Shade, reproductive effort and growth of the endangered native cactus, *Opuntia humifusa* Raf. in Point Pelee National Park, Canada[1]

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Abstract. *Opuntia humifusa* (eastern prickly pear cactus) is an endangered species in Canada, found principally in only one remaining location nationally, at Point Pelee National Park (PPNP). This study quantifies fruit and flower production in the population, the pad yellowing phenomenon that has been observed, overlying coverage and shade, and a variety of plant size metrics in order to assess the relationships between these factors. A variety of parametric (ANOVA, Pearson product-moment correlation, *t* tests) and nonparametric (Spearman's rank correlation, Kruskal-Wallis test) statistical analyses were conducted. Pad yellowing, a presumed sign of ill health, was not significantly related to any aspect of plant size or reproduction, and was statistically related only to shade (less yellowing with greater shade). Shade also affects plant height, with taller plants associated with greater shade. Reproductive effort is lower in shadier sites, and shade also appears to delay reproduction to later in the season. Published research generally suggests that increases in sexual reproduction are a sign of stress, suggesting an overall decrease in stress in the cactus population in the Park. However, I observed that reproduction decreased with shade, and increasing shade is known to cause population decline, making the effects of light stress at PPNP difficult to determine.

Key words: cactus (Cactaceae), conservation, endangered species, fish-eye photography, reproduction

Opuntia humifusa (Raf.) Raf. is a member of the Cactaceae family that is also known as eastern prickly pear, synonyms include *Opuntia compressa* and *Opuntia cespitosa* (Weakley in press). It is listed as endangered, the highest level of classification after extinct and extirpated, by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), which describes such species as "facing imminent extirpation," and it has been placed on the list of species at risk (SARA). *Opuntia humifusa* is only found in two places in all of Canada today, though there are historical records of it elsewhere in Ontario (Reznicek 1982), and it is known to tolerate more extreme, colder climates (Gorelick, Drezner, and Hancock 2015). The Fish Point Provincial Nature Reserve on Pelee Island is a very small population, with perhaps as few as six (numbers vary over time) individuals (Van Der Wal *et al.* 2006). Most plants are found in the only other Canadian location, at

Point Pelee National Park (PPNP), where two genetically distinct subpopulations (element occurrences) are found (Lovett-Doust *et al.* 2003).

Several studies, primarily unpublished, have been conducted at PPNP on this endangered species. Number of plants, pads, and other measures of cactus presence have been quantified at PPNP (*e.g.,* Ross 1971; Jock 1984; Chiarot 1992; Whitehead 1995; Swain 1998; VanDerWal *et al.* 2006), though VanDerWal *et al.*'s (2006) most recent survey yielded high numbers of plants, which suggests that past surveys likely underestimated the number of plants from less thorough sampling. VanDerWal *et al.* (2006) use historical data to estimate population size, noting not more than 60 microsites (24,000 pads) in 1971, and in secondary succession, average microsite size declined from 352 to 79 pads between 1995 and 2005. Between 1984 and 2004, a series of studies recorded the number of microsites over time. In the first study (1984), 258 microsites were recorded; subsequent studies recorded 290, 293, 306, 309, 310, and, in 2004, 345 microsites were recorded (adjusted estimates by VanDerWal *et al.* 2006). The number of pads per microsite (a group of closely spaced individuals; see Field Methods) has been substantively declining since 1995 due either to increasing juvenile recruitment or decline of larger and older microsites through successional closure of the canopy (VanDerWal *et al.* 2006). Due to the shrinking size of microsites, fruit production per microsite has decreased, but,

number of fruits per pad has been increasing (VanDerWal *et al*. 2006). Decreasing numbers of pads combined with increasing sexual reproduction, particularly in secondary succession where canopy closure continues, is a suggested sign of stress (VanDerWal *et al*. 2006, and references cited therein). Past work at PPNP suggests that most new plants establish vegetatively from dislodged cladodes (Jock 1984; Swain 1998). Vegetative reproduction is more effective than sexual reproduction in other populations as well (Baskin and Baskin 1977).

Various adaptations are evident in this wide-ranging species to deal with seasonal cold and competition with other plants. *Opuntia humifusa* ranges from Alabama to Ohio (Jennings 1908; Noelle and Blackwell 1972) and New Jersey (Hanks and Fairbrothers 1969a), and sites in between (*e.g.*, Baskin and Baskin 1977), though it is found primarily in sunny, relatively dry sites locally with sandy and well-drained soil. Its success in xeric microsites may be related to competition as a Crassulacean acid metabolism plant, though limited data are available to confirm this. As a CAM photosynthesizer, *O. humifusa* would have the greatest competitive advantage in those sites that are driest, compared to C_3 and C_4 plants, and with *O. humifusa*'s prewinter strategy of reducing water volume, more xeric sites would also limit winter injuries (Koch and Kennedy 1980).

High levels of shade have been found to be detrimental to *O. humifusa*, which has low survivorship and strong etiolation response (elongation of pads) in very low light levels (*e.g.*, 90% shade), and thus, plants grow taller (Lovett-Doust and Levi 2003; VanDerWal *et al*. 2007). Chiarot (1992) suggested that *O. humifusa* need at least 30% light for survival. Abella and Jaeger (2004) report *O. humifusa* in northern Ohio are not found in areas with more than 50% canopy cover. As succession progresses, the canopy matures and light levels decrease, resulting in poorer conditions for *O. humifusa* (VanDerWal *et al*. 2006).

Over many decades, research at PPNP has quantified abundance, population increases, and other aspects of ecology of this cactus, but little is known about pad yellowing (observed casually by PPNP staff) and other aspects of the species' health. In fact, little has been published about the species in Canada beyond anecdotal observations and government reports associated with its endangered status. There is a general need for more information about individual and population health and reproduction and possible indicators, along with general information about possible linkages between these variables, particularly in this northern population at the periphery of its range. Management actions to protect and help maintain and recover the population within the Park are possible as there are threats to the species that can be mitigated (T. Dobbie, Park Ecologist, personal communication).

This study has several purposes. This study aims to provide data for a site with little published information, focusing on understanding the relationships between plant size, shading, reproduction, and the poorly studied yellowing of pads observed in some individuals. More specific questions to be tested include: (a) how does shading affect reproductive effort, (b) is the yellowing observed on these plants related to shade and solar radiation receipt, and (c) are yellowing and reproductive effort linked? Although plant health is not specifically assessed in the current study, some insight may be gleaned about stress through this study's assessment of yellowing and of sexual reproduction, which may be responsive to stress and overall plant health, and shade, which is itself an important component of the success and failure of *O. humifusa* populations. An increase in yellowing and in sexual reproduction would imply increased stress in the population, which, based on past work, should be greatest (stress, reproduction) in high and low shade, and greatest population health (least sexual reproduction and yellowing) should occur in low to moderate levels of shade.

Materials and Methods. Study Site. Point Pelee, Ontario, is a peninsula that extends southward into Lake Erie. Point Pelee National Park (PPNP) contains the southern portion of this peninsula, including the southernmost point in continental Canada, with land south of the 42nd parallel. Data from Environment Canada for the nearby Kingsville Moe, ON (climate ID# 6134190), Canada, weather station (42°2′35.064″N, 82°40′26.088″W) show that mean rainfall in July is 84 mm, and average precipitation is about 900 mm annually (30-yr normals, 1981–2010). Average daily high temperatures are −0.3 °C in January and 26.8 °C in July. In 2014, mean maximum temperature in July (recognizing that data collection was complete before the

end of the month) was 24.5 °C and 25.4 °C in June. Total rainfall in July of 2014 was 83.9 mm, but this sum is from only 24 days of data available for these days from Environment Canada.

In PPNP, *O. humifusa* is found exclusively on sand spit savanna environments in varying successional stages (VanDerWal *et al*. 2007). *Opuntia humifusa* is concentrated primarily in two areas naturally, one near the beach on the west side of the peninsula in an area known as West Beach (WB). This is a primary successional red cedar (*Juniperus virginiana*) savanna (VanDerWal *et al*. 2007). About 2 km north of WB is the DeLaurier Homestead (DeL), home to most of the remaining natural (not planted) cacti. This area was abandoned nearly a century ago, and represents a secondary successional savanna environment (VanDerWal *et al*. 2007) whose openness has been maintained through managed clearing (cutting), as the closure of the canopy is known to be detrimental to the natural *Opuntia* populations (*e.g*., Kraus 1991; Chiarot 1992). The DeL site has a more developed A horizon with organic matter buildup after historical use (Lovett-Doust and Levi 2003), and elevated soil nutrients in the secondary succession (VanDerWal *et al*. 2006). This species is generally found on sandy, well-drained soils. At PPNP, proportion of moisture, organic matter, concentrations of N and P are higher in the secondary successional habitat than in the primary successional habitat, and pH was closer to neutral, while K was higher in the primary successional habitat (VanDerWal *et al*. 2007).

The WB and DeL populations have been shown to be genetically distinct (not requiring taxonomic distinction) using amplified fragment length polymorphism (AFLP), which produces genomic fingerprints (Lovett-Doust *et al*. 2003). DeLaurier Homestead is inland on the peninsula and is comprised of two distinct areas or "patches" of plants that are perhaps 100–200 m apart, separated by the local roadway, parking lot, and some buildings. These two areas that together represent DeL are identified as DeLaurier North (DN) and DeLaurier South (DS).

Field Methods. In July 2014, *O. humifusa* data were collected for 100 plants from natural populations (not planted ones) at WB ($n = 50$) and at DeL ($n = 50$), both in the north ($n = 30$) and south ($n = 20$) subpopulations. Identifying and defining a single plant was complicated, as *O. humifusa* is known to spread vegetatively when

cladodes separate from the main plant, fall to the ground or are transported, and then set root. Researchers at PPNP have previously elected to identify so-called microsites, which include all cladodes on a "plant," as well as any plants or cladodes within one meter of the plant (*e.g*., VanDerWal *et al*. 2006). This system has some obvious drawbacks, as two identifiable concentrations of pads (*i.e*., "individuals") whose nearest pads are two meters apart, are readily lumped into one microsite if a single cladode is found midway between them. Many seemingly independent plants are thus classified as a single microsite using this system. The density of plants in some areas may make this approach particularly problematic. In this study, no such one-meter rule was applied. Instead, plants were assessed on a case-by-case basis, based on the distribution of pads and of nearby plants, and particularly large or complex networks were excluded. Unless excluded (noting that the very large networks were), plants were sampled randomly and without any size stratification. Fig.1 (top) is an example of a large individual that is likely made up of several independently rooted plants that established vegetatively when a pad or pads fell and rooted proximally to the original plant. Using the microsite approach, the smaller plant at the very bottom of Fig. 1 (top) would also be included as it is well within 1 m of the edge of the large "plant." This type of indistinguishable plant network would be excluded in the current study. Fig. 1 (bottom) shows four definable plants (some of which may be within 1 m of another) that would have been sampled in the current study, with no reason for exclusion.

Once an individual was identified, data were collected for plant size, reproductive structures, pad yellowing, and vegetation, or rarely, other shade-producing cover. Plant size included the north-to-south as well as the east-to-west diameters of the plant, to the furthest extent of the outermost cladodes excluding spines. Plant height was measured from the ground to the highest cladode point on the plant excluding spines. Finally, number of cladodes for each individual was counted. Two counts were made for larger plants and averaged. These four measures of plant size were sampled as they provide useful information about different aspects of the species' ecology. Height tends to be related to ambient light and other conditions (and could not be used as a reliable surrogate for diameter, for example), while
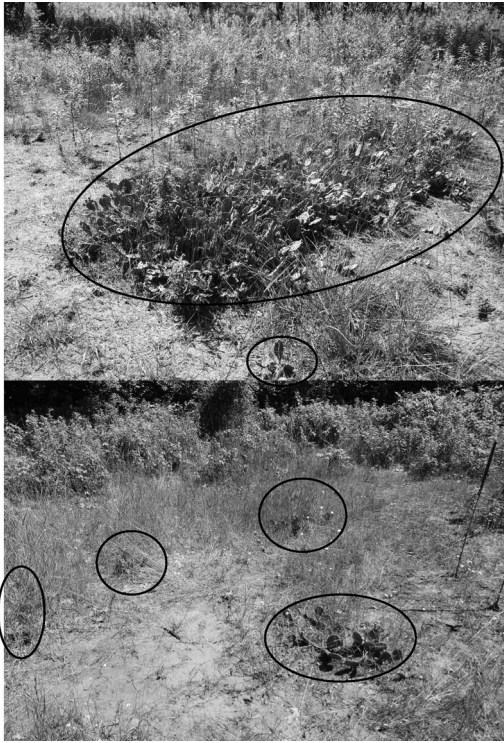
Fig. 1.   *Opuntia* at Point Pelee National Park. Top: A large patch likely made up of several vegetatively formed and indistinguishable individuals. At the bottom of the image, a smaller plant can be seen, noting that it is within 1 m of the larger plant. Bottom: Four distinct plants are visible in the image.
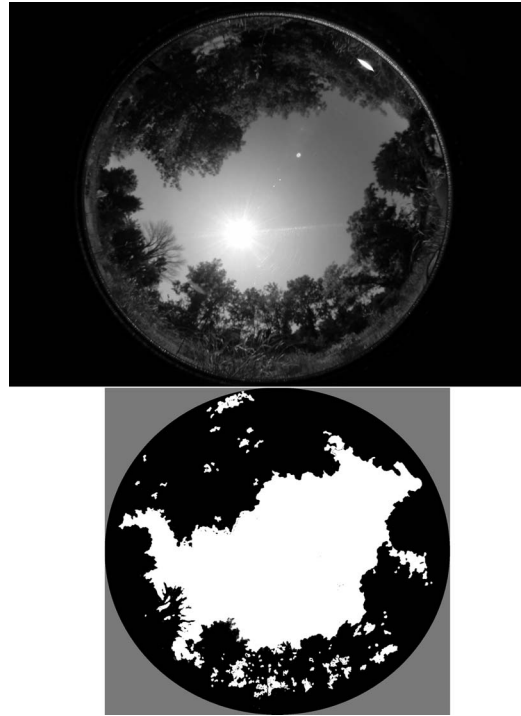

Fig. 2.   An example of a fish-eye image taken at DN. Top: The raw image (original is in color). Bottom: The processed image converted to black (cover) and white (sky) pixels. Gray pixels at the corners are not part of the image and were not counted.

number of pads is important as an overall control for other variables (yellowing, reproductive structures) and absolute vegetative growth. Data for reproductive structures included counting all flowers (including buds) and fruits on each plant. Pad yellowing is often observed in PPNP, and number of pads with yellowing were counted. Any amount of yellow was included in the counts.

A full-sky hemispheric Nikon FC-E8 fish-eye lens (Nikon, Minato, Tokyo, Japan) was placed immediately above the center of the individual facing skyward, immediately above the plant rather than at a fixed height (Fig. 2). Thus, camera height was lower above lower plants. This hemispheric fish-eye approach is efficient (*e.g.*, Drezner 2007) and the upgraded camera and lens used have been found to be accurate for measuring coverage (Grimmond *et al*. 2001). Image processing is described below. Multiple photographs were taken at each plant to ensure at least one image was

not blurry, and on one image, a marker was placed on the lens denoting north.

Statistical Methods. Fish-eye photographs were processed to quantify overlying coverage and shade. First, each image was cropped into a circle representing the full sky, with the perimeter approximating the horizon (in the absence of vegetation). Next, each image was carefully converted manually to black pixels (vegetation and any other cover), and white pixels (open sky, including clouds and other visuals on the image that are part of the open sky, such as birds; Fig. 2). In some cases, sections of images had to be converted pixel-by-pixel in high zoom. Each image had roughly two million pixels. The conversion to black and white was accomplished with a variety of software packages with different tools, most notably Adobe Photoshop (Adobe, San Jose, CA). Once the images were converted to black and white, they were cropped into four semicircular images of the four cardinal directions.

Thus, one image represented the northern half of the sky, and its compliment represented the southern half, and repeated for east and west images. Direction of solar radiation receipt is very important as not only does this change seasonally, but also during the summer growing season, east and west shade differ in the air temperatures associated with each and potential photosynthesis, which may be reduced as the day progresses in this CAM plant. A pixel count in Photoshop yielded a count of black pixels and white pixels for each of the five images, for each of the 100 plants. The total number of black (vegetation and cover) pixels was divided by the total number of pixels in the image to get percent shade. Thus, five variables were created: % total shade, % north shade, % south shade, % east shade, and % west shade.

The other variables in this study included those for plant size, reproductive structures, and yellowing. A variable for the percentage of pads identified as having some degree of yellowing relative to the total number of pads was generated (%Yellow). Plant size variables included NS (north-south) diameter, EW (east-west) diameter, the ratio between these variables (NS/EW), Plant Height, and number of cladodes (#Pads). Six reproductive variables were created from the raw counts to control for plant size: #Flowers/#Pads, #Fruits/#Pads, and #Reprod/#Pads (flowers plus fruits), and also #Flowers/NS-EW avg, (average of the two plant diameters), #Fruits/NS-EW avg, and #Reprod/NS-EW avg. As flowers wilt and develop into fruits, these values will shift, necessitating the variable Reproduction (controlling for plant size) that quantifies all structures devoted to reproduction.

The Kolmogorov-Smirnov test for normality was used to evaluate these 17 variables. Variables deviating significantly from a normal distribution were transformed and normalized. In order to assess the relationships between variables, I used Pearson product-moment correlation for all the normal and normalized variables ($P > 0.05$), which were all the variables except the six reproductive variables. The six reproductive variables were correlated to all the variables using Spearman's rank correlation (Spearman's rho). Next, in order to assess whether these variables differed across the sites, one-way ANOVA was used. Data for each variable were grouped by site (WB, DN, DS). For the six reproductive variables, the Kruskal-Wallis test was used. Finally, the ratio of the NS diameter to the EW diameter of each

plant was used to determine if one dimension was longer than the other. A t test was run to see if this ratio significantly deviated from a value of one. The correlated Bonferroni technique (Drezner and Drezner 2016) was applied to each set of analyses (*i.e.*, in the output tables) to correct for false positive results from repeated tests, and all the significant results reported are those confirmed by the correlated Bonferroni technique.

Results. The Kolmogorov-Smirnov test confirmed that the four directional shade variables, and the NS/EW diameter variable did not significantly deviate from a normal distribution ($P < 0.05$). Plant NS and EW diameters, Plant Height, #Pads, %Yellow, and %Total shade did not deviate from a normal distribution with transformation ($P < 0.05$). The remaining six reproductive variables could not be normalized.

Significant Pearson product-moment correlation results show that plant diameters (both north-south and east-west), and #Pads are all significantly related negatively to West Cover (Table 1). The variable %Yellow was significantly related negatively to West Cover, South Cover, and Total Cover. The relationship between %Yellow and South Cover is graphed in Fig. 3. Plant Height was significantly related to South and East Cover, positively (Table 1, Fig. 3). Spearman's rho correlations yielded many significant results (Table 2). Number of Flowers (adjusted for plant size) is related to both plant diameter variables, Plant Height and #Pads, positively (Table 2). Results also suggest a significant positive relationships for the two flowering variables ($P = 0.036$ and $P = 0.033$) with East Cover (data not shown). The two fruit variables were significantly related to both plant diameters and #Pads, all positively, and negatively related to the five cover variables (Table 2). For example, the relationship between Number of Fruits (as well as Number of Flowers) and South Cover is provided (Fig 3). The two reproductive variable correlations largely follow those of the fruit variables, though with some exceptions including a nonsignificant relationship with East Cover and one of the two reproductive variables showing a relationship with Plant Height. Finally, the relationship between the two flower and two fruit variables were significant ($P < 0.05$, data not shown). None of the six reproductive variables were related to %Yellow. Finally, the t test confirmed that the NS/EW diameter ratio was

Table 1. Results of Pearson product-moment correlation analyses. The sign $(-, +)$ indicates the nature of the relationship, and all r values are provided. Significance levels $(n = 100)$ are: *$(P < 0.05)$ and **$(P < 0.01)$, and results with no asterisk(s) are not significant $(P > 0.05)$. $P = 0.05$ when $r = 0.1966$, and when $r = 0.1292$, $P = 0.10$. Variables used in the analyses include Plant Height, #Pads, the north-south (NS) and the east-west (EW) diameters of the plant, the ratio of these two (NS/EW), percent of pads showing yellowing (%Yellow), and total shade (Total cover) and coverage in the four cardinal directions (North cover, South cover, East cover, West cover). All variables are normally distributed or transformed. Plant Height and #Pads are positively correlated $(P < 0.001)$. Not surprisingly, Plant Height and both diameters, and #Pads and both diameters are significantly related, positively $(P < 0.001)$, and neither Plant Height nor #Pads are significantly related to the NS/EW ratio.

Variable	North cover	South cover	East cover	West cover	Total cover	%Yellow
Plant Height	+0.07	+0.20*	+0.21*	+0.04	+0.13	−0.14
#Pads	−0.19	−0.06	+0.02	−0.26**	−0.10	+0.11
N-S diameter	−0.18	−0.08	−0.00	−0.24*	−0.10	+0.09
E-W diameter	−0.15	−0.07	+0.05	−0.26**	−0.10	+0.14
NS/EW	+0.02	+0.04	−0.07	+0.13	+0.07	−0.08
%Yellow	−0.07	−0.29**	−0.12	−0.23*	−0.20*	

significantly different from 1; the NS diameters were significantly longer than the EW diameters across the sites sampled (the average ratio for each site is given in Table 3).

All five cover variables and plant height were significantly different across the three (WB, DN, DS) sites in the one-way ANOVA analyses (Table 3). Plants were tallest at DS, followed by DN with WB averaging shorter plants. West Beach had consistently lower cover then DeL,

and although the difference between the two DeL subsites were less striking, DN consistently had higher cover values than those at DS for all five cover variables (Table 3). At least one site was significantly different in %Yellow in the three site comparison (DS was much lower than the other two sites). For the six reproductive variables, only the two flower variables were significantly different across the three sites (Kruskal-Wallis test; Table 3).
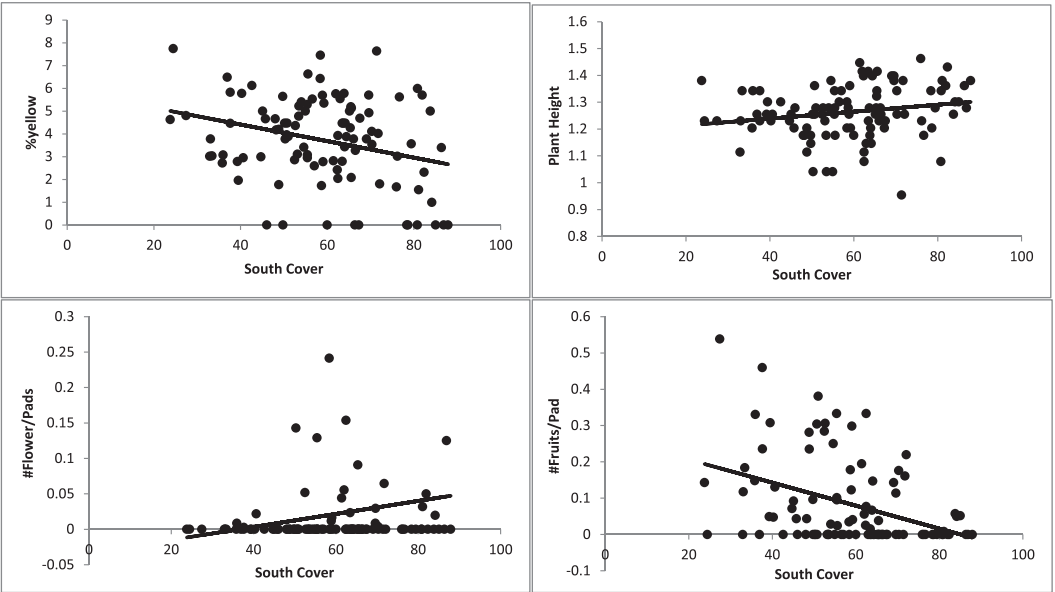
Fig. 3. Line fit plots (regression) for South Cover (normally distributed) and four variables. Top left, %Yellow (percent of pads with yellowing, normalized with square root), $P = 0.0038$, $y = 5.87 - 0.036$ (south cover). Top right, Plant Height (normalized with log), $P = 0.0489$, $y = 1.19 + 0.0013$ (south cover). Bottom left, #Flowers/Pad (not normal), Spearman's rho $P = 0.098$ and one outlier is not shown on graph (78.6, 0.75). Bottom right, #Fruits/Pad (not normal), Spearman's rho $P < 0.001$.

Table 2. Results of Spearman's rank correlation (rho) analyses for the six reproductive variables (#Flowers, #Fruit, and both, (Reprod.) adjusted for mean plant diameter and #Pads). The correlation coefficient is given with the significance level ($n = 100$) marked as ***($P < 0.001$), **($P < 0.01$), *($P < 0.05$). Variables used in the analyses include the NS and the EW diameters of the plant, Plant Height, #Pads, and Total cover (shade) and coverage in the hemispheres (half circle) of the four cardinal directions.

	#Flowers/#Pad	#Flowers/NS/EW
NS diameter	+0.27**	+0.29**
EW diameter	+0.30**	+0.32**
Plant Height	+0.25*	+0.26**
#Pads	+0.25*	+0.28**
	#Fruits/#Pad	#Fruits/NS/EW
NS diameter	+0.58***	+0.64***
EW diameter	+0.59***	+0.66***
#Pads	+0.58***	+0.66***
Total cover	−0.39***	−0.38***
North cover	−0.32**	−0.32**
South cover	−0.38***	−0.36***
East cover	−0.26**	−0.24*
West cover	−0.40***	−0.41***
	#Reprod/#Pad	#Reprod/NS/EW
NS diameter	+0.41***	+0.59***
EW diameter	+0.52***	+0.64***
Plant Height	+0.14	+0.21*
#Pads	+0.47***	+0.61***
Total cover	−0.29**	−0.29**
North cover	−0.23*	−0.25*
South cover	−0.28**	−0.27**
West cover	−0.29**	−0.32**

Discussion. While studies have looked at the complex taxonomy of *Opuntia* and the *Humifusa* clade (Majure *et al*. 2012), as well as at other characteristics of *O. humifusa* (Baskin and Baskin 1973; Koch and Kennedy 1980; Loik and Nobel 1991; Deotare *et al*. 2014), less has been published on the ecology of the species. Point Pelee National Park currently protects nearly 50 federally listed species at risk, and *O. humifusa* is one of the highest priority species for conservation action due in part to the fact that most of the Canadian population is at PPNP, making it key for the recovery of the species in Canada (T. Dobbie, Park Ecologist, personal communication).

SHADE AND STRESS. Like elsewhere, *O. humifusa* at PPNP is found in successional habitats, with excessive shade limiting the long term success of that species (VanDerWal *et al*. 2006). As the forest closes, long-term survival declines and highly shaded individuals show a tendency toward etiolation as the plant tries to increase light receipt through upwards growth (Lovett-Doust and Levi 2003; VanDerWal *et al*. 2006; Drezner in press). Experimental studies have shown that the greatest increases in cladode numbers occurred with about 30% shade, not 0% shade (VanDerWal *et al*. 2007), and survival may be compromised with more than 70% shade (Chiarot 1992). Thus, *O. humifusa*'s optimal environment for growth involves some, but not excessive, shade.

The ecological literature generally suggests that some species increase sexual reproduction under conditions of stress (West *et al*. 2001; Van Zandt *et al*. 2003), while in other cases, stress may bring about senescence of reproductive structures and reduce reproduction, particularly when stress occurs at certain times during the reproductive process (Aragon, Escudero, and Valladares 2008 and citations therein). How *O. humifusa* specifically responds to light stress is unknown. General research and unpublished work from PPNP suggests stress drives increases in reproduction (VanDerWal *et al*. 2006 and references therein). The current study shows that reproduction decreases with shade, including relatively high amounts of shade which causes this species to decline and sometimes become locally extirpated. Conversely, Bennett, Bomar, and Harrington (2003) suggested that improved microsite conditions resulted in an increase in flowering in *Opuntia fragilis* in Wisconsin; thus, improved conditions contribute to greater effort towards sexual reproduction in that congeneric species. Stress levels are currently uncertain at PPNP.

PAD YELLOWING. Pad yellowing has been observed in the cacti at PPNP. It is presumably a response to poorer conditions or a reflection of poorer plant health. The literature offers limited information about yellowing. Thornber (1911) describes *Opuntia* pads that are "yellowish" as a response to severe winter freezes and summer heat and drought. Ribbens and Myrom (1997) note that *Opuntia fragilis* "pad appearance was closely correlated with apparent pad health: . . . yellow pads generally appeared to be dying" (p. 9). Whether these color descriptors even represent the same yellowing observed in the Point Pelee populations is uncertain. Some possible causes of pad yellowing may be a nutrient deficiency (or deficiencies), response to high or low temperatures, or sunburn. Considering the relatively high

Table 3. Comparisons of means of different variables across study sites ($n = 100$). West Beach (WB), DeLaurier North (DN), and DeLaurier South (DS) represent the three populations at Point Pelee National Park. Variables compared include total shade (Total cover); percentage of North cover, South cover, East cover, and West cover; percentage of pads with yellowing (%Yellow); the ratio between the NS to the EW diameter of the plant (NS/EW ratio); and Plant Height (cm) were compared across three sites using one-way ANOVA. Statistical significances are based on normal and normalized variables. The mean values presented are taken from the raw data, regardless of whether the original variable was transformed for normality. In the lower half of the table are the six reproductive variables that could not be transformed: number of flowers per pad (#Flowers/#Pad), number of flowers adjusted for mean plant diameter (#Flowers/diameter), and the same for number of fruits (#Fruits/#Pad, #Fruits/diameter), and number of flowers + fruits (#Reprod/#Pad, #Reprod/diameter). The significance values are given for the Kruskal-Wallis tests.

	Mean					Standard error			
Variable	WB	DeL	DN	DS	P-value	WB	DeL	DN	DS
Total cover (%)	55.6	70.1	72.7	66.2	< 0.001	1.7	1.5	1.6	2.5
North cover (%)	59.5	73.9	77.1	69.0	< 0.001	1.9	1.6	1.8	2.8
South cover (%)	51.6	66.4	68.4	63.4	< 0.001	2.0	1.7	2.0	2.8
East cover (%)	54.7	71.2	71.8	70.2	< 0.001	2.0	1.8	2.1	3.4
West cover (%)	56.5	69.0	73.5	62.3	< 0.001	1.9	2.1	2.6	3.0
%Yellow (%)	18.1	16.8	21.7	9.4	< 0.05	2.0	1.9	2.5	1.8
NS/EW ratio	1.117	1.201	1.215	1.180	0.60	.052	.069	.106	.070
Plant Height	17.4	20.2	19.8	20.8	< 0.01	0.5	0.6	0.8	1.0
#Flowers/#Pad	.0073	.0342	.0530	.0061	< 0.05	.0039	.0160	.0262	.0029
#Flowers/diameter	.0050	.0205	.0292	.0075	< 0.05	.0023	.0062	.0097	.0039
#Fruits/#Pad	.1004	.0650	.0613	.0706	0.67	.0198	.0133	.0164	.0228
#Fruits/diameter	.1075	.0705	.0714	.0692	0.75	.0264	.0166	.0225	.0249
#Reprod/#Pad	.1078	.0992	.1143	.0766	0.76	.0200	.0204	.0302	.0233
#Reprod/diameter	.1125	.0911	.1007	.0767	0.85	.0271	.0182	.0253	.0255

latitude of the study site at the northern end of the species' range, high temperature cannot be discounted but it does not seem to be the most likely explanation (particularly as mean maximum July temperature is less than 27 °C; see Study Site). The analyses conducted in the current study show only three statistical relationships with yellowing (negatively to South Cover, West Cover, and Total Cover). Pad yellowing occurs less where there is more shade, lending support to the possibility of sunburn, though the reason why DS had particularly low values compared to DN is unclear (Table 3). Other work on *Opuntia* shows that plants growing in areas with greater sunlight produce longer and denser spines compared to plants growing in more shaded areas (Jock 1984; VanDerWal et al. 2007; Majure and Ervin 2008), reinforcing the idea that plants in areas with excessive sunlight invest more resources into spine production to reduce solar exposure. However, yellowing was observed on multiple pads in some plants in areas with greater than 80% overlying cover in the current study (data not shown). It is possible that soil nutrients play a role in pad yellowing. Nobel (1988) describes chlorosis as "loss of green color, yellowing" (p. 188), which

can occur with a sulfur deficiency, for example. Soil differences may thus play a role, particularly as soils at DeL have more developed A horizons as well as organic matter buildup following historical agricultural use (Lovett-Doust and Levi 2003). VanDerWal et al. (2007) suggest *O. humifusa* would benefit from increased nutrients at PPNP, but they note that benefits would only occur with increased light, and that light conditions are more important than nutrients for growth. In New Jersey, Hanks and Fairbrothers (1969a, b) found that *O. humifusa* presence was not related to increased nutrients, presence of organics, or particular soil types.

Perhaps surprisingly, yellowing is not related to any of the six reproduction variables. If yellowing is a sign of poorer health or conditions (i.e., a change in plant health is reflected in the yellowing of pads), reproduction may change in response, yet no statistical relationships were observed. It is possible that the yellowing observed at PPNP is not a strong indicator of plant health. Yellowing is also not significantly related to plant size (#Pads, Plant Height, EW and NS diameters, and NS/EW diameters).

SHADE AND SIZE. Shade was significantly higher at DeL than at WB (all five variables), and all five cover variables were significantly different across the three sites as well, with DN consistently having the highest cover, followed by DS, with WB the lowest. Plant Height was also significantly different across the three sites, with WB the lowest (mean of 17.4 cm), followed by secondary successional DN (19.8 cm) and DS (20.8 cm), confirming previous unpublished work (VanDer-Wal *et al*. 2007) that secondary succession *O. humifusa* plants are taller. Plants shaded to the south and east are taller. Increased plant height and etiolation are expected in areas with greater shade and overlying cover (Lovett-Doust and Levi 2003; Drezner in press). *Opuntia* stems are longer and become etiolated when plant development occurs in the dark or under low light conditions (MacDougal 1903; Nobel 1981). *Opuntia humifusa* is taller in the shade in Florida, where height growth is emphasized over pad production in areas where the overlying canopy is dense (Abrahamson and Rubinstein 1976). Abrahamson and Rubinstein (1976) suggest that the controlling factor for growth form is canopy cover rather than soil, as plants may be light-seeking, or possibly, subcanopy wind reductions may also be influencing growth form. Other cacti have also shown a strong relationship with the height of surrounding vegetation, which has been associated with available PAR (Nobel 1980, 1981). The height of the columnar cactus *Trichocereus chilensis* in South America dramatically increases with vegetation cover as height nearly quadrupled (Nobel 1981). Nobel (1981) suggests that light is the most reasonable factor affecting height (of those suggestions made in the literature), and that rapid upward growth is important in low light environments that can limit CO_2 uptake, and, spine and glochid production decrease in low light environments (Jock 1984; VanDerWal *et al*. 2007; Majure and Ervin 2008). The low light conditions in the forest may be initially beneficial for seed germination due to greater moisture and nutrients, but without adequate light, seedlings die (VanDerWal *et al*. 2007). North-South diameters are longer on average than EW diameters across PPNP. This may reflect nonrandom pad distribution in order to maximize PAR receipt (Nobel 1982).

REPRODUCTION AND SHADE. I observed that plants under greater shade tended to have fewer fruits. This may be a sign of ameliorated microclimate in the shade, or a reflection of poorer conditions that hinder or result in reduced reproductive effort. The number of fruits per plant, adjusted per number of cladodes, was lower than in previous studies at PPNP. VanDerWal *et al*. (2006) found approximately one fruit per two cladodes in WB (0.49 fruits/cladode) and a general average of 0.45, with data from two previous studies showing about one fruit per four cladodes (0.25–0.27 fruits/cladode). The current study observed 0.10 fruits/cladode at WB and 0.065 fruits/cladode at DeL. This may be partly explained by the current study's exclusion of very large microsites, which could have proportionately more fruits, though the average for the plants with over 100 pads is only 0.17 fruits/cladode (data not shown). Timing of field collection may also contribute to some degree, as may consumption and dislodgement of fruits, and natural interannual variability in reproduction, which is unknown. Although stress levels at PPNP are not well understood and likely fluctuate over time, the reduced fruiting (in light of VanDerWal *et al*.'s (2006) proposal of greater fruiting being a sign of greater stress) would be a favorable sign suggestive of decreased stress.

While fruiting was negatively related to shade, presence of flowers was not significantly related to shade or cover. However, flowering was significantly different across sites, with more flowers at DeL than at WB, particularly at DN. I suggest this is due to timing rather than to a direct relationship. While flowering may be delayed due to genetic differences across subpopulations or to the different microenvironmental conditions, such as better soils in secondary succession (VanDerWal *et al*. 2007), I suggest flowering is delayed (at least in part) to later in the season in more shaded areas, resulting in no statistical trend or a positive relationship with cover. In WB and areas with less shade, flowering had already occurred and counts were thus of the fruits that subsequently formed. In highly shaded areas (DN having the greatest shade of the three sites and the most flowers per pad), delayed flowering resulted in proportionately greater counts of flowers. Number of reproductive structures representing flowers plus fruits (per pad) is not statistically different at WB and DeL. However, DN has significantly more flowers, and although not significant, both DeL sites have lower numbers of fruits (Table 3). When all reproductive structures are counted (flowers + fruits), there is still a significant negative relation-

ship with overlying cover and thus, moderate to relatively high shade reduces reproduction. Eight plants experienced more than 80% cover (though they were relatively small individuals) and these only averaged about one fruit or flower per 54 pads (five reproductive structures on a total of 272 pads that comprise these eight plants; data not shown), compared to the overall average of about one reproductive structure per 10 pads for all sampled plants. Jock (1984) found that shaded *O. humifusa* at PPNP had fewer flowers and fruits, indicating less reproductive vigor, though his survey was early in the season. One casual observation made during the current field collection period was of the last plant (#100), which was relatively large and spatially extensive, and was also located primarily under a large, shading tree: its flowers and fruits appeared more concentrated along the pads at the outside edge of the plant with the least shade, and pad density appeared higher along this periphery as well (Drezner, personal observation). Fruiting differences across sites were not significant, but the trend was for greater fruiting at WB. Reproductive structures were not significantly different across sites but did decrease with increasing shade. Reproduction is lower in the shade and higher with greater sun.

Lovett-Doust and Levi (2003) found that the mass of mature seeds was positively correlated with incident light but negatively related to number of viable seeds (*i.e.*, there is a trade-off between seed size and number of seeds). Nobel and Castaneda (1998) and Rae (1995) found increased flowering with increased light in other cactus species. Unpublished work at PPNP suggests that *O. humifusa* plants tend to flower together to promote long-distance pollination (Aiello and Kevan 2002). If so, a temporal lag in flowering across sites may further contribute to genetic differentiation. However, PPNP populations are thought to primarily reproduce vegetatively (Swain 1998).

REPRODUCTION AND SIZE. The relationship between reproduction and plant size shows that larger plants (larger NS and EW diameters, and #Pads) have more flowers, fruits, and total reproductive structures per cladode than smaller plants, as well as when adjusting by plant diameter. The relationship between Plant Height and #Fruits/Pad and with #Reprod/Pad are not significant. Flowering however, does increase with plant height, though this may be a presumed

artefact of the delay in reproduction discussed above, as DeL plants are taller on average than WB plants. Fruits from DS are narrower and longer than fruits from other sites at PPNP as well (Lovett-Doust and Levi 2003).

Conclusions. While excessive light may increase yellowing, not enough causes an etiolation response and premature mortality in established plants. Intermediate shade appears to be where that the best growth occurs (*e.g.*, VanDerWal *et al.* 2007), recognizing that at PPNP, none of the sampled plants were in low shade locations. The plant with the lowest shade was 36% (total cover), and 82 of the 100 plants had > 50% total cover.

The decreased reproductive effort observed in the current study compared to past work (e.g., VanDerWal *et al.* 2006) suggests decreased light stress or stress in general in the population. Lower presumed light stress in shade (or at least in the absence of excessive shade) decreases reproduction, while greater shade reduces yellowing. If intermediate shade is indeed ideal for *O. humifusa*, and greater than 80–90% shade is detrimental and results in high levels of postestablishment mortality to the point where canopy closure should be monitored at PPNP as has been suggested (Chiarot 1992; VanDerWal *et al.* 2007), then the very low reproductive effort in high shade requires further study and attention. Stress needs to be assessed more directly in these populations and then linked with sexual reproduction, yellowing, and other variables.

Future work should also assess whether *O. humifusa* engages in facilitative interactions. The low light conditions in the forest are initially beneficial for seed germination due to greater moisture and nutrients (VanDerWal *et al.* 2007). Although several studies suggest that *O. humifusa* is not associated with any particular species (Hanks and Fairbrothers 1969a; Abella and Jaeger 2004), regular association with certain species is not essential. Some cacti require nurse plants (Turner *et al.* 1966) but not with any particular species, and sometimes even with a nurse rock that ameliorates microsite conditions (Drezner 2006, 2014). Many of the plants at PPNP were found within patches of thinner understory herbaceous coverage. Whether *Opuntia* acts as a nurse to these plants (directly or indirectly through substrate modification) or vice versa is unclear.

Managers should continue to maintain intermediate shade conditions at PPNP. Further, the drivers of pad yellowing and potential implications for plant health need to be assessed more directly, such as through observational multiyear or controlled experiments that vary light receipt and intensity as a possible factor. Particularly in light of some of the historical inconsistencies in the quantification of plants (pads, patches, microsites), regular monitoring of plants and more complete demographic data would be useful for long-term monitoring and assessment of the populations.

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