete with red (hummock) *Sphagnum* better than *D. intermedia*, and *D. intermedia* can probably compete with green (hollow) *Sphagnum* better than *D. rotundifolia*. This explanation of competition is even more relevant in relation to the above discussion of differential morphology supported by Gleason and Cronquist (1991) and Rydin (1993); *D. intermedia*'s growth strategy is more conducive to competition with faster-growing green (hollow) *Sphagnum* than *D. rotundifolia*'s strategy. Competition may thus be a factor contributing to explanations of vertical distribution and microhabitat preferences of *Drosera* species.

Future studies could address abiotic factors in more detail as discussed above. Another question this study raises is the influence of competition on species interactions between *Sphagnum* and *Drosera*, as well as within both genera. Investigations could also attempt to confirm and further clarify some of Thum's (1986) findings by focusing on differential insect capture between species of *Drosera*, perhaps including its possible relation to microhabitat preferences.

I conclude that *D. rotundifolia* and *D. intermedia* occur in different microhabitats within Mud Lake Bog, and that these microhabitats coincide with the microhabitat preferences of red and green *Sphagnum spp.*, respectively. Factors determining this preference for hummocks or hollows probably include height above nearby low points (perhaps indicative of height above water level and species desiccation tolerance), pH, or conductivity, and may include several elements of asymmetrical competition or other types of interspecies interaction, but probably do not include dissolved oxygen levels.

LITERATURE CITED

- Crum, H. A. 2004. Mosses of the great lakes region. University of Michigan Herbarium, Ann Arbor, Michigan, USA.
- Ellison, A. M., and N. J. Gotelli. 2001. Evolutionary ecology of carnivorous plants. *Trends in Ecology and Evolution* 16:623-629.
- Gibson, T. C. 1991. Competition among threadleaf sundews for limited insect resources. *The American Naturalist* 138:785-789.
- Gleason, H. A., and A. Cronquist. 1991. Manual of vascular plants in northeastern United States and adjacent Canada. New York Botanical Garden. Bronx, New York.
- Krafft, C. C., and S. N. Handel. 1991. The role of carnivory in the growth and reproduction of *Drosera filiformis* and *D. rotundifolia*. *Bulletin of Torrey Botanical Club* 118:12-19.
- McQueen C. B. 1990. Field guide to the peat mosses of boreal north America. University Press of New England, Hanover, Maryland, USA.
- Rigg, G. B. 1940. The development of *Sphagnum* bogs in North America. *The Botanical Review* 6: 666-693.
- Rydin, H. 1985. Effect of Water Level on Desiccation of *Sphagnum* in Relation to Surrounding *Sphagna*. *Oikos* 45: 374-379.
- Rydin, H. 1993. Interspecific competition between *Sphagnum* mosses on a raised bog. *Oikos* 66: 413-423.
- Steven, G., and J. H. Dickson. 1991. The vegetational history of glen diomhan, north arran, site of endemic whitebeams, *Sorbus arranensis* Hedl. and *S. pseudofennica* E.F. Warb. *New Phytologist* 117: 501-506.
- Svensson, B. M. 1995. Competition between *Sphagnum fuscum* and *Drosera rotundifolia*: a case of ecosystem engineering. *Oikos* 74: 205-212.
- Thorén, M. L., J. Tuomi, T. Kämäräinen, and K. Laine. 2003. Resource availability affects investment in carnivory in *Drosera rotundifolia*. *The New Phytologist* 159:507-511.
- Thum, M. 1986. Segregation of habitat and prey in two sympatric carnivorous plant species, *Drosera rotundifolia* and *Drosera intermedia*. *Oecologia* 70:601-605.
- van Breemen, N. 1995. How *Sphagnum* bogs down other plants. *Trends in Ecology and Evolution*. 10: 270-275.

FIGURES AND TABLES

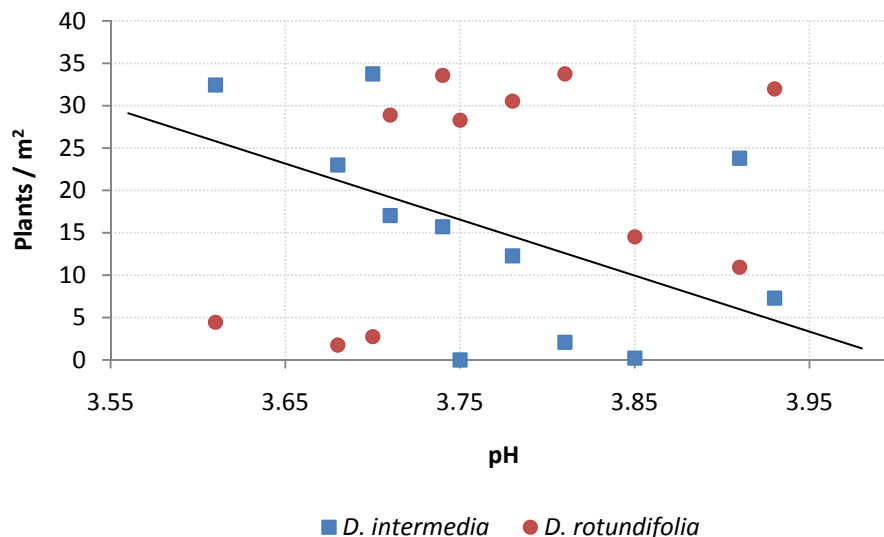


Figure 1. Densities of *D. rotundifolia* and *D. intermedia* as a function of quadrat pH. There was no significant relationship between pH and *D. rotundifolia* density, while there was a significant negative relationship between pH and *D. intermedia* density ($r^2=.286$, $N=11$, $p=.005$).

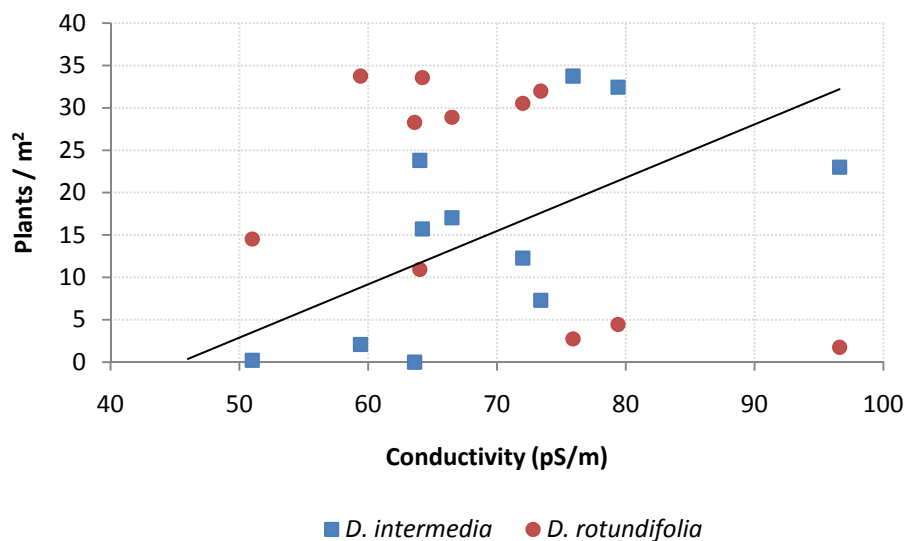


Figure 2. Densities of *D. rotundifolia* and *D. intermedia* as a function of quadrat conductivity. There was no significant relationship between conductivity and *D. rotundifolia* density, while there was a significant positive relationship between conductivity and *D. intermedia* ($r^2=.386$, $N=11$, $p=.018$).

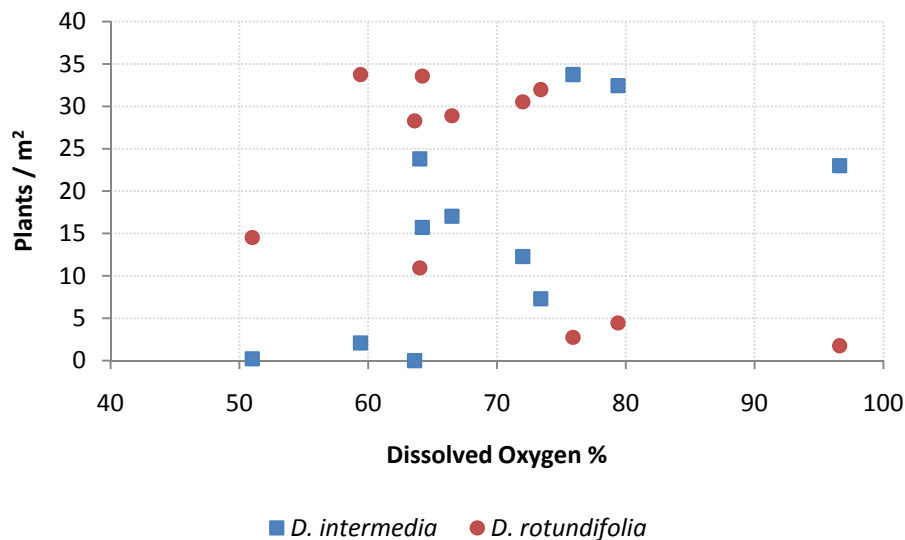


Figure 3. Densities of *D. rotundifolia* and *D. intermedia* as a function of dissolved oxygen content. There was no significant relationship between either *D. rotundifolia* density ($r^2=.266$, $N=11$, $p=.864$) or *D. intermedia* density ($r^2=.386$, $N=11$, $p=.188$).

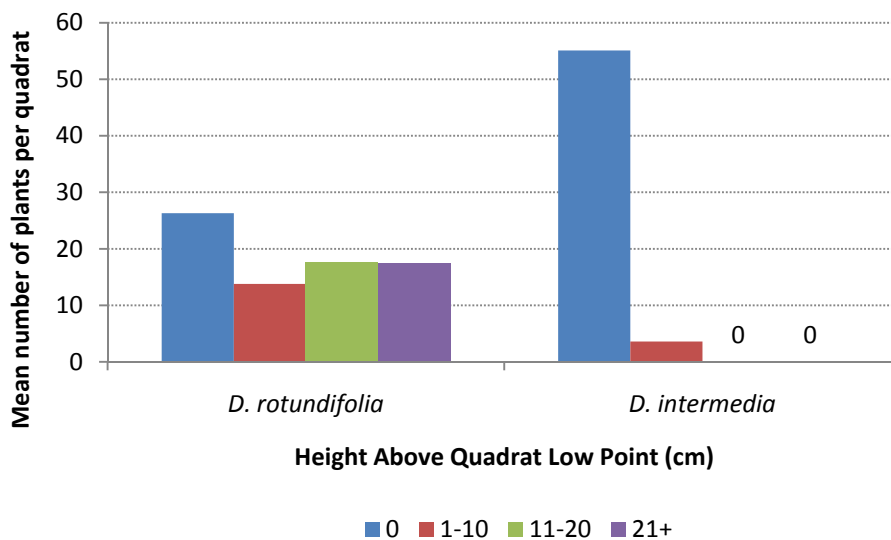


Figure 4. Mean number of *D. rotundifolia* and *D. intermedia* plants as a function of height above quadrat low point (divided among four categories: 0 cm, 1-10 cm, 11, 20 cm, and 21+ cm). Both species showed a significant decrease in number as height increased, though their specific distributions were significantly different (see Table 1).

Table 1. Results from 2-Way ANOVA of the number of *Drosera* plants testing for the effects of species, height category, and an interaction between these two factors. There was no significant difference in the number of plants of each species, but there was a significant difference in the number of plants in each height category. In addition, there was a significant difference in the species-specific distribution of plant heights.

	F	df	p
Species	1.47	1, 42	.23
Height category	5.86	3, 42	.002
Species * height category	6.45	1, 42	.015

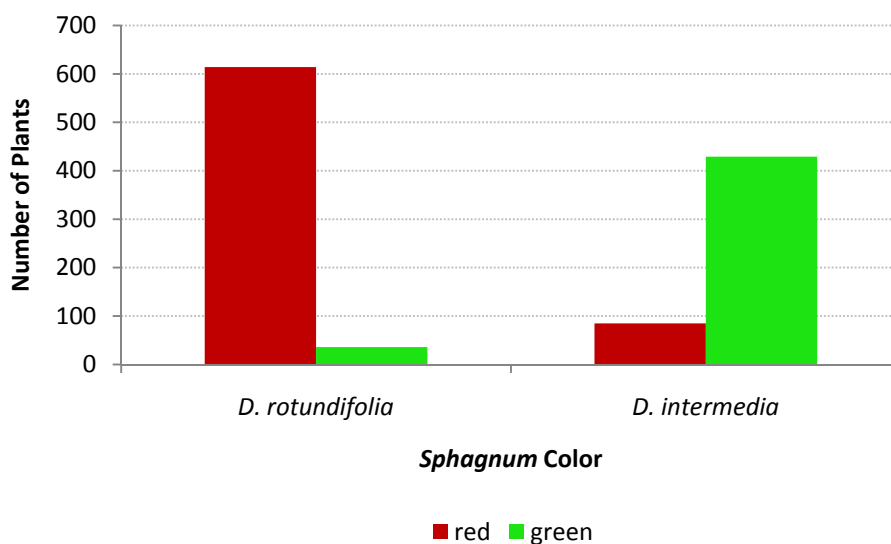


Figure 5. Number of *D. rotundifolia* and *D. intermedia* plants growing on red and green *Sphagnum*. There was a significant association between *Drosera* spp. and *Sphagnum* color ($\chi^2=726$, $df=1$, $p<.001$).

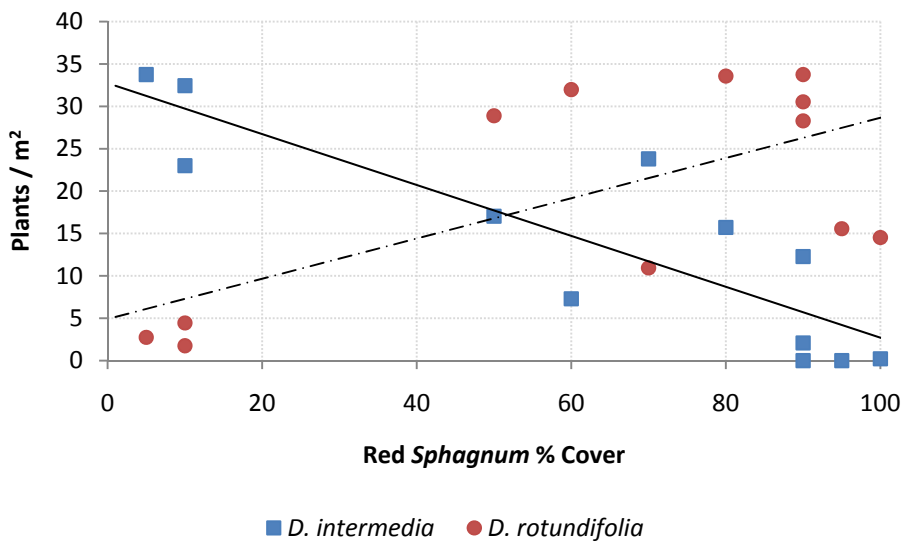


Figure 6. Densities of *D. rotundifolia* and *D. intermedia* as a function of the percent cover of red *Sphagnum* in each quadrat. There was a significant positive relationship between percent cover and *D. rotundifolia* density ($r^2=.446$, $N=12$, $p=.018$), and a significant negative relationship between percent cover and *D. intermedia* density ($r^2=.750$, $N=12$, $p<.001$).