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Mechanisms of Native Shrub Encroachment on a Virginia Barrier Island

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Mechanisms of Native Shrub Encroachment on a Virginia Barrier Island

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University

by

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Abstract

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Species composition, temperature, soil nutrients, and leaf area index (LAI) were recorded across three encroaching *Morella cerifera* thicket edges and three free-standing shrubs on Hog Island, Virginia to characterize the effect of shrub thickets on the plant community and microclimate. Electron transport rate (ETR) was taken on shrub leaves to determine if microclimate benefits *M. cerifera* physiology. Species richness was lowest inside shrub thickets. Soil water content and LAI were higher in shrub thickets compared to grassland. Soil organic matter, N, and C were higher inside shrub thickets. Summer and fall maximum temperatures were more moderate in shrub thickets and at free-standing shrubs. Fall and winter minimum temperatures were higher inside shrub thickets. ETR was higher at the free-standing shrubs compared to the thicket edge. *Morella cerifera* impacts microclimate characteristics and species composition immediately upon encroachment. Improved shrub physiology was neither supported nor rejected by the research presented here.

Introduction

Shrub encroachment into grassland habitat has occurred globally for decades (Archer 1995 and Rundell et al., 2014). The northern advance of woody species around the Arctic Circle has been attributed to an increase in global temperature averages (Tape et al., 2006 and Sistla et al., 2013). Shifts in precipitation regimes and atmospheric CO_2 drive the encroachment of shrubs into African savannas (Sankaran et al., 2005 and Higgins and Scheiter, 2012). Overgrazing by cattle, often with a subsequent change in fire regime is linked to shrub expansion in the American west and southwest, especially in the Chihuahuan Desert (Ansley and Rasmussen 2005, Archer 1995, Bestelmeyer et al., 2013, Briggs et al., 2005, Brown and Archer, 1999, Goslee et al., 2003, Grover and Musick, 1990, and Van Auken 2009). Due to the dense growth form that shrubs exhibit, many species reinforce a microclimate which ameliorates abiotic conditions and enhances plant growth. This positive feedback mechanism plays an important role for many encroaching shrub communities (D'Odorico et al., 2010).

Recent shrub encroachment is generally recognized as a response to anthropogenic disturbance and often a threat to ecosystems, although historically, shrubs represent a shift in successional states after a natural disturbance (Connell and Slatyer, 1977). Shrub encroachment differs from successional shrub recruitment in that it is an abrupt response to a disturbance event such as overgrazing or climate change (Bestelmeyer et al., 2011) Negative effects associated with recent shrub expansion include decreased species diversity (Crawford and Young, 1998, Briggs et al., 2002, Isermann et al., 2007, Knapp et al., 2008, and Dows, unpublished data), extreme alteration in community structure (Huxman et al., 2005 and Rundell et al., 2014), the creation of alternate stable states (D'Odorico et al., 2012), nutrient cycling shifts (Brantley and Young, 2010), and increased susceptibility of shrubland to disturbance compared to previous ecosystems (Knapp et al., 2008 and Parizek et al., 2002). On Virginia barrier islands, *Morella cerifera* thickets clearly represent a different community structure compared to grasslands, and decreased plant diversity as well as increased soil nitrogen has been observed with the shift to shrubland (Crawford and Young, 1998, Brantley and Young, 2010). However, the stability of the shrubland habitat and the effect it has on fine scale abiotic and biotic conditions are yet to be determined.

Native shrub encroachment may have positive interactions with the community (Battaglia et al., 2007 and Valles et al., 2010). These interactions include increased soil nutrients and biomass with minimal effects on diversity. Effects of shrub encroachment cannot universally be described as ecologically negative, but some ecosystems may be more susceptible to degradation upon encroachment (Eldridge et al., 2011 and Zinnert et al., in press). On the barrier islands, aeolian and hydrological transport of sediment are land-moving forces that grasslands are known to tolerate, even in overwash events caused by large hurricanes (Miller et al., 2010). If shrublands cannot remain stable in such disturbance events, then islands will be at higher risk of erosion upon shrub encroachment. Given the importance of the stability of the barrier islands, it is critical to gain a better understanding of shrub encroachment so that risk may be assessed and management implemented, if necessary.

The dominant shrub on the Virginia barrier islands, *Morella cerifera L. Myricaceae*, is an evergreen nitrogen fixer which is native to the southeastern United States. It exhibits a vigorous physiology and remarkable resource use efficiency in a variety of conditions (Naumann et al., 2007, Naumann et al., 2008, Shiflett et al., 2013, Shiflett et al., 2014, Vick 2011). Sudden expansion in recent decades is unprecedented and could be a divergence from successional trends, although historical records of the barrier islands are limiting (Zinnert et al., 2011). *Morella cerifera* expanded on the northern end of Hog Island by 400% between 1949 and 1989 and by 273% since 1984 (Young et al., 1995 and Zinnert et al., 2011). On the southern end of Hog Island, *M. cerifera* has expanded by 304% since 1984 (Zinnert et al., 2011). Encroachment has been associated with an increase in air temperature and atmospheric CO_2 concentration (Zinnert et al., 2011), but mechanisms promoting expansion have not been identified and underlying causes are not well understood.

Shrub microclimates can create a positive feedback with plant growth as a mechanism for expansion. Distinct microclimates under shrub canopies have been documented the desert, arctic, and other more moderate climates (D'Odorico et al., 2010, D'Odorico et al., 2013, Kennedy and Sousa, 2006, Sturm et al., 2005, and Valles et al., 2011). Shrub microclimates are more stable because temperatures are moderated such that winter temperatures are warmer and summer temperatures are cooler (Ramirez et al., 2015). There is protection from harsh external conditions while soil nutrients and water availability increase (Valles et al., 2011). Enhanced hydraulic conductivity (Shiflett et al., 2014) and fog precipitation (Kennedy and Sousa et al., 2006) of shrub thickets can increase water availability while leaf litter and root leachate can increase soil nutrient composition (Brantley and Young, 2010). Decomposition of leaf litter and retention of ground-emitted thermal radiation are sources of warmth under the canopy (He et al., 2010 and D'Odorico et al., 2013). Canopy cover also reduces convectional heat loss by decreasing exposure to wind. The conditions of shrub microclimates suggest an environment that favors shrub growth and reproduction.

A warmer and less variable winter microclimate can have large implications for evergreen shrub physiology; nighttime cold-induced ‘photoinhibition’ decreases efficiency of daytime productivity through several mechanisms. Shrubs exposed to cold nighttime temperatures increase retention of xanthins (Adams and Demmig-Adams, 1995), decrease respiration of soluble sugars (Turnbull et al., 2002), and decrease leaf to air vapor pressure gradient (Curtis, 1936). These trends correlate to a decrease in daytime productivity. Warmer temperatures can also extend the active period of soil microbes and invertebrates, leading to more nutrient cycling, and possibly more activity by the nitrogen fixing bacterium *Frankia*, associated with *M. cerifera*.

My objective was to identify fine-scale microclimate characteristics of *Morella cerifera*, a thicket forming shrub which is encroaching on Virginia barrier islands, and to quantify the effect on neighboring plant and soil composition in order to better understand a potential mechanism of expansion. My specific hypotheses are as follows:

1. Shrub thickets will harbor fewer species than adjacent grasslands.
2. *Morella cerifera* thickets will increase soil nitrogen, carbon, organic matter, and water availability due to the redistribution of organic matter in leaf litter and accumulation of fixed nitrogen.
3. *Morella cerifera* thickets will increase minimum temperature during winter months and moderate summer temperatures, creating a more stable environment compared to adjacent grassland. Warmer winter temperature will correlate with

increased photosynthetic capacity, as shown by higher ETR in shrubs exposed to beneficial effects of microclimate versus the free-standing shrubs growing in the grassland, out of influence of the thicket.

Materials and Methods

Study site:

My research focuses on the expansion of *Morella cerifera* on Hog Island, a barrier island on the Virginia Coast Reserve (VCR, Figure 1). The VCR is a chain of about 18 islands on the coast of Virginia, the longest stretch of undeveloped coastline on the eastern United States (Badger, 1993). Hog Island lies south of Parramore Island and north of Cobb Island, from about "37°27'54.1"N, 75°39'51.4"S to 37°22'00.8"N, 75°43'20.1"W. While vulnerable to erosion and ecological degradation, barrier islands are extremely important for protecting the westward marsh habitat, inland, and all economic commodities they behold (Rood 2012). The islands are dynamic in their response to the physically dominated environment, being in a constant state of change as a result of powerful wind and water which determine their geomorphology (Ehrenfeld, 1990). There are beaches and dunes on the ocean side of the island and tidal salt marshes on the lagoon side (Figure 1). On the interior of the island the dune-swale community is composed of mixed grass-shrubland, with small trees occurring sparsely. My study is concerned with the encroachment of shrubs on the interior dune-swale community, which has shown a substantial increase in shrub cover in recent decades. Each habitat is associated with a specialized assemblage of species and functional types, many of which play an important role in island stability (Young et al., 2011).

Meteorological data was gathered from a station on Hog Island 10 km north of my field site (Porter and Spitler, 2015).

Morella cerifera thickets on the barrier islands are extremely dense. Although generally less than 5 m tall, thickets can have leaf area indices (LAI) higher than those of mature temperate forests (Brantley and Young, 2007) and should be capable of retaining warmth and acting as a barrier to external climate. Leaf litter and root leachate is nitrogen rich because of the symbiotic association with N-fixing *Frankia* and formation of root nodules (Brantley and Young, 2008). *Morella cerifera* shows a strong positive correlation between leaf temperature and net CO_2 assimilation up to 30° Celsius (Young et al., 1992, Shiflett et al., 2013). Hog Island lies within the northern edge of *M. cerifera*'s native range, where freezing temperatures can cause damage and may be a limiting factor for growth. Thus, increased minimum temperatures could have observable impacts on *M. cerifera* physiology and growth.

Field work was conducted on Hog Island from May 2015 to March 2016. In order to quantify the effect of the shrub thicket on microclimate, three transects were established on Hog Island that traverse the edge of three shrub thickets. The first transect was located at 37°22'46.37"N, 75°42'49.28"W and the second at 37°22'47.04"N, 75°42'52.58"W. These two transects ran east to west, perpendicularly through the thicket edge, with the eastern side of the transect inside the thicket and the western side of the transect outside of the thicket. The second transect was 85 m west of the first transect, and had a partially opened canopy due to recent shrub mortality. The third transect was located 180 m north of the first two transects, at 37°22'51.00"N, 75°42'45.06"W. It ran north to south, with the northern side of the transect inside the thicket. Each transect began 10 m inside the shrub thicket, crossed perpendicularly through the thicket edge, and ended in the open canopy grassland, 10 m away from the thicket edge. Along these 20 m transects were sampling points every 5 m such that a point existed 10 m inside the thicket, 5 m inside the thicket, at the thicket edge, 5 m outside the thicket, and 10 m outside the thicket. The midpoint of each transect which coincided with the edge of the thicket was defined as the location where shrub cover overcame grass cover. The thickets were chosen because they were at least 20 m wide, roughly level elevation and same age, and the adjacent grassland was free of shrubs that may influence the grassland plots. There were also three sampling points 500 m south of the transects, inside free-standing, grassland shrubs which were beyond influence of the thicket.

Species Composition and Soil Attributes:

In order to determine the relationship between plant composition and soil nutrient content, species cover was measured and soil taken from all plots in the summer. Species cover was measured in two 1 m^2 plots at each plot using the Daubenmire cover classes method (Daubenmire, 1959). Soil samples were collected in order to measure nitrogen, carbon, organic matter, and relative water content. Leaf litter was removed and soil was taken from the top 15 cm of the mineral layer. Soil samples were sent to the UGA stable isotope lab for determining total nitrogen and carbon content. Organic matter was measured by loss through ignition in a muffle furnace, as outlined in Crawford et al., (2007). Relative water content was calculated by dividing the fresh weight of the soil from the oven (80 °C) dry weight.

Leaf Litter Depth and Leaf Area Index (LAI):

Leaf litter depth was measured in the summer at all points along each transect using a ruler from ground level. Leaf area index (LAI) was measured in the growing season of 2015 in constant sunlight between 1100 and 1400 hours using a plant canopy analyzer (Model LI-3100C, LI-COR, Lincoln, Nebraska, USA).

Temperature Data:

Three temperature sensors (T Buttons, Thermodata) set at different heights, ground level, 20 cm, and 1 m, recorded bihourly measurements at each of the six plots along each transect (n=3) including the free-standing shrubs. Temperature will be discussed as mean daily maximum and mean daily minimum during summer (June 1-August 31), fall (September 1 – November 30), and winter (December 1 – February 29).

Electron Transport Rate:

To determine photosynthetic capacity, ETR was measured on *M. cerifera* free-standing shrubs and thicket edge shrubs in winter (n=30). Leaves measured were 1 m above the ground or lower. This procedure was chosen to differentiate the condition of leaves exposed to (thicket) or not exposed to (free-standing) the shrub microclimate. All measurements were made between 1100 and 1400 hours, in constant lighting conditions and temperature. ETR, and leaf temperature were measured using a pulse amplitude modulated leaf fluorometer (PAM-2000, Walz, Effeltrich, Germany) as in Shiflett et al., (2014).

Analyses:

Bray-Curtis ordination (Bray and Curtis, 1957) using Bray-Curtis distance and endpoint method, and Euclidean residual distance was used to determine relationships between species composition and plots. One-way ANOVA ($\alpha = 0.05$) was used to determine differences among treatments in soil composition, leaf litter, and LAI between all plots. Two-way ANOVA was performed to test height × plot interaction for temperature data for all seasons. If two-way interactions were significant, one-way ANOVA was performed across plots at each given height to test interactions across transects. One-way ANOVA was used to determine the difference in ETR between thicket and free-standing shrubs. All data were visually inspected for normality. Bartlett's test was used to test equality of variances (Snedecor and Cochran, 1989). Post-hoc Tukey tests were conducted if significant differences were detected in order to determine what factors differed (Tukey, 1949). Coefficient of variation was calculated for summer maximum and winter minimum temperatures.

Results

Species Composition:

Species cover for each location is recorded in Table 1. Axis 1 of the Bray Curtis ordination explained 42.9% of variation, while Axis 2 explained 36.3%, for a total of 79.2% of variation explained when all species are considered (Figure 2). Four distinct groups were identified. The thicket plots were most similar, with all plots having near 100% *M. cerifera* cover, and only one individual *Baccharis halimifolia* found (Table 1). Two groups consisted of all grassland plots, and were separated from one another by transect, where the third transect had a slightly different species assemblage than the first two transects. These plots had relatively high species richness, with low average cover of each species. The last group consisted of all thicket edge and free-standing shrub plots, grouped together due to a combination of high species richness and high average cover of each species.

Leaf Area Index (LAI):

Leaf area index (LAI) increased significantly from grassland (0.59±0.07) to thicket edge (2.18±0.12), and inside thicket (4.27±0.34) (F=153.8, p<0.001; Figure 3). All grassland plots were significantly lower than all thicket edge plots and all thicket edge plots were lower than all thicket plots.

Leaf Litter Depth:

Leaf litter depth was deepest 10 m inside the thicket (11.7±0.9 cm), and was significantly deeper than all other plots except for the plot 5 m inside the thicket (F=33.38, p<0.001; Figure 4). Leaf litter 5 m inside the thicket was significantly deeper than the thicket edge and grassland plots but was not deeper than the litter under the free-standing shrub. The thicket edge plot had a litter depth of 3.7±1.7 cm and was statistically similar to the free-standing shrub and the grassland plots outside the thicket.

Soil Attributes:

Soil organic matter was measured at each plot and was not significant, though there was a trend of more organic matter when inside the thicket (F=2.75, p=0.07; Figure 5). Thicket plots had significantly higher soil water content than grassland plots (F=14.94, p<0.001; Figure 6). The free-standing shrub resembled thicket and thicket edge plots while grassland plots had the lowest soil water content. Soil N and C were not significantly different across plots, but there was a trend of increasing nutrients inside the shrub thicket and at the free-standing shrub compared to outside the thicket (F=2.15, p=0.129 and F=2.01, p=0.15, respectively; Figure 7). Variability was higher within thicket plots.

Temperature:

Summer mean maximum air temperature was 28.2 °C and the mean minimum temperature was 21.3 °C. There was an interaction between height and location on transect for mean summer maximum and minimum temperatures (F=393.9, $p<0.001$, and F=6.1, p=0.002, respectively). Summer ground temperatures were much hotter outside the thicket compared to inside the thicket and at the free-standing shrub (F=818.2, $p<0.001$; Figure 8). The mean maximum ground temperature 5 m outside the thicket was 45.9 ± 0.4 °C while 5 m inside the thicket, it was 26.2 ± 0.2 °C. At 20 cm and 100 cm height, air temperature was significantly hotter outside the thicket compared to inside the thicket and at the free-standing shrub (F = 159.5, $p<0.001$ and F=56.91, $p<0.001$, respectively). At 100 cm, the difference in air temperature from 5 m outside the thicket to 5 m inside the thicket was 3.4 ±0.3 °C. Mean maximum summer temperatures at all thicket edge and free-standing sensors differed by less than 2 °C. Summer mean minimum ground temperature differed between plots, but with no discernible pattern (F=3.21, p=0.0069; Figure 9). However, at 20 cm height, thicket and free-standing shrub plots had significantly warmer mean minimum temperatures than plots outside the thicket (F=8.20, $p<0.001$). There was no difference in air temperatures at 100 cm height.

During fall, mean maximum air temperature from the meteorological station on Hog Island was 21.6 °C and the mean minimum temperature was 14.8 °C. There was a significant interaction across plots and heights for mean fall maximum temperatures (F=48.7, $p<0.001$) Mean maximum ground temperature was significantly warmer outside the thicket compared to inside the thicket and at free-standing shrubs (F=103.3, $p<0.001$; Figure 10). This difference was also significant at 20 cm and 100 cm (F=29.6, p<0.001 and F=10.9, p<0.001, respectively). Mean minimum ground temperature and air temperature at 20 cm was significantly warmer inside the thicket and at the free-standing shrub at ground level (F=6.3, p<0.001, and F=5.04, p<0.001, respectively; Figure 11). Mean minimum air temperature at 100 cm was significantly warmer at the free-standing shrub compared to grasslands, but no other temperatures differed significantly (F=3.18, p=0.007)

Winter mean maximum air temperature on Hog Island was 11.2°C, while mean minimum temperature was 3.6°C. There were significant interactions across plots and heights for mean winter maximum and minimum temperatures (F=14.3, p<0.001 and F=6.2, p=0.002, respectively). Mean maximum temperature was significantly warmer at the thicket edge and outside the thicket compared to inside the thicket and the free-standing thicket at ground level, 20 cm, and 100 cm. (F=59.51, p<0.001, F=16.5, p<0.001, and F=10.36, p<0.001, respectively; Figure 12). For each height, the thicket edge had the warmest mean maximum temperature across plots. Mean minimum ground temperature was significantly warmer inside the thicket, at the thicket edge, and at the free-standing shrub compared to the grassland (F=8.68, p<0.001; Figure 13). For example, the plot 10 m inside the thicket was 2.2 ± 0.5 °C warmer than the plot 10 m outside the thicket. At 20 cm, air temperature was significantly warmer inside the thicket compared to outside the thicket (F=2.58, p=0.025). There was no significant difference in temperature across plots at 100 cm, but thicket and free-standing shrub plots were all warmer than plots outside the thicket. The free-standing shrub also had warmer minimum ground temperatures than grassland plots (F=5.95, p=0.0027).

Coefficient of variation:

Summer maximum temperature coefficient of variation was about 0.05 lower in the thicket than the grassland (Figure 14). At 20 cm and 100 cm, coefficient of variation was about 0.01 lower inside thicket (Figure 14). During winter, minimum ground temperatures had a coefficient of variation that was 1-1.5 lower inside the thicket and at the thicket edge (Figure 15). At 20 cm, coefficient of variation was 0.6-1.2 lower inside the thicket and at the edge compared to the grassland (Figure 15). Coefficient of variation was 0.2-0.4 lower at the thicket edge and inside the thicket than in the grassland (Figure 15).

Electron Transport Rate:

ETR was significantly higher in free-standing shrub leaves compared to thicket edge leaves (F=7.18, p=0.009; Figure 16).

Discussion

This study evaluated the effects of *Morella cerifera* on fine-scale abiotic and biotic factors upon encroachment into grassland. My results, consistent with those of similar studies on other shrubs, indicate that *M. cerifera* significantly changes the microenvironment including air temperature, soil components, and plant species composition (Crawford et al., 1998, He et al., 2010, Valles et al., 2011, and Ramirez et al., 2015). Previous studies have shown the effects of *M. cerifera* on the habitat of the barrier islands at large scales, but none have shown change in habitat attributes on a fine scale (Crawford and Young, 1998 and Brantley and Young, 2008). These results show that the expansion of *M. cerifera* in coastal systems can have an immediate and significant impact on the surrounding environment. In other words, the presence of shrubs at any scale has a significant effect on microenvironmental factors on Hog Island.

Species richness was lower in the shrub thickets, as expected (Crawford et al., 1998). Only one individual of another species (*Baccharis halimifolia*) than *M. cerifera* was found inside the thicket and it was mostly dead. Species cover was highest at the thicket edge and free-standing shrubs, and species richness was similar at these plots compared to the grassland. The reason for the sudden die off of species upon entering the thicket is not known, but is likely related to lower light availability (Brantley and Young, 2007).

My hypotheses concerning soil attributes were partially supported; higher water availability and litter depth were found in the thicket compared to the grassland. Organic matter, N, and C resembled each other closely across plots, with higher variability in the thicket. Organic matter content and soil C was higher in the thicket due to litter deposited over the sandy soil. The amount of organic matter inside the thicket was smaller than that found in older thickets (Crawford et al., 1998). More time may be needed to decompose litter (Graziani and Day, 2015). Higher soil N was caused by the nitrogen fixing effects of *Frankia*, the symbiotic bacteria living in root nodules of *M. cerifera*. In the grassland N is very low, sometimes undetectable, and leaches out of the sandy soil quickly. Nitrogen levels were lower than Graziani and Day's (2015) thicket and thicket edge plots, and resembled more the lower dune near the thicket edge. Their thickets, however, were north of mine, and thus older.

The cause of higher soil water content in the shrub thicket seems to be two-fold. First, the shrubs occupied a slightly lower elevation (< 1 m) than their adjacent grassland. The second probable cause is the protection of the soil water from solar and wind evaporation by a dense canopy and thick layer of leaf litter, slowing evaporation relative to the grassland. These causes, however, remain speculative.

Cooler summer temperatures in the thicket compared to adjacent grassland were likely caused by dense canopies which decreased sunlight inside the thicket. The grassland adjacent to the shrub thickets had high sand cover, usually with more sand than plant cover. Solar radiation had a high heating effect on the sand, causing daytime ground temperatures to regularly exceed 50 °C, with mean maximum temperatures at 44.0 ± 0.3 °C. One recording was as high as 58.0 °C while air temperature was 33.0 °C. On the same day and time, ground temperature 5 m inside the thicket was 29.5 °C, nearly half the temperature to that just 10 m away. Grouping all thicket and free-standing shrub summer temperatures, the average was 29.3 ± 0.1 °C while the average grassland temperature was 37.0 ± 0.2 °C. Considering that *M. cerifera's* photosynthetic optimum is around 30 °C (Young, 1992), with a drop in physiology at higher temperatures, the shrub thicket and free-standing shrubs may benefit from microclimate effects during the summer, where temperatures are moderate and remain close to the 30 °C optimum. Although I predicted that summer temperatures would be moderated by the shrub microclimate, I do not know if the cooler climate benefits shrub physiology. Additionally, it appears free-standing shrubs form significant microclimates of their own, in terms of soil attributes and temperature. This finding was not predicted by the original hypotheses, as the free-standing shrubs were designed as a control for thicket shrubs exposed to microclimate benefits. Instead it appears even young pioneering shrubs alter the microclimate significantly.

As I hypothesized, warmer minimum temperatures occurred inside the thicket during the winter time. Ground temperature was 2.1 ± 0.3 °C warmer on average inside the thicket and at the thicket edge compared to the adjacent grassland. Air temperature at 20 cm was 1.1 ± 0.4 °C warmer inside the thicket compared to outside the thicket, and at 100 cm the thicket was 0.4 ± 0.4 °C warmer inside the thicket, though the latter was not significant. Again, free-standing shrubs unexpectedly had warmer minimum temperatures compared to grassland plots. Compared to the plot 10 m outside the thicket, free standing shrub ground temperatures were 1.4 ± 0.4 °C warmer. Air temperature was slightly warmer in free-standing shrubs compared to grassland, but not significantly. The warming caused by shrub thickets and free-standing shrubs can be expected to have significant positive impacts on the shrub thicket, especially in extreme cold temperatures (Young, 1992). However, the similarity in microclimate conditions between free-standing shrub and thicket edge plots may explain the respective similarity in ETR between the two locations. My hypothesis that the thicket leaves would outperform leaves on a free-standing shrub rested on the assumption that free-standing shrubs would not form a microclimate like that of shrub thickets. Greater shading in the thicket may have contributed to lower ETR in thicket shrubs, while lack of competition for light and soil resources may have led to higher ETR at free-standing shrubs. Additionally, *M. cerifera* has been documented to conserve physiological traits across shrub age (Shiflett et al., 2014).

Several studies have shown microclimate effects at the patch scale on non-thicket forming shrubs, but shrub thickets may cause greater effects than single shrubs alone; my study looks at and compares both (Ramirez et al., 2015 and Valles et al., 2011). Although most of the variables measured at 10 m inside the thicket were not significantly different from those 5 m inside the thicket, some variables such as soil water content and leaf litter depth did noticeably increase suggesting that the thicket's immediate effects upon encroachment remain significant long enough for the thicket to advance into the grassland. These effects may be diminished after the thicket progresses forward, beyond the reach of the transects studied here, however at this point other species have been outcompeted.

The similarity in microclimate characteristics between the free-standing shrub and the thicket edge was unexpected. For this reason, methods other than sampling thicket edge leaves and free-standing shrub leaves will be needed to identify physiological benefits of microclimate on shrubs. In terms of temperature, edge and free-standing shrub plots were more moderate in the summer and warmer in the winter. Soil water content and leaf litter depth were higher than the adjacent grassland and less than inside the thicket. Plant cover was relatively high at these points, which clearly grouped all edge and free-standing shrub plots together in the Bray-Curtis ordination (Figure 2). Plants were dense at these plots because of access to soil nutrients without the depletion of sunlight observed inside the thicket. These results support the idea that *M. cerifera* acts as a "fertile island", if only temporarily, in what is otherwise a physically harsh, nutrient and water limiting environment (Schlesinger et al., 1990).

Barrier islands are a novel system for studying shrub thicket microclimates as a mechanism for expansion. Most studies have been in arid or arctic environments, where causes of shrub encroachment are better understood and benefits of a microclimate, such as water and warmth retention, are more apparent. Overgrazing sparked the encroachment of shrubs in the American southwest, where shrub microclimates offer significant protection from freeze damage and drought (He et al., 2014). Climate warming has allowed shrubs to expand north in the Arctic, while the microclimates they form further increase annual biological activity in the soil and woody vegetation. My study shows that encroaching shrubs may also benefit from a microclimate in locations where the need for relief from pressures such as freezing temperatures and water availability is not as apparent as in arid or arctic environments. Shrubs in my study occupy a temperate environment; however, they have similar effects on the environment around them, including increased soil nutrient content, increased litter depth, increased minimum temperatures, and more moderate summer temperatures.

It is well known that average global temperatures have been rising for thousands of years, with an accelerated rate of increase in recent history (IPCC, 2014). The VCR lies within the northern limit of *M. cerifera's* native range, which is likely constrained from higher latitudes by temperature and temperature-dependent functions such as evapotranspiration and ETR (Shao and Halpin, 1995 and Shiflett et al., 2013). It is possible that climate warming has surpassed a tipping point, or threshold, allowing *M. cerifera*, with the help of an ameliorating microclimate, to encroach on neighboring island species that are no longer able to compete with its increasingly robust physiology. Increased shrub microclimate temperatures recorded in New Mexico at the landscape scale were comparable to the amount of temperature increase expected over a century under global warming conditions (He et al., 2014). On Hog Island, winter warming caused by shrub thickets is also comparable to about a century of global warming (~2 °C), but on a fine scale. Warmer minimum temperatures could be considered a possible cause of expansion because *M. cerifera* physiology is tightly correlated with temperature, which is also a constraining factor for *M. cerifera* expansion north of this region.

There are several concerns with shrub encroachment on Hog Island. Primarily, can *M. cerifera* thickets withstand a storm-induced overwash event as well as grassland habitat? It is well known that native grasses are critical for island resistance and resilience to disturbance events (Snyder and Boss, 2002). If the island is dominated by monospecific stands of shrubs, recovery from a powerful disturbance event could take more time than if the island were dominated by grassland communities. Further, plant productivity generally increases with biodiversity (Zhang et al., 2012). There is evidence in this system, including increased LAI and organic matter inside the thicket, to believe the opposite is true (Crawford et al., 1998 and Brantley and Young, 2008). Other species that reduce diversity while increasing productivity often fall in the category of invasive, which are well known to damage ecosystem services (Vilà et al., 2011). Although native, it is possible that *M. cerifera* behaves as an invasive species on Hog Island. More research is needed to better understand the effect of shrub encroachment on island stability and whether or not management is required to encourage regrowth of grassland habitat.

Islands on the VCR have varying histories of anthropogenic disturbance. These disturbances include prescribed fire, cattle grazing, lumbering, and farming (Levy 1990). Although the island communities may still be responding to historical disturbances, the VCR is considered “free of human disturbance” because humans no longer inhabit the area (Hayden et al., 1991). Historic disturbances varied temporally and spatially across the barrier islands, yet *M. cerifera* expansion has been practically ubiquitous across habitable areas of the VCR in recent decades and has not been associated with any human disturbances (Young, personal communication). My research has proposed a potential mechanism, in concert with climate change effects, driving island encroachment by *M. cerifera* (Zinnert et al., 2011).

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Table 1. Mean (± standard error) species cover (%) for all species and plots sampled on Hog Island, VA.

	10 m inside thicket	5 m inside thicket	thicket edge	5 m outside thicket	10 m outside thicket	Free-standing shrub
Spartina patens	-	-	53.3 ± 15.8	25.0 ± 12.5	17.5 ± 10.9	-
Panicum amarum	-	-	-	5.83 ± 4.6	5.83 ± 4.6	-
Rumex acetosella	-	-	10.8 ± 4.2	2.5 ± 0.0	6.67 ± 4.2	-
Morella cerifera	97.5 ± 0.0	97.5 ± 0.0	61.7 ± 13.7	-	-	61.7 ± 13.7
Baccharis halimifolia	-	8.66 ± 5	-	-	-	5.83 ± 4.6
Cirsium horridulum	-	-	-	0.83 ± 0.8	0.83 ± 0.8	0.83 ± 0.8
Rubus pensilvanicus	-	-	5.83 ± 4.6	0.83 ± 0.8	-	-
Conyza canadensis	-	-	5.83 ± 4.6	6.67 ± 4.2	1.67 ± 0.8	1.67 ± 0.8
Dicanthelium sp.	-	-	10.0 ± 5.0	1.67 ± 0.8	-	0.83 ± 0.8
Nuttallanthus canadensis	-	-	0.83 ± 0.8	-	0.83 ± 0.8	0.83 ± 0.8
Schizachyrium scoparium	-	-	5.0 ± 5.0	28.3 ± 28.3	21.7 ± 20.4	45.8 ± 8.3
Aristida tuberculosa	-	-	-	-	0.83 ± 0.8	0.83 ± 0.8
Oenothera humifusa	-	-	-	-	0.83 ± 0.8	-
Lepidium virginicum	-	-	-	-	0.83 ± 0.8	-
Solidago sempervirens	-	-	12.5 ± 12.5	5.0 ± 5.0	5.0 ± 5.0	4.83 ± 4.6
Euthamia caroliniana	-	-	-	0.83 ± 0.8	-	-
Teucrium canadense	-	-	-	0.83 ± 0.8	-	-
Physalis walterii	-	-	-	-	-	-
Solanum carolinense	-	-	0.83 ± 0.8	-	-	-
Hypericum hypericoides	-	-	0.83 ± 0.8	-	-	-
Strophostyles helvola	-	-	-	-	-	0.83 ± 0.8
Gamochaeta argyrinea	-	-	-	0.83 ± 0.8	-	0.83 ± 0.8
Average % Cover	97.5 ± 0.0	76.9 ± 20.6	24.1 ± 5.7	12.5 ± 4.8	10.6 ± 3.7	21.0 ± 6.2

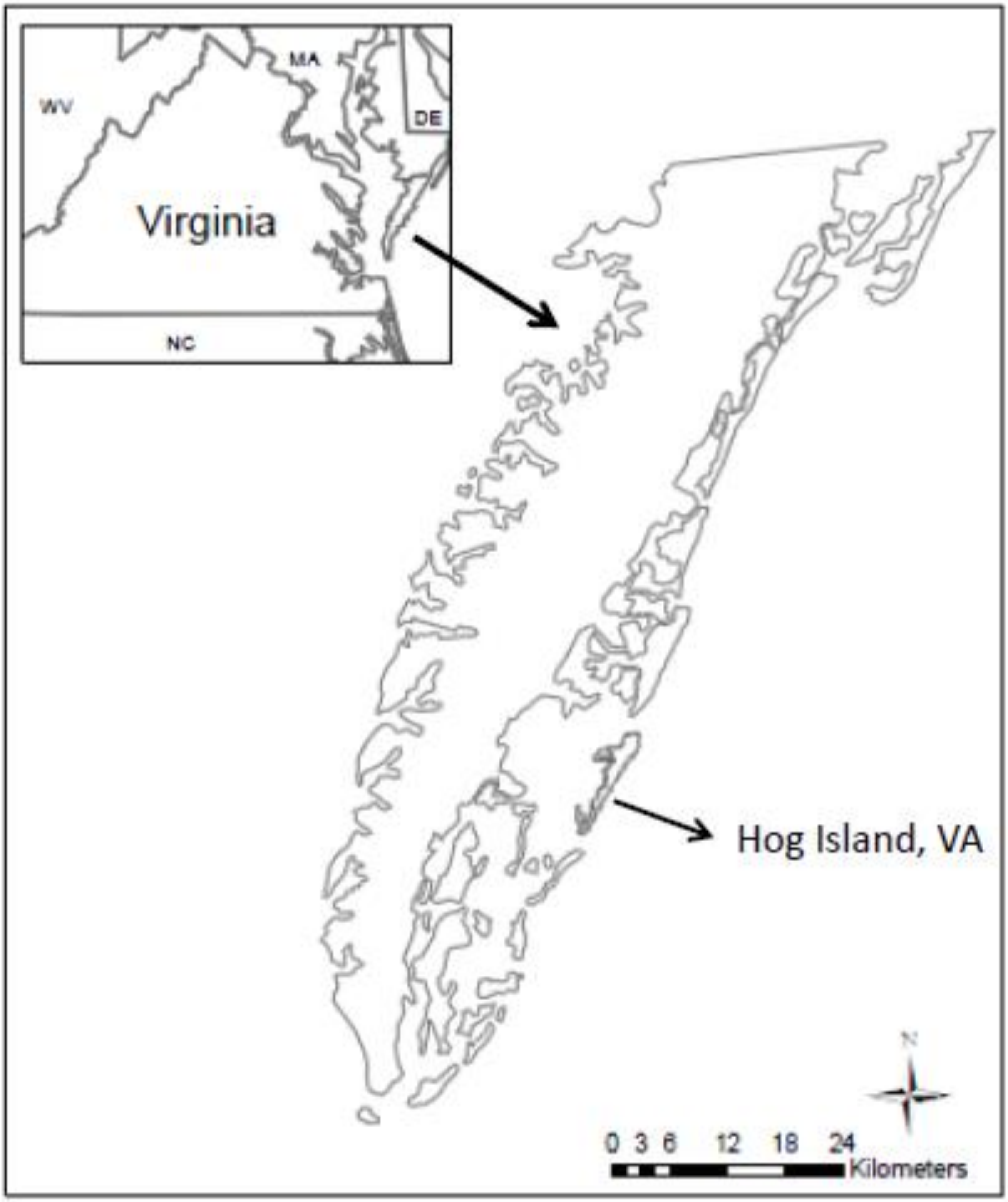

Figure 1. The Eastern Shore of Virginia showing the barrier islands which compose the Virginia Coast Reserve (VCR). Field work for this study was conducted on Hog Island.

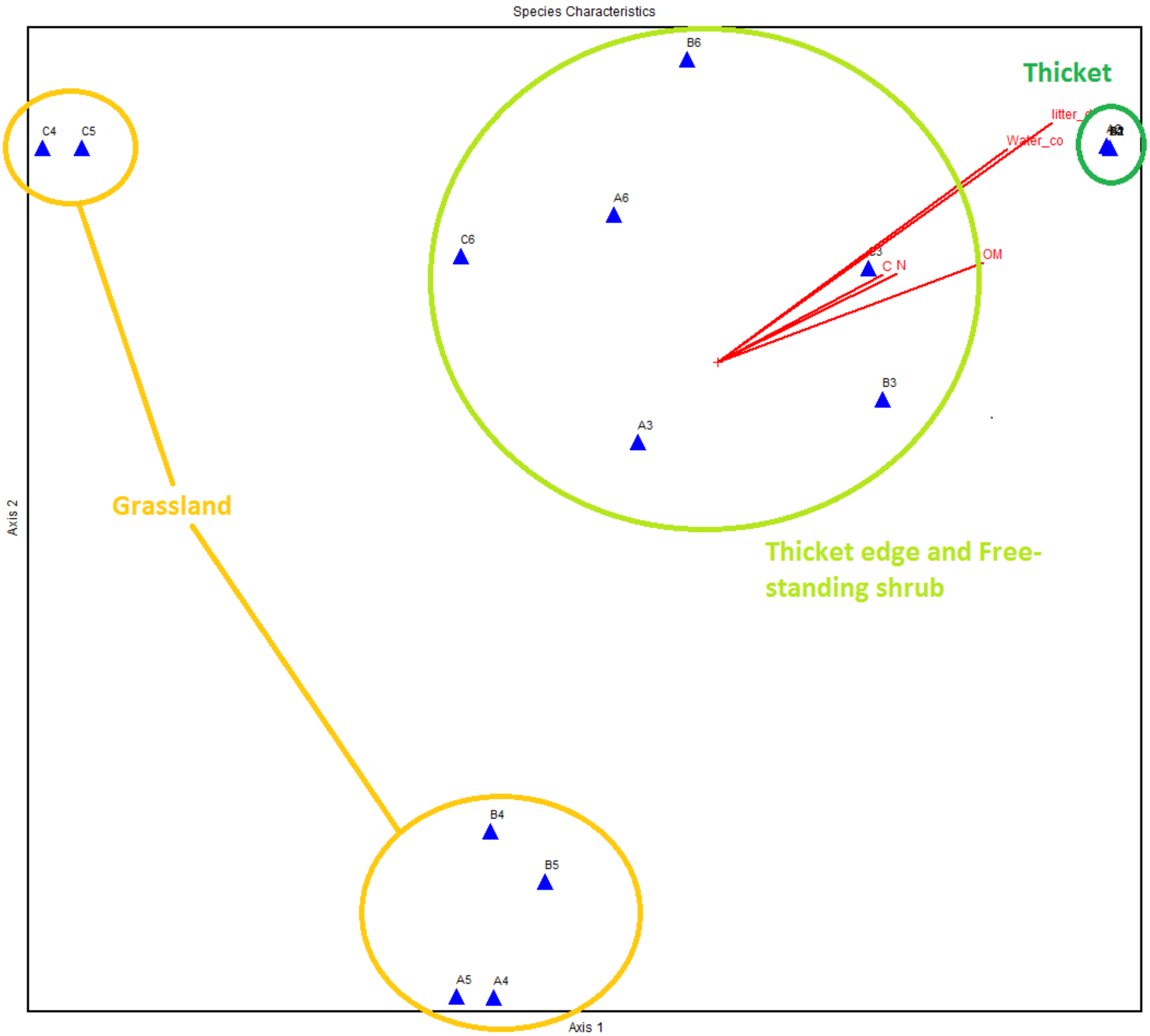

Figure 2. Bray Curtis Ordination for plant composition of plots sampled on Hog Island, VA. Axis 1 explained 42.9% of variation, Axis 2 explained 36.3%, for a total of 79.2% of variation explained when all species are considered. Environmental variables include litter depth, water content, organic matter (OM), N, and C.

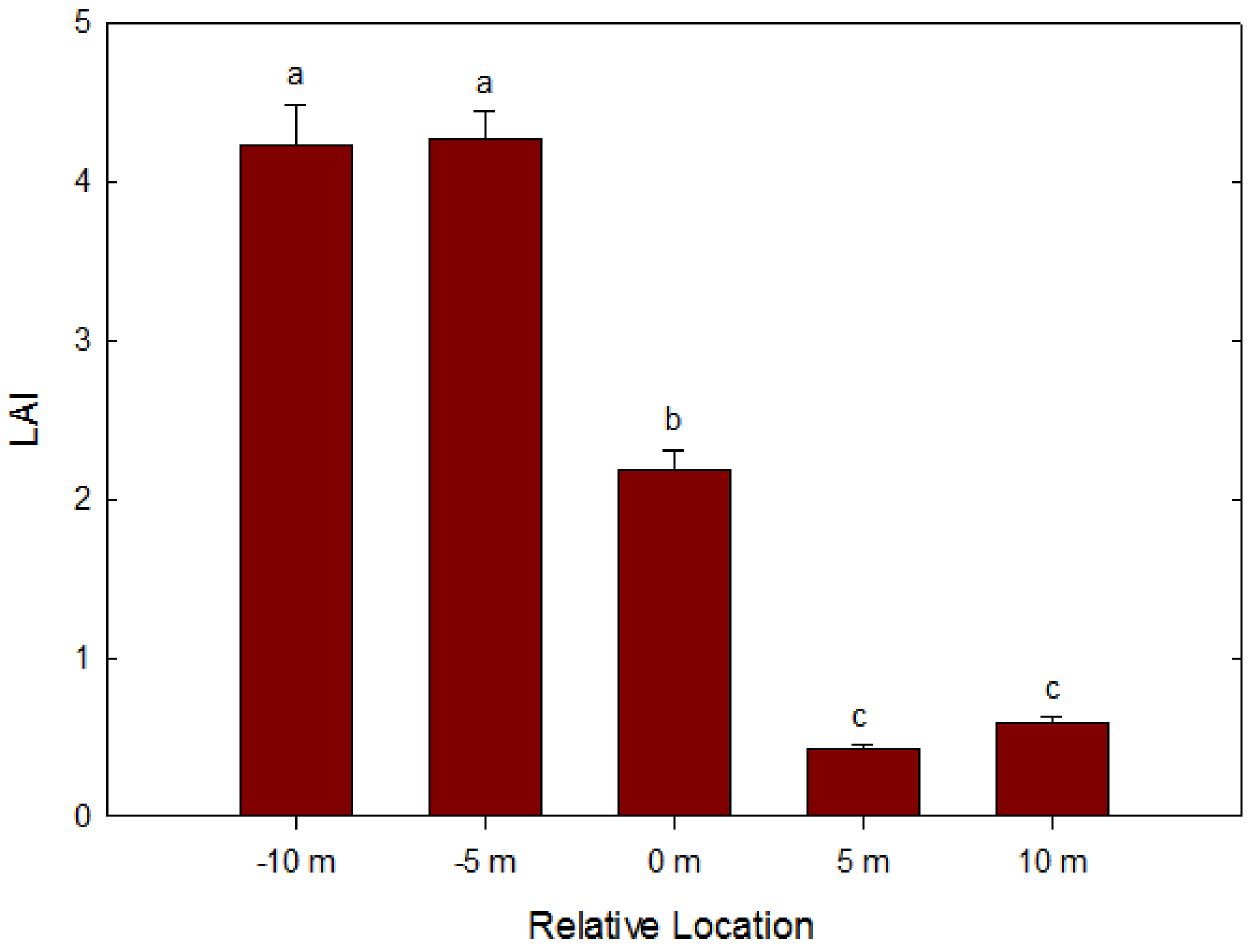

Figure 3. Leaf Area Index across transects on Hog Island, VA. Relative location refers to plot distance to thicket edge where -10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket. Error bars represent ± one standard error.

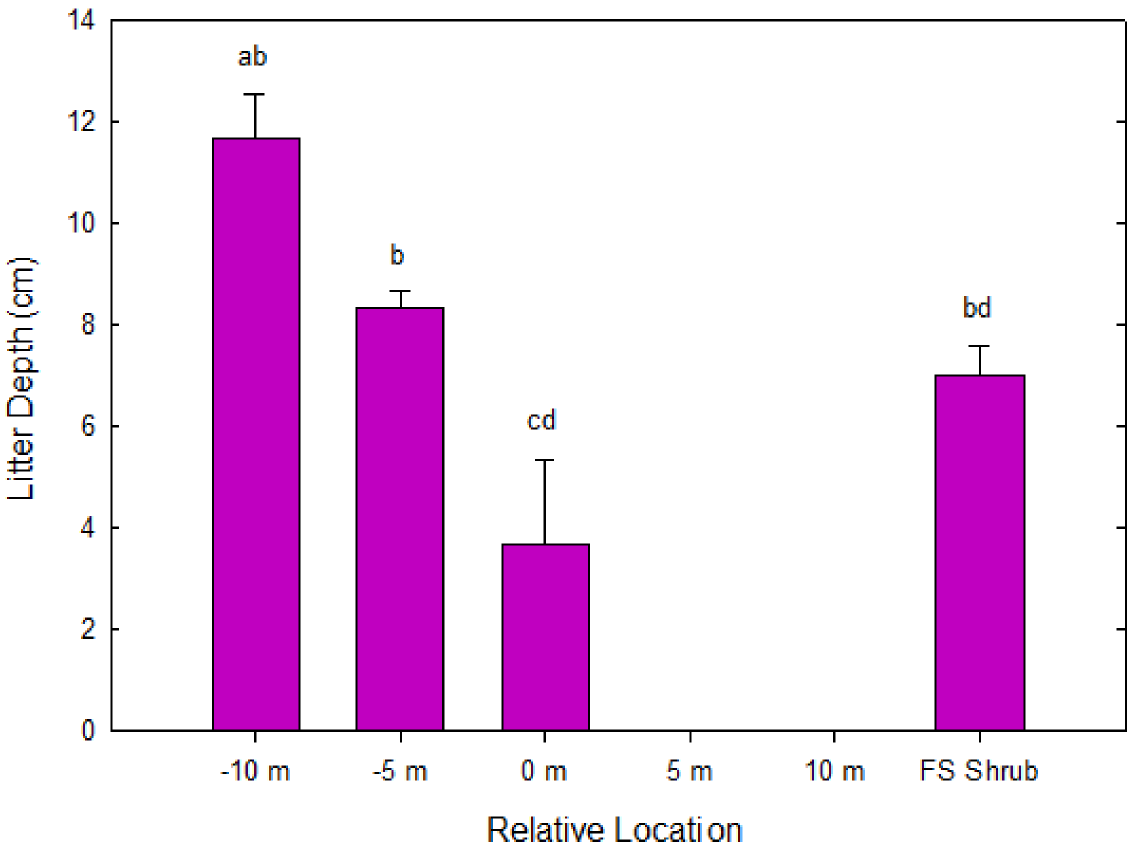

Figure 4. Litter depth across transects on Hog Island, VA. Relative location refers to plot distance to thicket edge where -10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Error bars represent ± one standard error.

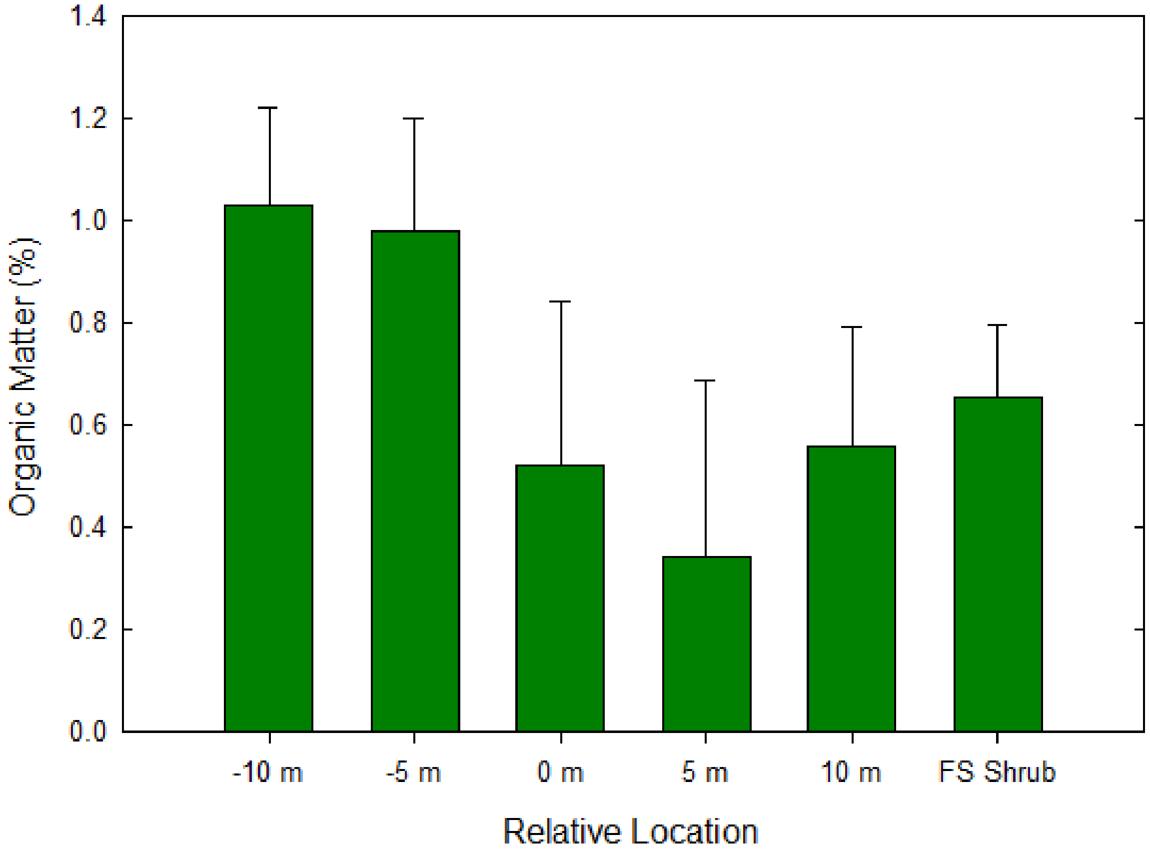

Figure 5. Soil organic matter across transects on Hog Island, VA. Relative location refers to plot distance to thicket edge where -10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Error bars represent ± one standard error.

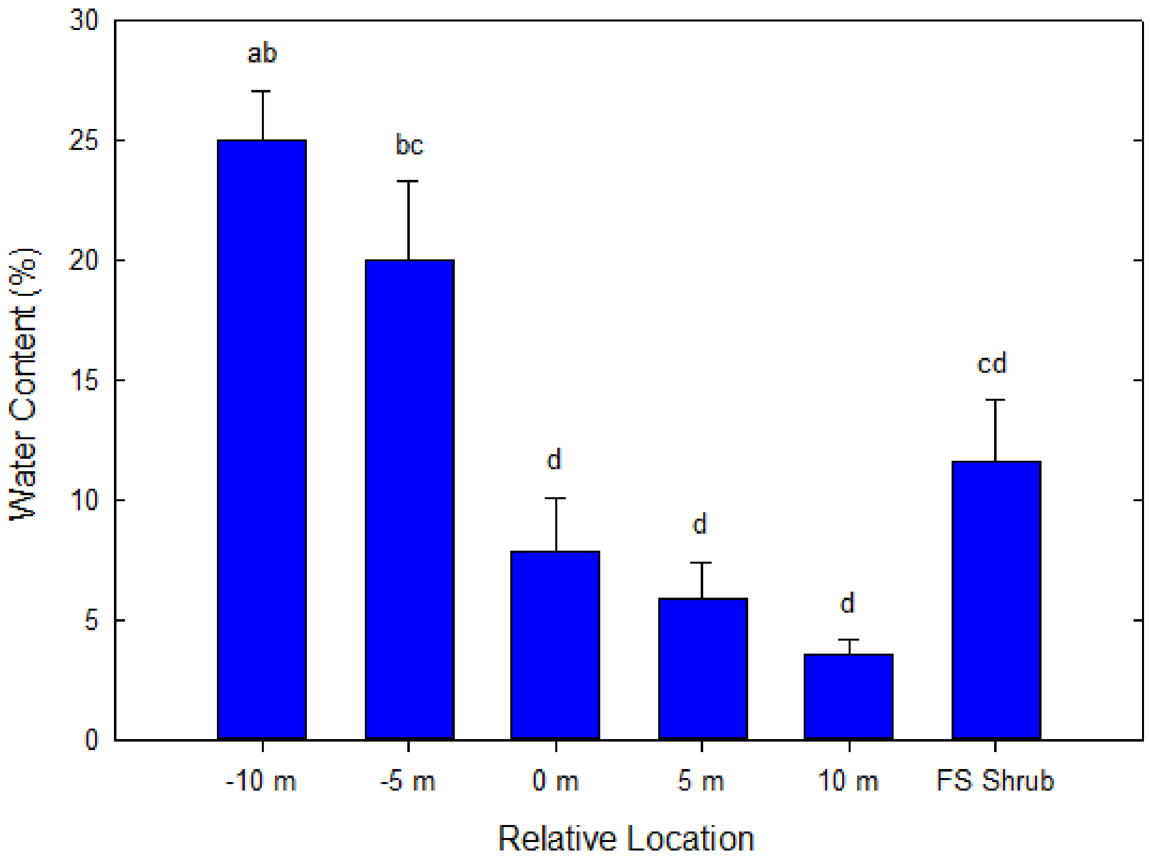

Figure 6. Soil water content across transects on Hog Island, VA. Relative location refers to plot distance to thicket edge where -10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Error bars represent ± one standard error.

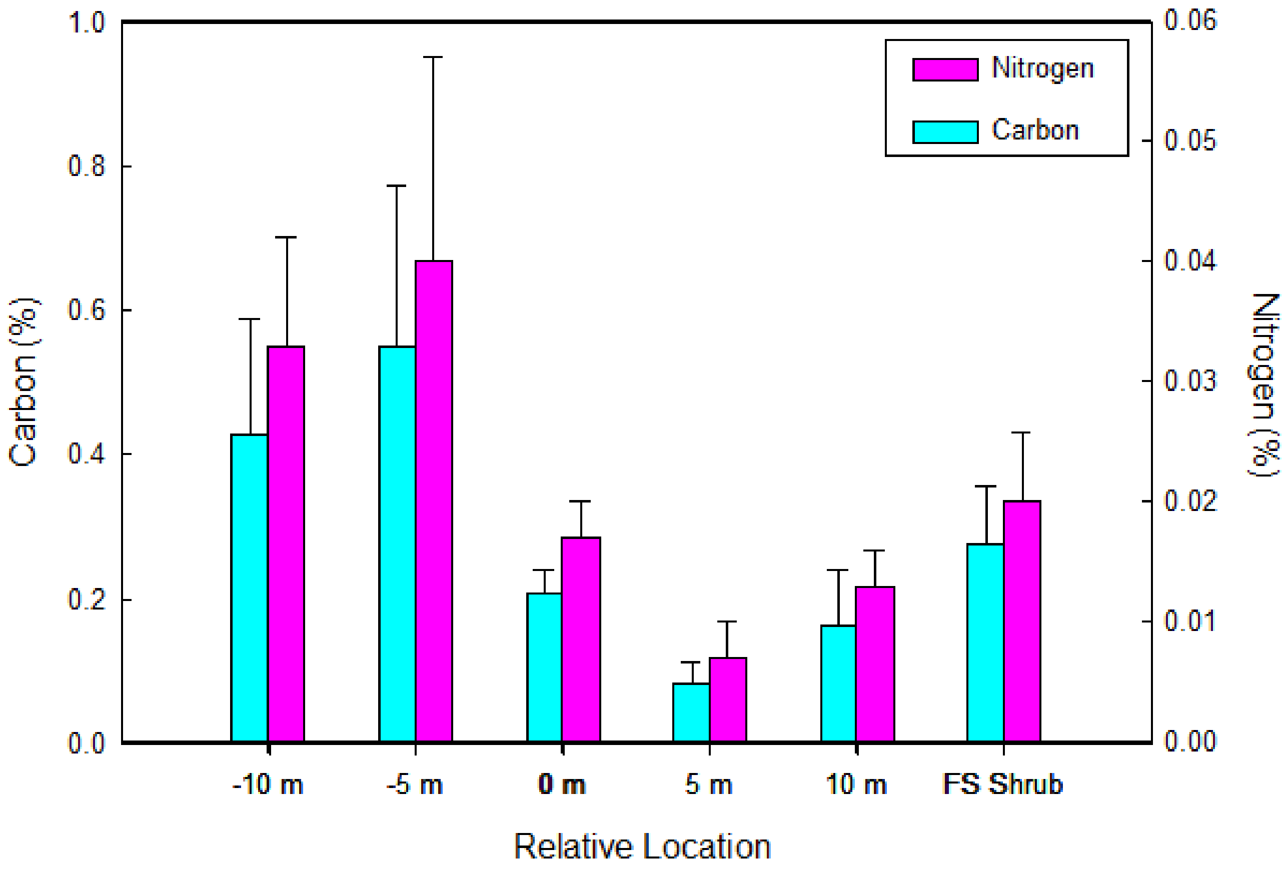

Figure 7. Carbon (%) and Nitrogen (%) composition of soils across transects on Hog Island, VA. Relative location refers to plot distance to thicket edge where -10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Error bars represent ± one standard error.

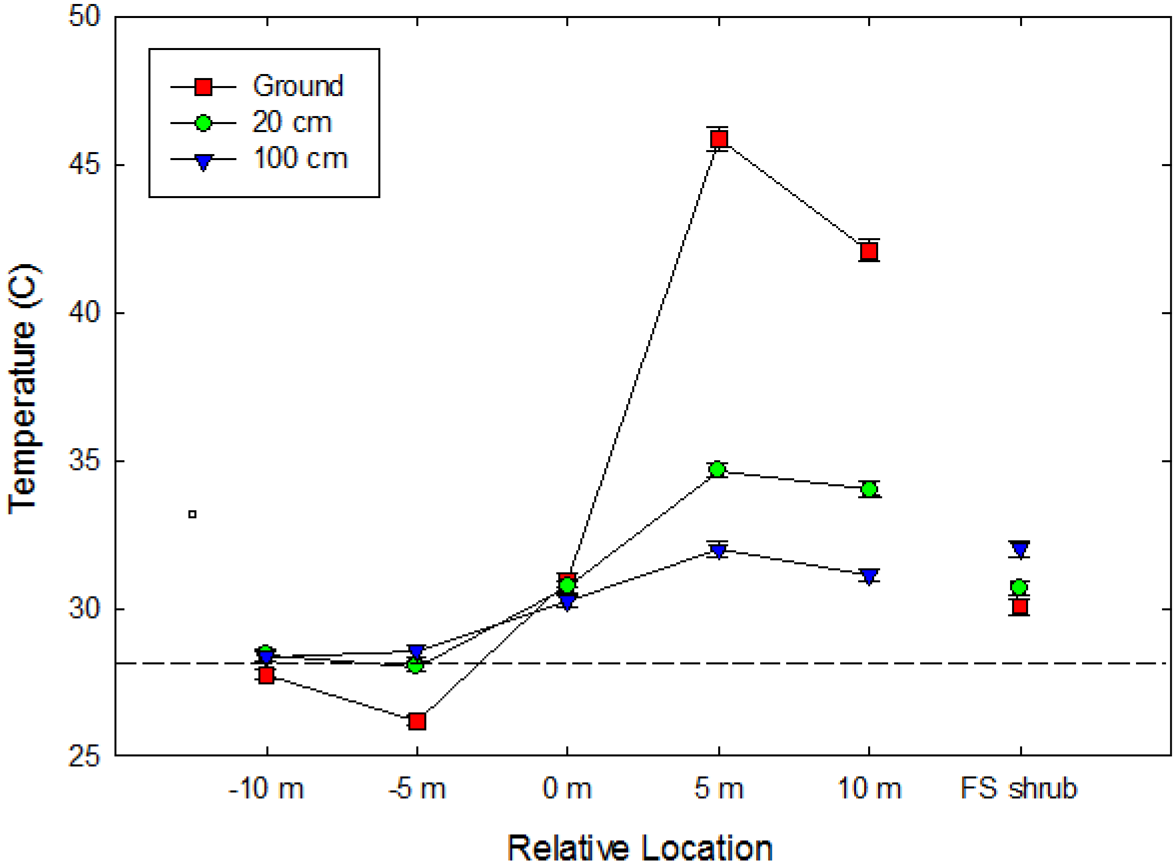

Figure 8. Mean summer maximum temperatures of plots across transects at ground level, 20 cm, and 100 cm. Dashed line represents mean summer maximum temperature according to meteorological station on Hog Island, VA. Relative location refers to plot distance to thicket edge where -10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Error bars represent ± one standard error.

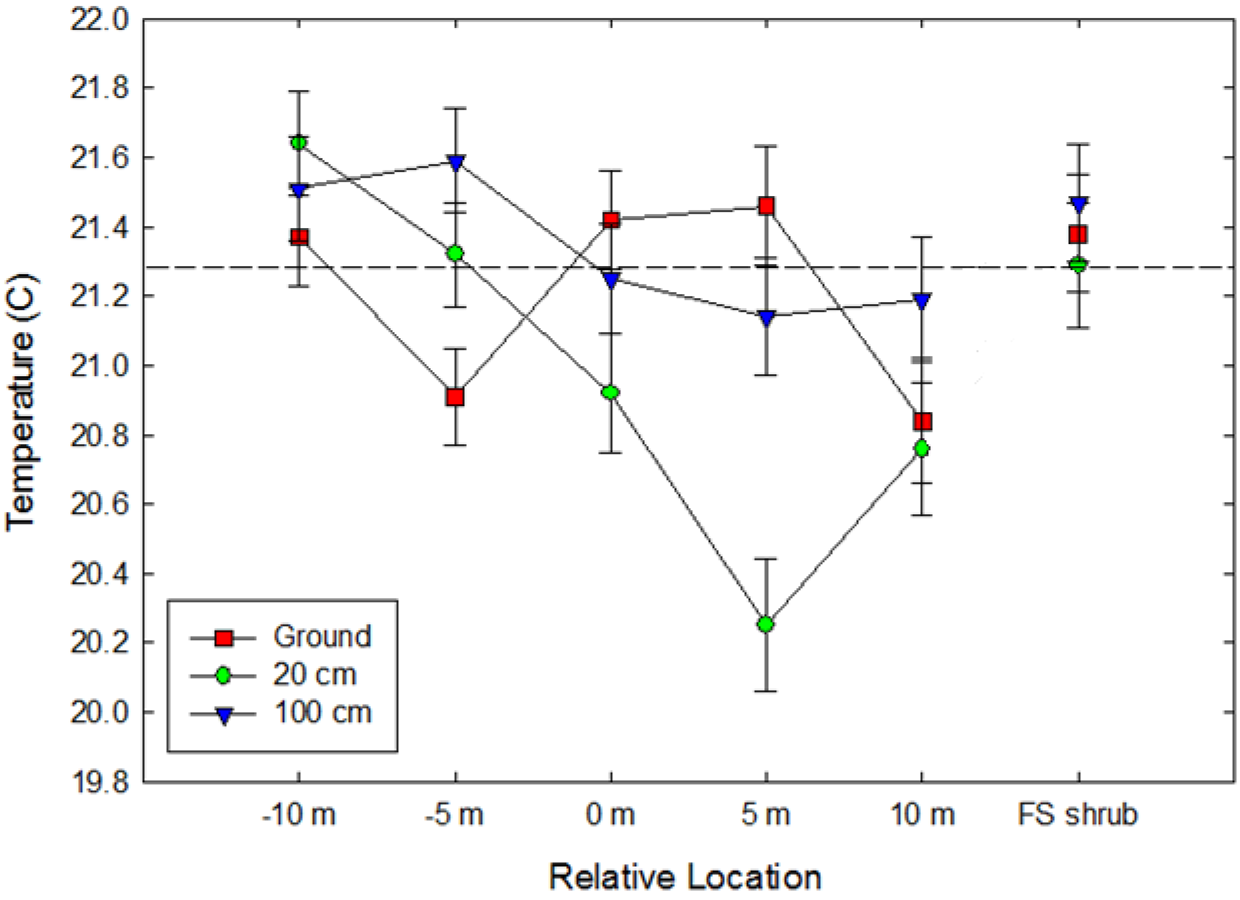

Figure 9. Mean summer minimum temperatures of plots across transects at ground level, 20 cm, and 100 cm. Dashed line represents mean summer minimum temperature according to meteorological station on Hog Island, VA. Relative location refers to plot distance to thicket edge where -10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Error bars represent ± one standard error.

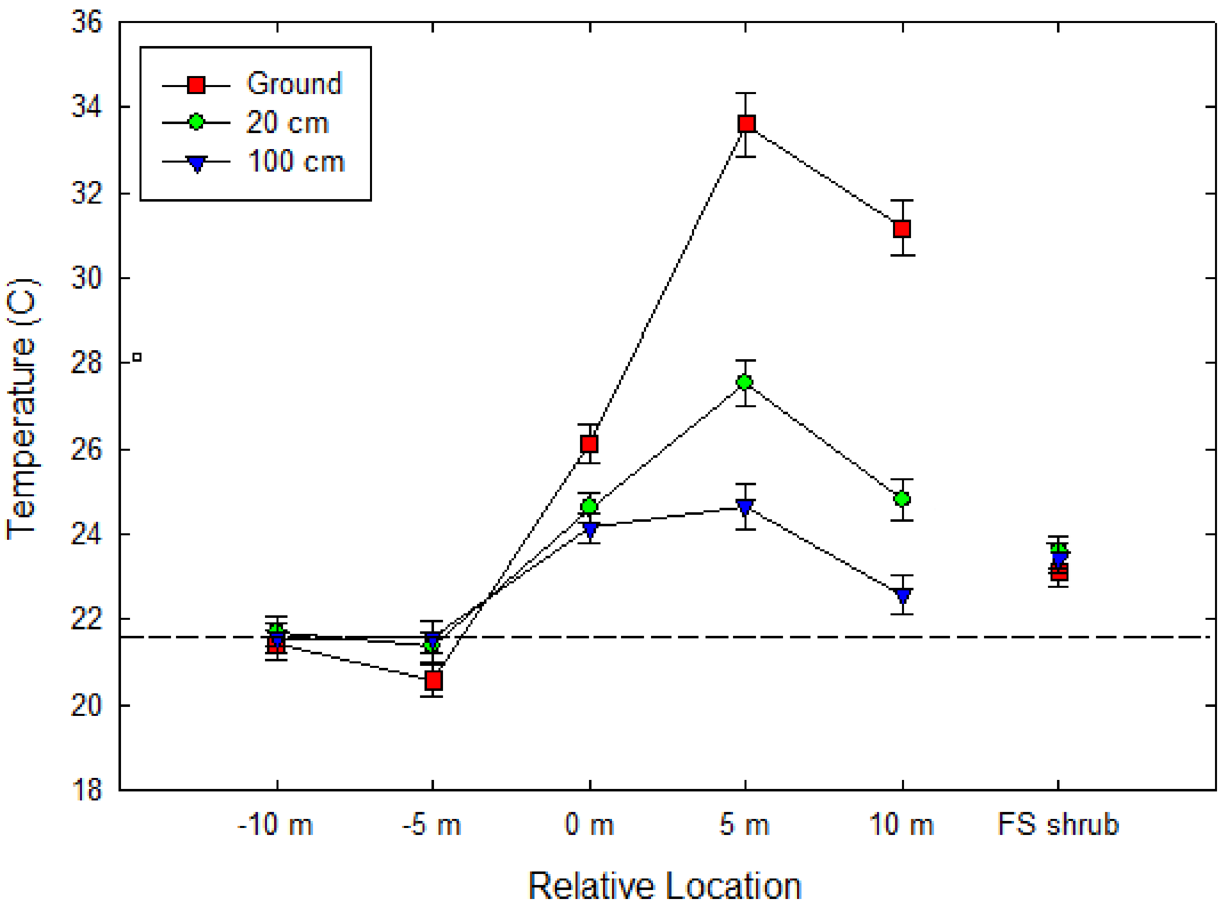

Figure 10. Mean fall maximum temperatures of plots across transects at ground level, 20 cm, and 100 cm. Dashed line represents mean fall maximum temperature according to meteorological station on Hog Island, VA. Relative location refers to plot distance to thicket edge where -10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Error bars represent ± one standard error.

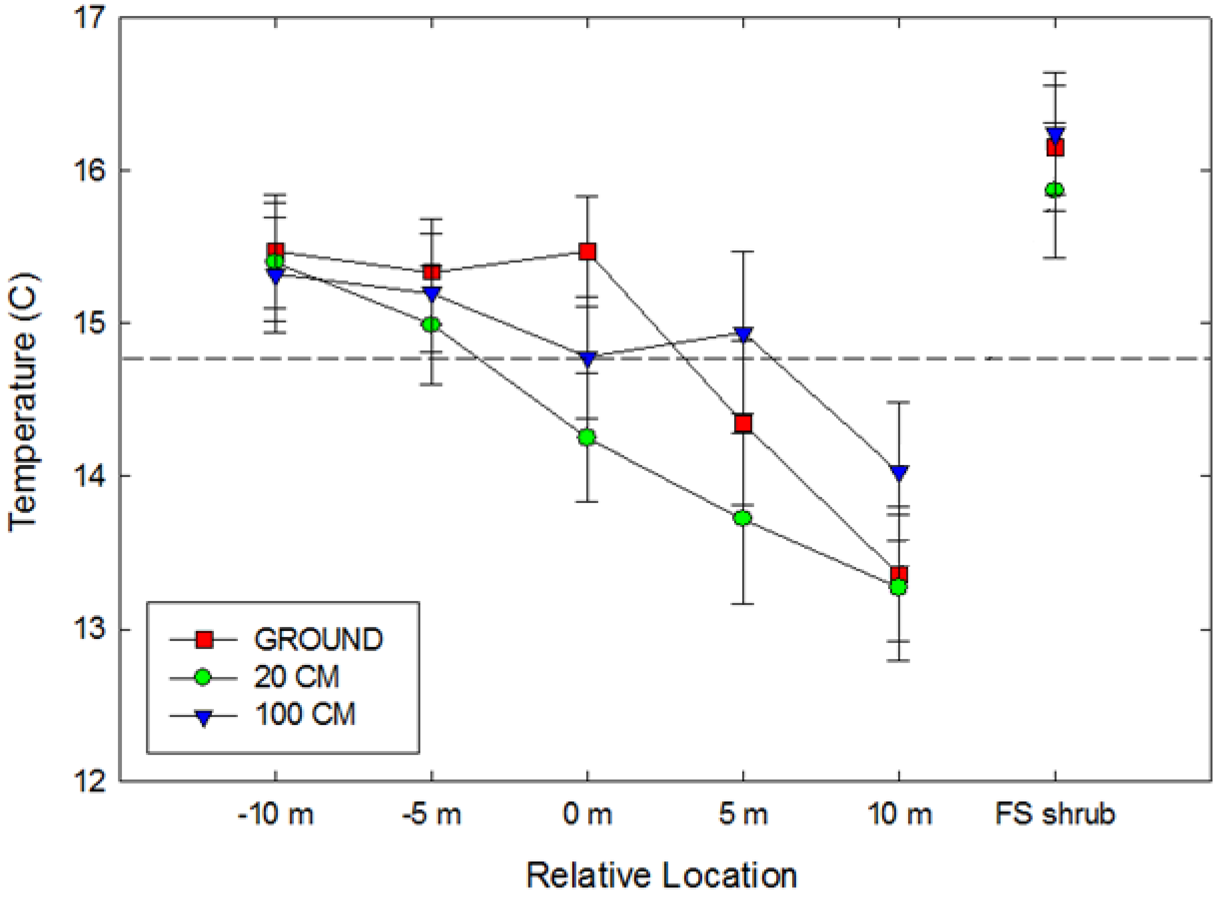

Figure 11. Mean fall minimum temperatures of plots across transects at ground level, 20 cm, and 100 cm. Dashed line represents mean fall minimum temperature according to meteorological station on Hog Island, VA. Relative location refers to plot distance to thicket edge where -10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Error bars represent ± one standard error.

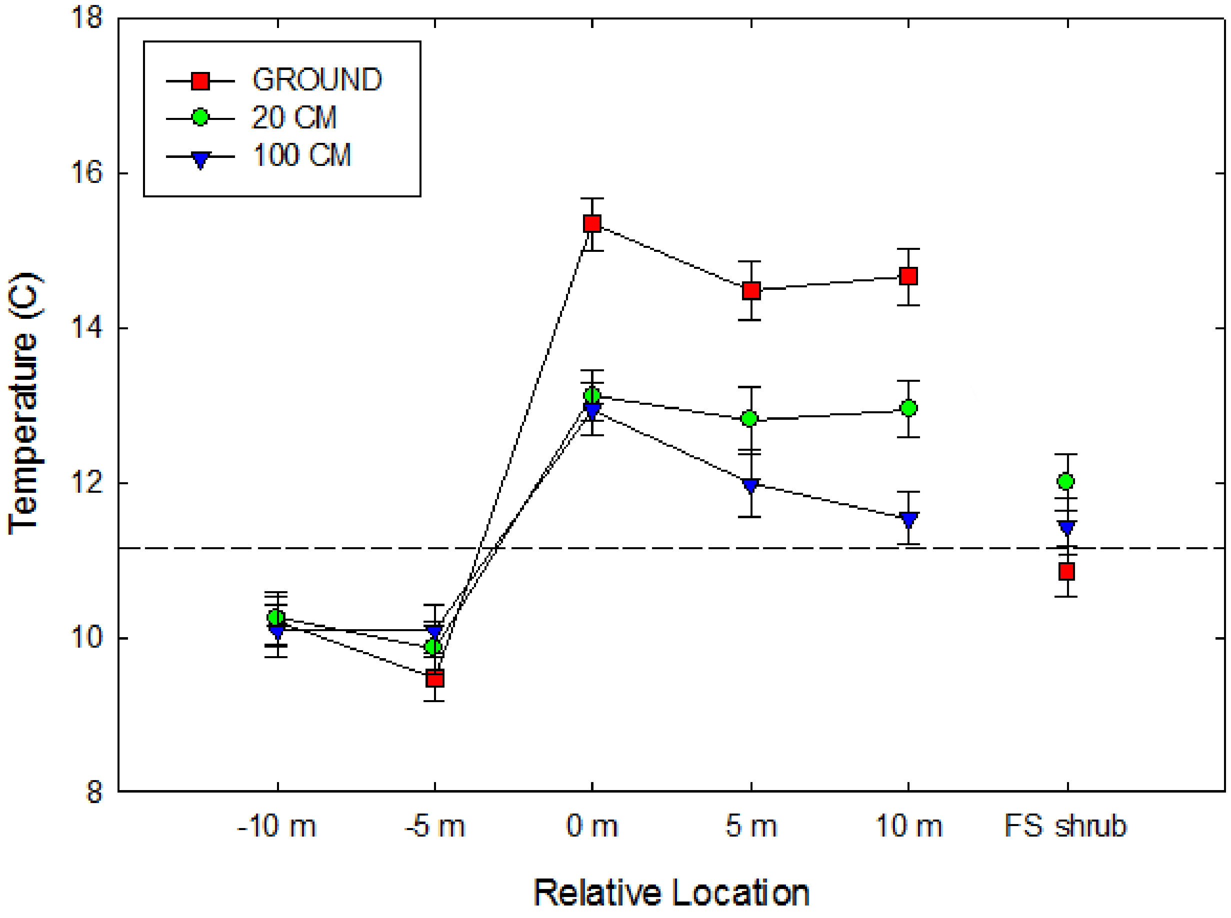

Figure 12. Mean winter maximum temperatures of plots across transects at ground level, 20 cm, and 100 cm. Dashed line represents mean winter maximum temperature according to meteorological station on Hog Island, VA. Relative location refers to plot distance to thicket edge where -10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Error bars represent ± one standard error.

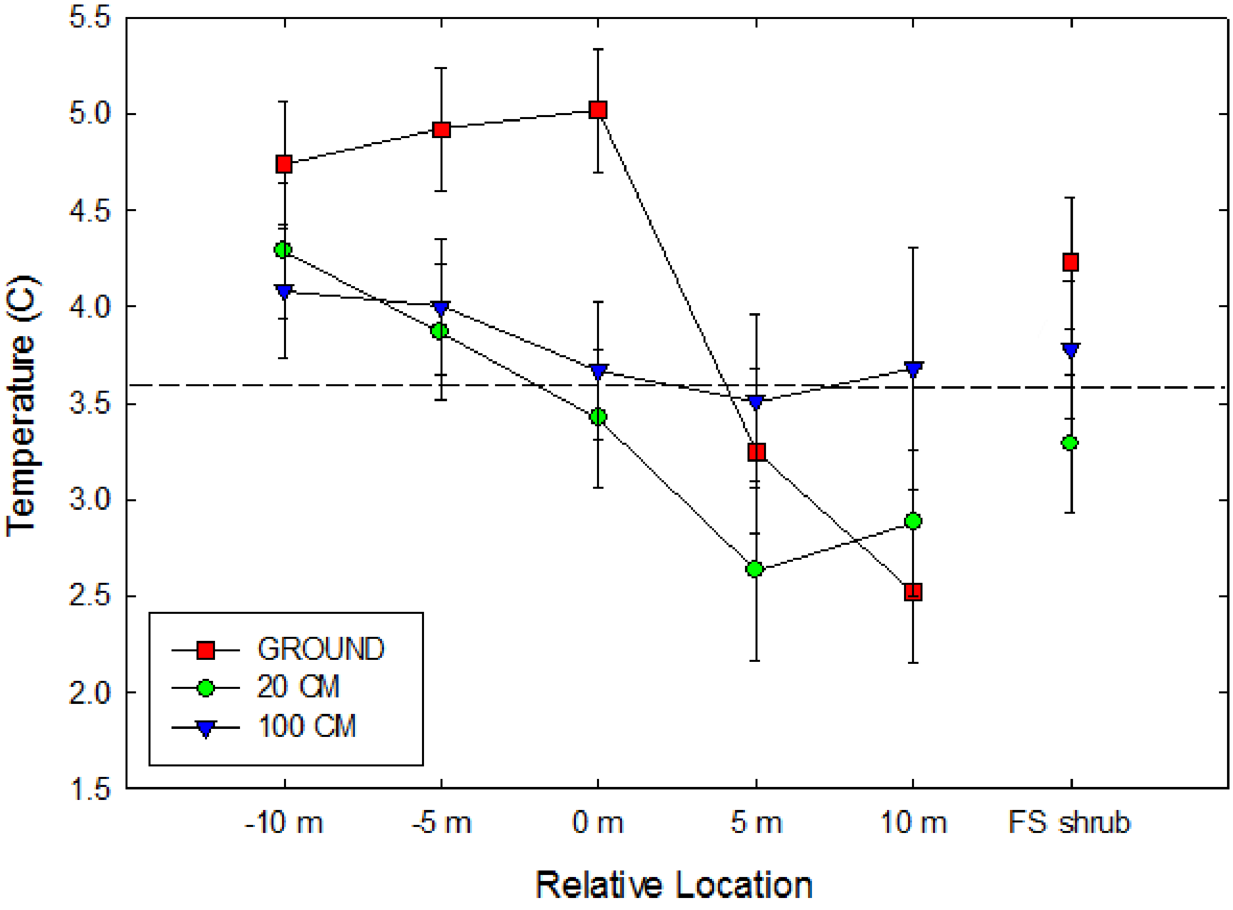

Figure 13. Mean winter minimum temperatures of plots across transects at ground level, 20 cm, and 100 cm. Dashed line represents mean winter minimum temperature according to meteorological station on Hog Island, VA. Relative location refers to plot distance to thicket edge where -10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Error bars represent ± one standard error.

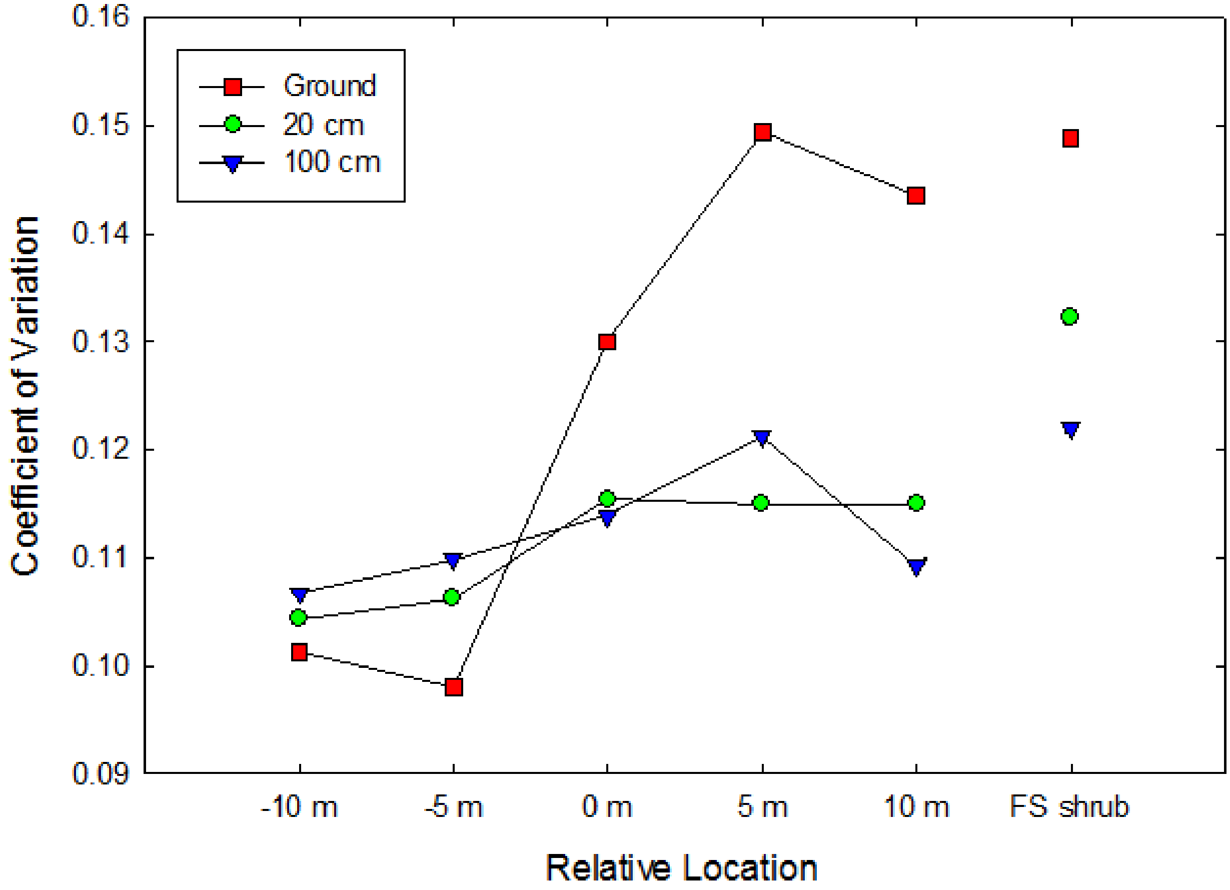

Figure 14. Coefficient of variation for mean summer maximum temperatures.

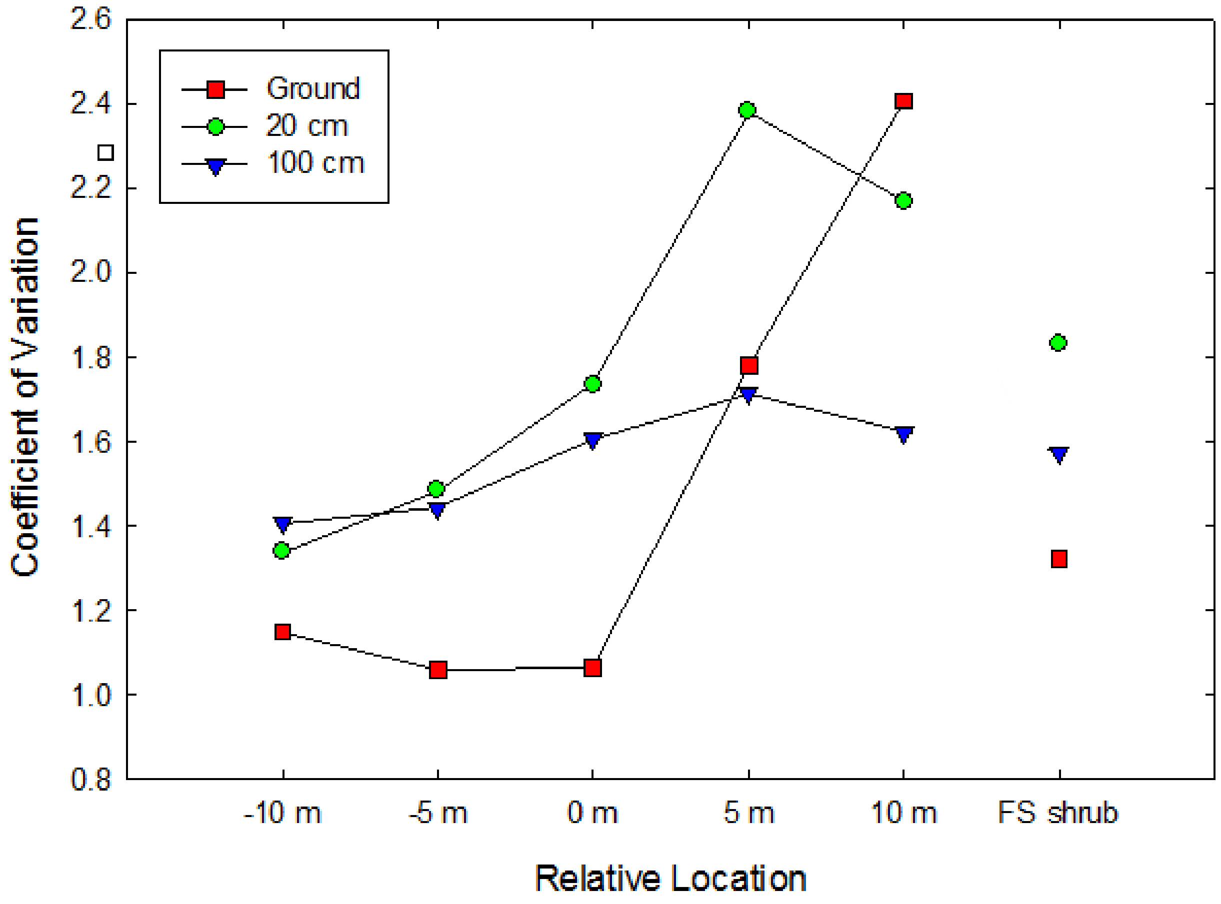

Figure 15. Coefficient of variation for mean winter minimum temperatures.

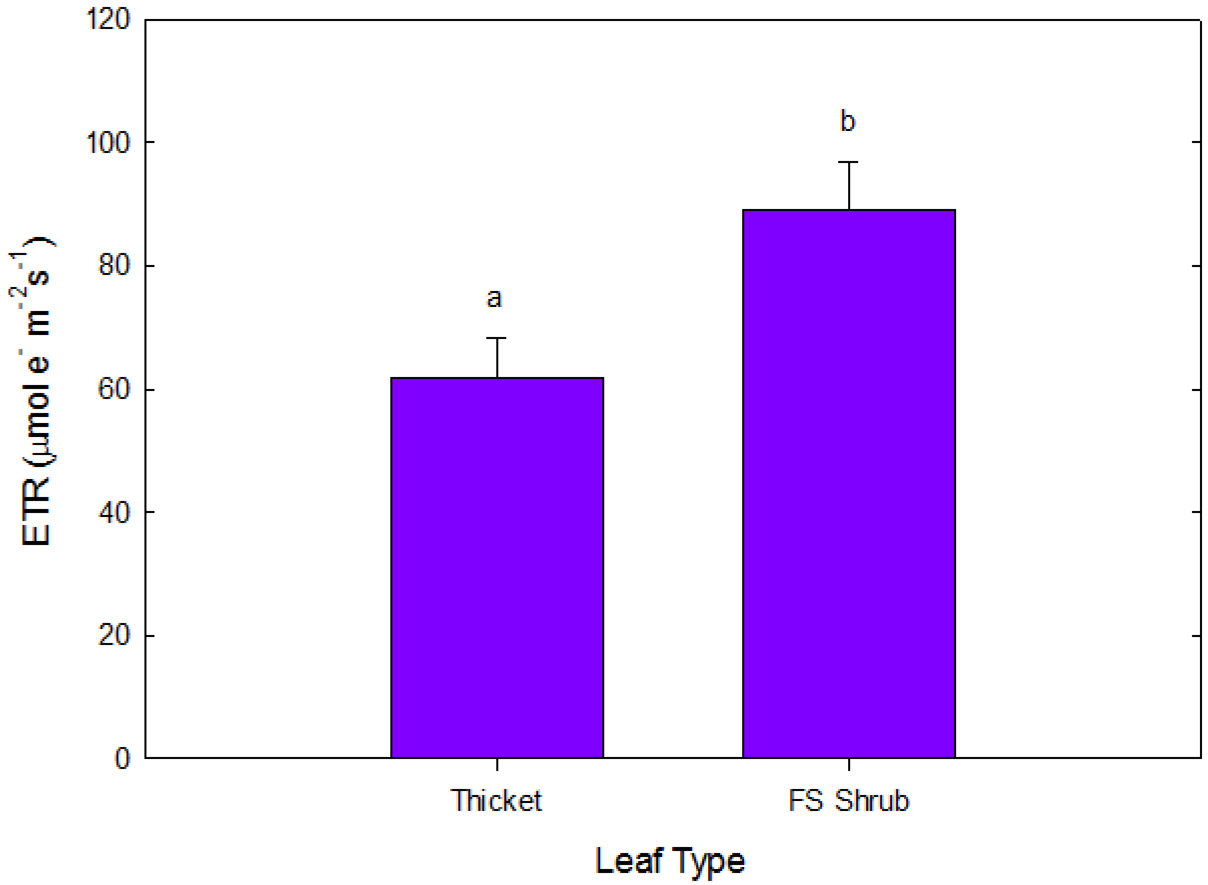

Figure 16. Electron transport rate of *M. cerifera* leaves on the thicket edge and at the free-standing shrub. Error bars represent ± one standard error.

Vita

Joseph Arthur Thompson was born on August 22, 1991 in Richmond, Virginia. Joey was stricken with a passion for the natural world before grade school and acted on that passion, exploring nearby woods and keeping various pets whenever possible. With the help of his parents, he graduated from St. Christopher's High School in Richmond, Virginia in 2010, where his teacher Billy McGuire supported and advanced his learning of the biological sciences. He went on to study biology and marine science at The College of William and Mary. There he participated in researching plant, bird, butterfly, and amphibian diversity of the Virginia Coastal Plain, and cared for the wonderful Millington Greenhouse under the guidance of Patty White-Jackson. His advisors Dr. Matthias Leu and Dr. Martha Case, and friends Alan Harris and Sean Chadwick inspired him to take his love for the natural world to the next level through establishing professional collection and identification techniques of a wide range of taxa, especially plants. After graduating from William and Mary in 2014, Joey went on to attend the Virginia Commonwealth University to acquire a Master's of Science in biology. Through his advisors Dr. Julie Zinnert and Dr. Donald Young, Joey fell in love with one of the rare wilderness areas left in Virginia, the barrier islands of the Virginia Coast Reserve (VCR), where he would conduct the thesis presented here. After his thesis at VCU, Joey plans to protect what he loves at Shenandoah National Park through invasive plant management and native plant restoration. He looks forward to expanding his knowledge of natural history, applying that information for the good of conservation, and sharing his passion with the public so that they too may take part in wonder of the natural world.