INTRODUCTION

Carnivory in plants has long been a topic of interest in the field of ecology, likely because it is such a unique and fascinating adaptation that goes against the normal, photosynthetic manner in which most plants acquire nutrients. It is an adaptation that allows certain species of plants to occupy habitats deficient in nutrients to the degree 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 is deficient in nitrogen, these species of plants can still survive (Ellison and Gotelli 2001). Due to this adaptation, we see carnivorous plants in highest numbers and diversity in low-nutrient environments, such as bogs, which are bodies of water generally low in nutrients, pH, and dissolved oxygen (DO) and are covered in large part by a floating layer of *Sphagnum* moss (*Sphagnum spp*.) (Ellison and Gotelli 2001).

Besides being nutrient poor, bogs are generally bright environments, lacking in larger vascular plants capable of shading out smaller species. Carnivorous plants are also found in such environments because the development of carnivorous adaptations is energy intensive; one tradeoff is between carnivory and photosynthesis. Carnivorous plants tend to have comparatively low maximal photosynthetic rates (Ellison and Gotelli 2001), which explains the tendency to find them in areas with high light levels. When they are in such environments, their photosynthetic rates can be maximized to lower the necessary energy investment in carnivory (Thorén et al. 2003). In environments which are less nutrient-stressed, having a higher percentage of plants more heavily invested in photosynthetic abilities, carnivorous plants would easily get shaded out by these larger, faster-growing plants, lowering their already limited photosynthetic capabilities, and have further inhibited growth in environments richer in nutrients (Ellison and Gotelli 2001).

This adaptation in favor of carnivory over nutrient-rich soils was exemplified in a feeding experiment performed on sundews (*Drosera spp.)* which showed no positive correlation between feeding via increased soil fertility and either growth or reproduction rates, however did show a positive correlations between increased insect feeding and the growth and reproductive rates of the plants (Krafft and Handel 1991). This study in particular demonstrates the adaptation at work in this genus of plants; it is so highly adapted to surviving in its environment through carnivory that, even if it is presented with advantageous soil conditions, the fitness of the plant is not improved by them.

Sundews, besides occurring in bright, nutrient-poor environments, tend to occur in fairly low densities because of high rates of intraspecific competition for insects when the plants are in dense clusters (Gibson 1991). Intraspecific competition for food as well as microhabitat has resulted in niche differentiation between different species of sundew (Thum 1986). Illustrating this difference is an experiment comparing two *Drosera* species (*D. rotundifolia* and *D. intermedia*) in a bog environment in Germany; the study showed that 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 mounds of *Sphagnum* moss called hummocks, whereas *D. intermedia* lived in the lower, more water-logged areas of *Sphagnum* between the hummocks, called hollows (Thum 1986).

The *Sphagnum* moss, with which the sundews grow, has been shown to have a significant impact on sundew distribution. The *Sphagnum*, however, is not merely a plant that is well adapted to the same conditions as are carnivorous plants, but is an “ecosystem engineer,” – an organism that alters the surrounding environment to increase its fitness (van Breemen 1995).

While all *Sphagnum* species share this same general tendency, there is significant interspecies competition such that they end up occupying microhabitats where they have the competitive advantage, not necessarily where they are the most productive (van Breemen 1995). This leads to a wet to dry gradient, or hummock-hollow sequence, where comparatively high areas in the *Sphagnum* mat are created by the *Sphagnum* species themselves, allowing different species to flourish at varying heights above the waterline (McQueen 1990). Specifically, it has been found that green species of *Sphagnum* are generally found in the lowest, most water-inundated areas of the mat, while colored species, usually a variation of red, are found to grow in the higher areas on top of hummocks (McQueen 1990). The reason for this difference lies in the different species' abilities to retain water as green species have little ability to do so and must remain effectively water-logged to survive, whereas red species can retain water more effectively and are able to live further above the water line without being subject to desiccation (Rydin 1985). This difference in adaptation was evaluated in a long-term study (Rydin 1993) where hummock species of *Sphagnum* were transplanted to hollows, and the hollow species were transplanted onto hummocks; when each were transplanted, the hollow species dried up as they were unable to deal with a lower water level, while the hummock species survived and slowly re-built a hummock habitat by growing atop its own dead matter (Rydin 1993).

While this intraspecies competition amongst *Sphagnum* species indirectly affects sundews through microhabitat alteration, direct intraspecies competition between *Sphagnum* and sundews, specifically the *Sphagnum fuscum* and *Drosera rotundifolia*, has been observed as well (Svensson 1995). The *S. fuscum* was found to have a competitive advantage as the *D. rotundifolia* was found to grow, either laterally or vertically, in response to the growth rate of the *S. fuscum* in order to avoid being covered over, reducing accessibility to insects and light

(Svensson 1995). Considering this fact that the sundew's growth rate is responsive to that of the *Sphagnum*, the relationship between them, then, is an integral facet in the evaluation of sundew microhabitat distribution; the *Sphagnum* not only creates the sundew's microhabitats though intraspecific competition by creating height variability in the mat (McQueen 1990), but also has been shown to directly affect the sundews themselves through interspecific competition (Svensson 1995).

Two species of sundew native to the bogs of Northern Michigan, *Drosera rotundifolia* and *Drosera intermedia*, will be the subjects of my study. They are both very small plants, measuring no more than six centimeters in diameter with leaves arranged in a basal rosette and grow very near the ground in the case of *D. rotundifolia* and in a more raised position in *D. intermedia* (Gleason and Cronquist 1991). The leaves themselves are sometimes modified to be active traps for insects, but are more frequently covered with irritable, mucilage-tipped tentacle-hairs called trichomes which function to passively trap insects, and its cymes of dainty white florets are held well above its leaves to avoid trapping potential pollinators (Gleason and Cronquist 1991). Of species of *Sphagnum* moss, two species of green, *S. cupisdatum* and *S. angustifolium*, and two species of red, *S. fuscum* and *S. magellanicium*, are known to exist in large quantities in Inverness Mud Lake Bog (Crum 2004), the site of my northern Michigan study.

In my study, I investigated the vertical distributions of both species of *Drosera rotundifolia* and *Drosera intermedia* within Inverness Mud Lake Bog, as well as their respective relationships to microhabitat features including *Sphagnum* color and species, and as the abiotic factors of conductivity, DO, and pH. Citing the general tendencies of carnivorous plant species as well as those found specifically concerning species of *D. rotundifolia* and *D. intermedia*

(Gleason and Cronquist 1991), I expect to find both *Drosera* species in open areas of the nutrient poor bog in low instraspecific densities, with the *D. rotundifolia* showing a preference for higher, drier areas (hummocks), and *D. intermedia* for lower, wetter ones (hollows). Due to its wetter habitat preference (Gleason and Cronquist 1991), I also expect the *D. intermedia* to be tolerant of conditions comparatively lower in pH, DO, and conductivity than is *D. rotundifolia*. Finally, as a correlation has been found between green *Sphagnum* and lower height levels as well as red *Sphagnum* and higher ones (McQueen 1990), I expect to find positive correlations between *D. intermedia* density and the presence green *Sphagnum* species, and *D. rotundifolia* and the presence of red *Spagnum* species.

METHODS

I studied the vertical distribution and microhabitat variations of *D. rotundifolia* and *D. intermedia* at the southern end of Inverness Mud Lake Bog in northern Michigan's Cheboygan County. Inverness Mud Lake Bog is located east of Pellston, MI, and the southern end is managed by the Little Traverse Land Conservancy with allowance onto the property granted only for educational or research-related purposes. The bog itself is covered by a *Sphagnum* mat between the shoreline and a line of trees dissecting the middle of the bog; on one side of the tree line is open water and a comparatively young sphagnum mat, and on the other is an older, uninterrupted sphagnum mat. It is in this older, contiguous section of the bog that I conducted my study.

I selected twelve quadrats which were each anchored with one hummock in a corner and side lengths measuring approximately double the diameter of the selected hummock, which typically comprised between 25 and 50 percent of the 4 square meter quadrat. Of the twelve quadrats, I placed 6 in areas with predominantly red *Sphagnum* species, and 6 in areas with predominantly green.

For each quadrat, I measured the actual perimeter to determine the area within each quadrat and then estimated a percent coverage of red and of green *Sphagnum* moss. Next, for each *Drosera* plant, I noted the species, either *D. rotundifolia* or *D. intermedia*, as well as the color of *Sphagnum* on which it is growing. Additionally, I measured the height at which each plant was growing above the lowest point of the quadrat. I measured this height by use of meter sticks, with one held vertically and the other being perpendicular (through the use of a level) to the ground and extending to the given plant being measured. I measured the abiotic factors last as to avoid unnecessarily standing within the quadrats and crushing the sundews. Lastly, I measured pH, DO, and conductivity with handheld digital meters by standing in a randomly selected place within each quadrat and depressing the bog mat until enough bog-water had collected to completely submerge the given test probes.

To evaluate the effect of height on sundew distribution, the heights at which sundews occurred were broken into four increasing categories of height (0, 1-10, 11-20, and 21+ cm) and tested by 2-way ANOVA by which variables of species, height category and the interaction term between them were analyzed. Linear regressions were run to test for correlations between the densities of the two *Drosera* species, and the abiotic factors of pH, DO, and conductivity as well as the percent of red and green sphagnum cover. Finally, a chi square test was run to evaluate whether there is an association between the species of sundew and the color of *Sphagnum*.

RESULTS

In comparing the variables of sundew species and height categories, it was found that there was no trend in total numbers sampled of either species (Table 1). This can be understood as the sum of all four height categories within one species does not appear to be greatly different from the other (Fig 1). There was, however, a significant difference found considering the height category (Table 1), as clearly larger numbers of sundews of both species were found at the lowest height category (Fig 1). A significant difference was also observed in the interaction between the species and height category variables (Table 1) as the progression from one height category to the next within each species is obviously dissimilar (Fig 1).

The first abiotic factor analyzed, pH, showed a significant negative correlation with the density of *D. intermedia* (Fig 2; r^2=.286, N=11, p=.005), but no trend with *D. rotundifolia*. It can be seen that, as pH increased, the density of *D. intermedia* fell. Additionally as conductivity rose, again there was no obvious trend relative to *D. rotundifolia*, however there was a significant positive correlation between the density of *D. intermedia* conductivity readings (Fig 3; r^2=.386, N=11, p=.018). There were no observable trends found in either species in relation to the DO data (Fig 4).

A significant difference between the *Drosera* species was also found reference to which color of sphagnum on they are respectively growing (Fig 5; χ^2=726, df=1, p<.001). A vast majority of *D. rotundifolia* were found on red sphagnum, and *D. intermedia* were predominantly found on green. There was also a strong relationship between the densities of each species and the percent cover of red and green *Sphagnum* (Fig 6). As the percent cover of red *Sphagnum* increased the density of *D. rotundifolia* showed a significant positive correlation (r^2=.446, N=12, p=.018), and inversely, *D. intermedia* showed a significant negative correlation to decreasing cover of green *Sphagnum* (r^2=.750, N=12, p<.001).

DISCUSSION

When considering the results from the two variable comparison between the two species and the different height categories, it is actually encouraging that the first aspect, which is testing to see whether there is a significant difference in total numbers of plants sampled in each species, was found to be statistically insignificant (Table 1). With similar total numbers sampled of each species, the other two variables within the same test, as well as many of the others, can thus be interpreted without considering the implications of grossly differing sample sizes between the two. The second variable considered within the same statistical analysis was height, or height category, which found a statistical difference between the height categories of the two species combined. In examination of the data (Fig 1), it is shown that, in both *D. rotundifolia* and *D. intermedia*, plants occurred with greatest frequency at a height of 0, and *D. intermedia* ceased to appear in significant quantities beyond this category, and at all beyond 10 centimeters in height; considering these two facets alone, the significant difference is clear. Finally, and perhaps most importantly relative to the study, the interaction term, one that evaluates whether there is a difference between the heights between species, was also found to be significant. Returning to the data (Fig 1), it is true that both species occur most frequently at 0 cm of height, but *D. rotundifolia* continues to appear in large quantities through the largest height category, while *D. intermedia* barely occurs at any increased height at all. The significance of this statistical analysis is in support of my first hypothesis that predicts *D. rotundifolia* to show preference for higher areas, and *D. intermedia* to show preference for lower areas.

These findings agree in important ways with those of Thum 1986, who surveyed the microhabitat differences between the same two species in a similar *Sphagnum* mat bog, and also found *D. rotundifolia* to occur most frequently on higher areas and *D. intermedia* at comparatively lower heights. Further, Thum's study found a nearly equivalent biomass of each of the species despite their respective preferences for different heights. While my finding of an insignificant difference in numbers of each species sampled certainly cannot be deemed substantiating evidence of a the same finding, but it speaks more towards similarity than it does difference. When comparing my actual data to these findings, the preference of *D. intermedia* is overwhelmingly congruous with Thum's results, but *D. rotundifolia* isn't quite as strongly comparable. It can be said that *D. rotundifolia* shows a preference for some level of height above zero, because if all height categories beyond zero are summed, there were markedly more found in the combined non-zero categories, and the results can be said to be similar. However, if each height category is to be evaluated individually, the greatest numbers of *D. rotundifolia* were actually found at a height of zero.

Perhaps explanatory of this possible point of contention between my findings and those of Thum's begins with the fact that, in addition to evaluating height differences, Thum evaluated the age differences of the *Sphagnum* mat upon which the species were growing. This fact, one that went unmeasured in my study, is an important one when considering the aging process of *Sphagnum* moss. It has been found that differences in mat thickness can occur within an area of the same general age as a result of interspecific competition (McQueen 1990), and also, the mat thickens and becomes drier with age as a natural part of succession (Crum 2004). With this in mind, the occurrence of *D. rotundifolia* on a height of 0 in one quadrat, may be a significantly different microhabitat than a height of 0 on another. Without a practical way to measure mat thickness, age, or moisture, I used "height above the lowest point" methodology to quantify these microhabitat differences, and considering the results to bear considerable similarity to the study of Thum 1986, a comparatively high number of *D. rotundifolia* occurring in the lowest height category is reasonably attributable to the unknown age and thickness differences between quadrats.

The second grouping of measurements and statistical analyses evaluated the abiotic factors of pH, conductivity, and DO. The pH data showed the density of *D. intermedia* to be negatively correlated with an increase in pH, meaning more *D. intermedia* were sampled per square meter where conditions were more acidic (Fig 2). Also, there was also a correlation between *D. intermedia* and conductivity, this one positive (Fig 3), indicating that as conductivity rose, so did the density of *D. intermedia*. Conversely, there were no significant trends to be found between *D. rotundifolia* and either of the aforementioned factors, nor were there between either species and DO (Fig 4). My second hypothesis, which predicted that, due to is lower and wetter habitat, *D. intermedia* was not wholly supported by the data though there are some interesting connections to be made.

To begin, the fact that the density *D. intermedia* is negatively correlated with increasing levels of pH, meaning a higher percentage of the plants are living in more acidic conditions is in support of my hypothesis. It is well understood that specific adaptations are needed on the part of plants in order to survive in such acidic conditions (Ellison and Gotelli 2001), and without any correlation between the particularly acidic areas and the *D. rotundifolia* that are not occurring in comparatively higher densities in general, it can be said, from this consideration at least, that the D. intermedia is more adapted, or tolerant, of more acidic conditions. The apparent oppositional finding is, of course, that *D. intermedia* is also positively correlated in density to an increase in conductivity. On an intuitive level, it seems that an association between *D. intermedia* and conductivity, an effective measure of nutrients would indicate a better fitness when in comparatively less harsh environments. This, then, appears oppositional to my hypothesis as well as the conclusions drawn from the previous data set. However, before nullifying the hypothesis completely, it must be remembered that normal plants are not being considered, but carnivorous ones. Recall that in a study by Kraftt and Handel 1991, there was no observed positive correlation between feeding via increased soil fertility and either growth or reproduction rates in sundews. This indicates that more nutrient-rich conditions, as long as this study is specifically applicable, should not affect the plants in a positive manner, indicating some other factor is at work in this case.

This other factor, I believe, has its basis in the findings of the study by Rydin 1993 where, among other things, he found that green *Sphagnum* species had a comparatively higher growth rate than its red counterparts, the reason for which having to do with the tradeoff of having lack of water-retention abilities, thus, being restricted to lower areas (Rydin 1986). Bear in mind, that there is an extremely strong association between *D. intermedia* and the green *Sphagnum* species (Fig 5). This association is especially important when competition is considered, particularly because *Sphagnum* has been shown to have a competitive advantage, with *Drosera spp.* being forced to respond in terms of growth to that of the *Sphagnum* to avoid being overgrown (Svensson 1995). At this point, there are several possible explanations of the original correlation between conductivity and increased *D. intermedia* populations including a negative effect of nutrients on *Sphagnum,* decreasing its growth, because, as an ecological engineer, creates low pH, and low nutrient conditions; this could decrease its growth and lower competition pressure with *D. intermedia*. Or perhaps, in this case, the increased growth rate of both species had an effect of increasing the density of *D. intermedia*, but for less direct causes than simple nutrient increases. Overall, it is clear that there is some reason to consider the merit of the hypothesis that *D. intermedia* is, in fact, more tolerant of certain conditions, but with only a pH correlation and speculation, as well as a complete lack of correlation to DO and *D. rotundifolia* to both pH and conductivity, it must be nullified in this study.

The final statistical analysis was to determine whether there was a significant association between the species of sundew and the color of *Sphagnum* moss. This test yielded convincingly significant associations between *D. rotundifolia* and red Sphagnum and *D. intermedia* and green *Sphagnum* (Fig 5). To supplement this test, an additional regression analysis was run to compare the densities of both sundew species and the two colors of sphagnum; again, a strong relationship between the densities of each species and the percent cover of red and green *Sphagnum* was found (Fig 6). Both of these tests yielded results consistent with my hypothesis that predicted to find positive correlations between *D. intermedia* density and the presence green *Sphagnum* species, and *D. rotundifolia* and the presence of red *Spagnum* species. These results are consistent with the findings of both Thum 1986 and McQueen 1990 who, respectively, found relationships between the height and the presence of *Drosera spp.* and the height and the presence of *Sphagnum spp.*

Ultimately, it can be concluded from this study that the species of *D. rotundifolia* and *D. intermedia* occupy different microhabitats within the bog environment with Sphagnum playing a significant role in this microhabitat creation. Additionally, it is clear that there are correlations between both sundew species and height, as well as *Sphagnum* color and height, but the nature of the correlation between the sundews and *Sphagnum* remains to be further explored.

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 economy 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 Botannical 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.

Rydin, H. 1993. Interpsecific competition between Sphagnum mosses on a raised bog. Oikos 66: 413-423.

Rydin, H. 1985. Effect of water level on dessication of *Sphagnum* in relation to surrounding *Sphagna*. Oikos 45: 374-379.

Svensson, Brita 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*. Oecologica 70:601-605.

van Breemen, N. 1995. How Sphagnum bogs down other plants. Trends in Ecology and Evolution. 10: 270-275.

FIGURES AND TABLES

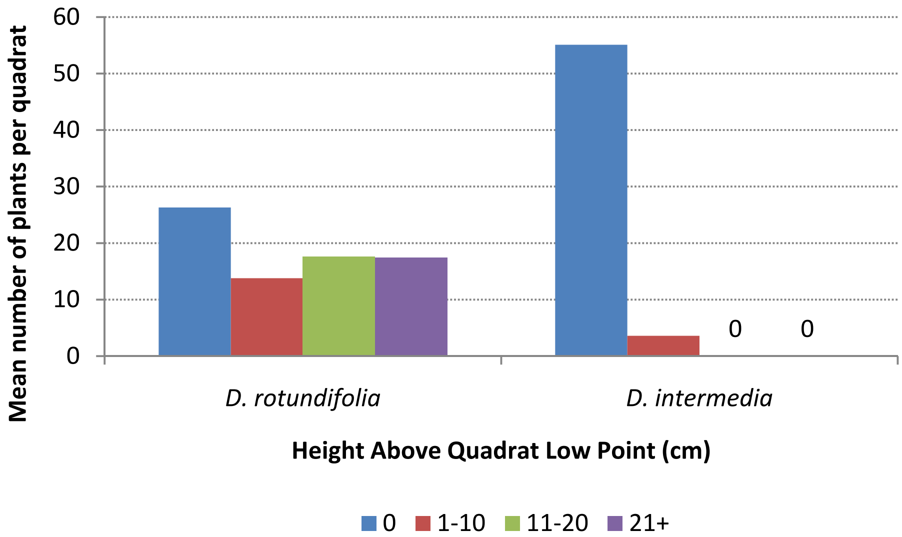

Figure 1. Mean number of *D. rotundifolia* and *D. intermedia* plants per quadrat for the four height categories above quadrat low point. Both species showed a significant decrease in number as height increased, although their specific distributions were significantly different (see Table 1).

Table 1. Results from 2-Way ANOVA of the number of *Drosera* plants per quadrat, testing for effects of species, height category, and the interaction between species and height category. 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 interaction between species and height category in number of sundews.

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

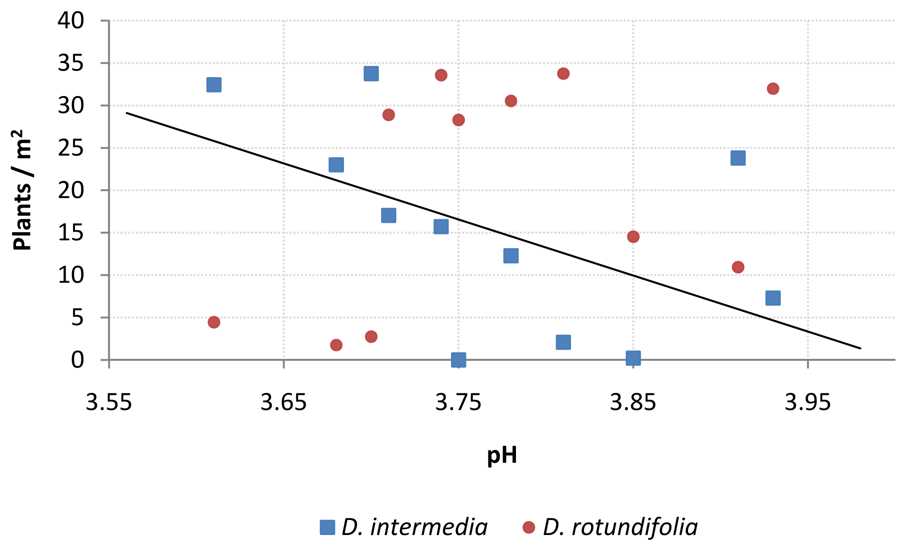

Figure 2. Densities of *D. rotundifolia* and *D. intermedia* in quadrats (plants/m^2) as a function of pH. There was no significant relationship between pH and *D. rotundifolia* density (r^2=.153, N=11, p=.235), while there was a significant negative relationship between pH and *D. intermedia* density (r^2=.286, N=11, p=.005).

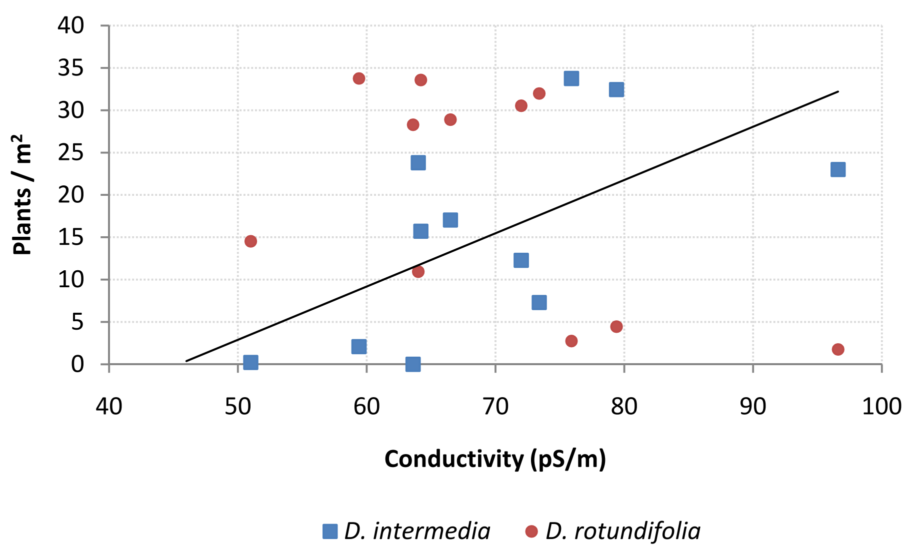

Figure 3. Densities of *D. rotundifolia* and *D. intermedia* in quadrats (plants/m^2) as a function of conductivity. There was no significant relationship between conductivity and *D. rotundifolia* density (r^2=.266, N=11, p=.104), while there was a significant positive relationship between conductivity and *D. intermedia* (r^2=.386, N=11, p=.018).

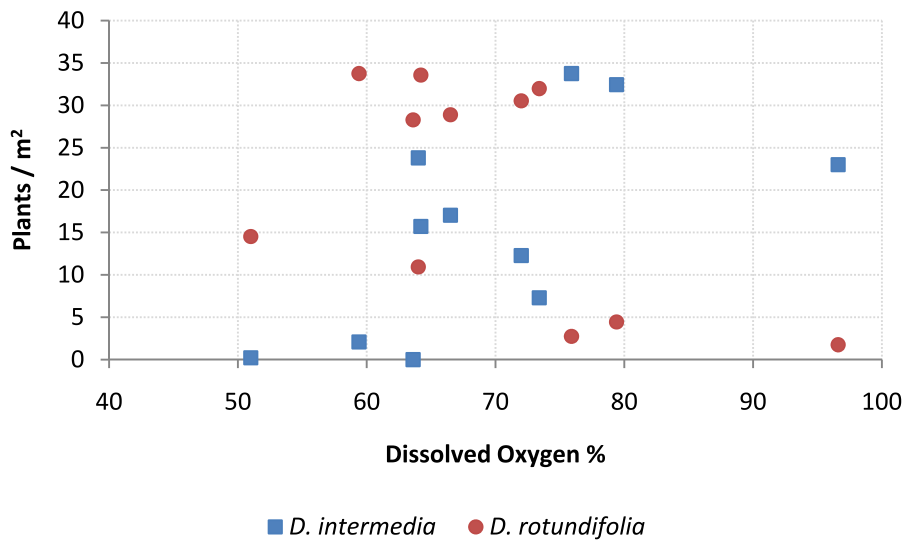

Figure 4. Densities of *D. rotundifolia* and *D. intermedia* as a function of dissolved oxygen content. There was no significant relationship between either *D. rotundifolia* density (r^2=.266, N=11, p=.864) or *D. intermedia* density (r^2=.386, N=11, p=.188).

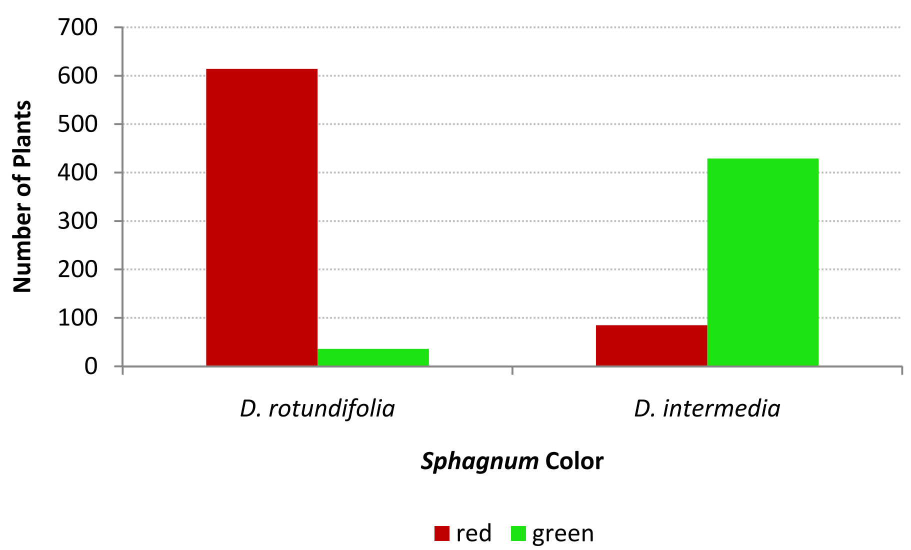

Figure 5. Number of *D. rotundifolia* and *D. intermedia* plants growing on red and green *Sphagnum*. There was a significant association between *Drosera* species and *Sphagnum* color (χ^2=726, df=1, p<.001).

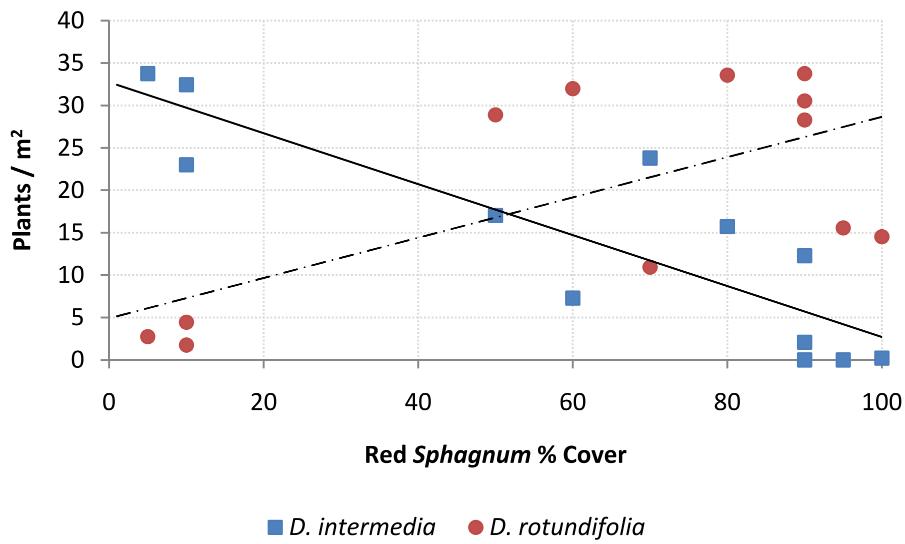

Figure 6. Densities of *D. rotundifolia* and *D. intermedia* as a function of the percent cover of red *Sphagnum* in each quadrat. There was a significant positive relationship between percent cover and *D. rotundifolia* density (r^2=.446, N=12, p=.018), and a significant negative relationship between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