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CORTICULAR PHOTOSYNTHETIC DYNAMICS FOR A COASTAL EVERGREEN

SHRUB: *MYRICA CERIFERA*

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

CORTICULAR PHOTOSYNTHETIC DYNAMICS FOR A COASTAL EVERGREEN

SHRUB: *MYRICA CERIFERA*

By Jaclyn Kimber Vick, M.S.

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

Virginia Commonwealth University, 2007

Thesis Director: Dr. Donald R. Young
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I quantified seasonal variations in corticular photosynthesis in 1st through 5th order branches of *Myrica cerifera* L. (Myricaceae) in order to determine whether corticular photosynthesis contributes to whole plant carbon gain by reducing respirational CO₂ loss. Maximum % refixation was 110 ± 39 % of CO₂ efflux in the dark (R_d) in 1st order branches during winter, minimum was 18 ± 3 % in 5th order branches during summer. Variations in % refixation paralleled changes in photosynthetically active radiation (PAR). As light attenuated with increasing branch order % refixation decreased. Increased PAR in the winter due to a more sparse canopy lead to increases in %

refixation. Total chlorophyll content and chlorophyll *a:b* ratios were consistent with shade acclimation as branch order increased. Corticular photosynthesis may be a mechanism to enhance shrub expansion due to increased whole plant carbon use efficiency (CUE) and water use efficiency (WUE) attributed to refixation.

CHAPTER 1

Thesis Introduction

Woody plant encroachment is occurring in many ecological systems worldwide such as grasslands, savannas, tallgrass prairies, the arctic, and barrier islands (Archer et al. 1995, Briggs et al. 2005, Sturm et al. 2005, Young et al. 1995). The expansion of shrubs into these systems has been attributed to changes in disturbance and resource abundance due to changes in climate, livestock grazing, agricultural use, and fire regimes (Archer et al. 1995, Briggs et al. 2005). Barrier islands may be a useful ecological system for studying shrub encroachment due to the sensitivity of the islands to the effects of global climate change, such as sea level rise and possible changes in storm frequency (Young et al., *in press*).

Barrier islands are highly dynamic with landscapes subject to disturbances that affect successional processes (Hayden et al. 1995). Winds, waves, tides, and currents regularly impact barrier islands, as do the occasional strong storms such as hurricanes and northeasters (Levy 1990). Succession typically does not proceed beyond grass and shrubs due to the frequency of these storms (Hayden et al. 1991). Plant community composition, species distribution patterns, and diversity are influenced by abiotic factors such as sea spray, sand movement, nutrient poor soils (Ehrenfeld 1990), depth to the water table, flooding, and groundwater salinity (Hayden et al. 1995). The ability of plants to tolerate

these factors frequently leads to the organization of vegetation into discrete zones mimicking dune formation patterns resulting from beach accretion (Ehrenfeld 1990, Young et al. 1995). Low nitrogen supply (Day 1996) and moisture stress (Shao et al. 1995) may be especially limiting to plants on barrier islands.

Myrica cerifera L. (Myricaceae) is the dominant woody shrub on the barrier islands off the southeastern coast of the United States (McCaffrey and Dueser 1990, Young 1992). *Myrica* is initially bird dispersed with dense thickets rapidly forming due to vegetative propagation (Young et al. 1995). Moisture stress may limit the distribution of *Myrica* to swales because they are more mesic relative to dunes (Young et al. 1992, Young 1992, Young et al. 1995). There are currently four distinct *Myrica* shrub thickets on Hog Island, Virginia, one of more than fifteen barrier islands along the Delmarva peninsula. These four thickets represent a chronosequence across the island, with younger thickets along the seaward edge and the oldest thicket on the westernmost or Hog Island Bay side (Brantley and Young 2007). Intolerance of salinity may also limit the distribution of *Myrica* in coastal environments including Hog Island (Young et al. 1992). Although barrier islands have little nitrogen in the sandy soils, *Myrica* is actinorhizal, having an association with the nitrogen-fixing bacterium *Frankia* (Young et al. 1992). This may be one mechanism facilitating the rapid growth of *Myrica* thickets.

Another mechanism enhancing the rapid growth may be photosynthetic branches. Photosynthesis has been measured in many plant parts, including flowers, fruits, woody stems, and roots (Pfanz et al. 2002). Most woody species, such as the Sahelian shrub *Guiera senegalensis*, have green tissues within the bark layers (Levy and Jarvis 1998,

Pfanz et al. 2002). Corticular chlorenchyma is chlorophyll-containing parenchyma tissue just beneath the periderm in woody plants (Manetas 2004a, Manetas 2004b, Pfanz et al. 2002, Wittmann et al. 2001). A cross-section of *Myrica* stems reveals green tissue from just inside the periderm all the way through to the pith indicating that the stems may be photosynthetic.

Photosynthesis within stems can be broken down into four categories: (a) CAM-driven photosynthesis in stems of succulent plants, (b) stem photosynthesis in stems with stomata that uptake atmospheric CO₂, (c) corticular or bark photosynthesis, and (d) wood photosynthesis within ray cells and even the pith (Aschan and Pfanz 2003). Both CAM-driven and stem photosynthesis result in net photosynthesis (Aschan and Pfanz 2003). Corticular and wood photosynthesis are characterized by internal CO₂ refixation (Aschan and Pfanz 2003). Since *Myrica* is neither succulent nor does it have stomata along the stem, the photosynthesis within the stem may be corticular and/or wood photosynthesis. With these types of photosynthesis, respirational CO₂ is internally refixed by chloroplasts within chlorenchymal tissues (Aschan and Pfanz 2003, Wittman et al. 2001). In certain species, up to 97% of the respired CO₂ can be refixed (Wittman et al. 2006).

One aspect of corticular photosynthesis that can vary depending on species is chlorophyll content of stems. Beech stem chlorophyll content is approximately 130 mg chl m⁻², whereas ash and oak have up to 500 mg chl m⁻² (Pfanz et al. 2002). More shaded stems have higher values than sunlit stems, which may be a shade adaptation (Pfanz et al. 2002, Wittman et al. 2001). In addition, bark chlorophyll a/b ratios can be comparable to those of shade adapted leaves (Wittman et al. 2001).

Corticular photosynthesis requires both light and CO₂. Photosynthetically active radiation has to pass through several layers including epidermal and peridermal tissue in order to reach the chloroplasts of the chlorenchyma (Pfanz et al. 2002). *Myrica* has evergreen leaves and so the stems are shaded year round by the canopy. Another evergreen shrub, *Ilex aquifolium*, showed shade adaption with only 250-300 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ needed for maximum photosynthetic rates (Schmidt et al. 2000). *Myrica* may or may not display this shade adaptation. *Pinus monticola* did not reach maximum photosynthetic rates even at 2000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ of photosynthetically active radiation (Cernusak and Marshall 2000).

Internal CO₂ refixation uses CO₂ from respiration of stem tissues rather than from the atmosphere (Levy and Jarvis 1998, Pfanz et al. 2002). Although some diffusion of CO₂ into the stem may occur through lenticels, it is more likely that lenticel chlorenchyma provides an opportunity for refixation as CO₂ is being respired out of the stem (Langenfeld-Heyser et al. 1996). Respired CO₂ does not easily diffuse into the atmosphere and can build up within the stem (Pfanz et al. 2002) due to alternating layers of suberin and wax in the cell walls of phellem (Esau 1965). Build up of CO₂ is coupled with low concentrations of oxygen to the point that anaerobic fermentation is possible (Pfanz et al. 2002). Wittmann et al. (2006) measured corticular CO₂ concentrations that were six times higher than those of leaves. High levels of CO₂ and low levels of O₂ may lead to enhanced PEPcase-driven dark CO₂ fixation and reduced photorespiration (Pfanz et al. 2002). The high CO₂ concentrations may also contribute to the high photosynthetic temperature optima characteristic of corticular photosynthesis (Cernusak and Marshall 2000).

Refixation of CO₂ reduces the amount of CO₂ diffusing to the atmosphere and can increase whole plant carbon use efficiency (CUE) (Cernusak and Marshall 2000). In addition, water use efficiency (WUE) may also increase because corticular photosynthesis does not use CO₂ obtained from the atmosphere through stomata, but rather recycles internally respired CO₂, thus avoiding unnecessary water loss (Pfanz et al. 2002).

Increased CUE and WUE may be very beneficial to plants in water-limited environments, such as barrier islands where sandy soils can have a water holding capacity as low as 20% (Shao et al. 1996). *Myrica cerifera* may be able to tolerate times of water stress (when stomata are closed) by employing corticular photosynthesis. Stems are generally more tolerant of stress than leaves (Nilsen 1992). Nilsen and Bao (1990) found that the contribution of stem photosynthesis to the total canopy carbon gain during times of water stress increased from 38% to 47% in the woody legume *Spartium junceum*. This suggests that stem photosynthesis is advantageous for plants growing in water-limited environments. For this reason, corticular photosynthesis may contribute to the success of *Myrica cerifera* on barrier islands and the rapid expansion into grassy swales.

For this study I quantified variations in corticular photosynthesis across seasons for five branch orders. Branch order is an indication of branch age because size and age increase with branch order. Younger branches have been shown to be more active and have higher rates of photosynthesis than older branches (Damesin 2003, Pfanz et al. 2002, Wittmann et al. 2001). The primary objectives of this study are (1) to determine the extent to which corticular photosynthesis occurs in 1st through 5th order branches of *Myrica*

cerifera at different times of the year and (2) to determine the associated whole plant carbon gain.

The following manuscript describes my thesis research on corticular photosynthesis dynamics for a coastal evergreen shrub, *Myrica cerifera*. The manuscript has been written in the form required by the journal *Functional Ecology*.

CHAPTER 2

Corticular photosynthetic dynamics for a coastal evergreen shrub: *Myrica cerifera*

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Running head: Coastal shrub corticular photosynthesis

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Summary

1. We quantified seasonal variations in corticular photosynthetic characteristics in 1st through 5th order branches of *Myrica cerifera* L. (Myricaceae) to determine the importance of corticular photosynthesis to whole plant carbon gain.
2. Maximum mean % refixation was 110 ± 39 % of CO₂ efflux in the dark (R_d) in 1st order branches during the winter. The minimum % refixation was 18 ± 3 % in 5th order branches during the summer.
3. Variations in % refixation paralleled changes in photosynthetically active radiation (PAR). As light attenuated with increasing branch order the % refixation decreased. Increased PAR in the winter due to a more sparse canopy lead to increases in % refixation.
4. Total chlorophyll content and chlorophyll a:b ratios were consistent with shade acclimation as branch order increased.
5. Corticular photosynthesis may be a mechanism to enhance shrub expansion due to the increase in whole plant carbon use efficiency (CUE) and water use efficiency (WUE) attributed to the refixation of respiratory CO₂.

Key-words: barrier islands, CO₂ refixation, light attenuation, photosynthetic pigments, shrub expansion

Introduction

Woody plant encroachment is occurring in many ecological systems worldwide including tallgrass prairies (Briggs et al. 2005), savannas (Archer et al. 1995), and the arctic (Sturm et al. 2005). The expansion of shrubs into these systems has been attributed to changes in disturbance and resource abundance due to changes in climate, livestock grazing, agricultural use, and fire regimes (Archer et al. 1995, Briggs et al. 2005). Coastal systems and barrier islands in particular may be sensitive to the effects of climate change and for this reason are ideal for the study of shrub expansion (Young et al., *in press*). For example, Hog Island, an Atlantic coast barrier island, has experienced rapid shrub expansion of *Myrica cerifera* L. (Myricaceae), which forms dense thickets in grass-dominated swales and has become the dominant woody shrub on many barrier islands along the southeastern coast of North America (McCaffrey and Dueser 1990, Young 1992, Young et al. 1995). Despite these observations on Hog Island and for other ecological systems, physiological mechanisms that facilitate shrub expansion are not well understood. For *M. cerifera*, mechanisms that enhance rapid expansion in coastal environments may include its evergreen leaf habit, its association with the nitrogen-fixing bacterium *Frankia* (Young et al. 1992), and possibly corticular photosynthesis.

Fruits, flowers, branches, and even roots may be photosynthetic (Pfanz et al. 2002). Branch, or corticular, photosynthesis is characterized by the refixation of CO₂ from respiring living cells of xylem parenchyma, cambium, and phloem (Aschan and Pfanz 2003, Levy and Jarvis 1998), and it occurs in chlorenchyma tissue located beneath the periderm (Manetas 2004a, Manetas 2004b, Pfanz et al. 2002, Wittmann et al. 2001). The

periderm is permeable to light and highly resistant to the diffusion of gas even when lenticels are present (Damesin 2003, Manetas 2004a, Manetas 2004b). This leads to a build-up of CO₂ in the chlorenchyma tissue just beneath the periderm (Cernusak and Marshall 2000, Pfanz et al. 2002) due to alternating layers of suberin and wax in the cell walls of phellem (Esau 1965). The high CO₂ concentrations effectively eliminate photorespiration and enhance photosynthetic potential within branches (Damesin 2003, Rachmilevitch et al. 2004, Wittmann et al. 2006).

While corticular photosynthesis rarely results in a net carbon gain, it may improve whole plant carbon use efficiency (CUE) and water use efficiency (WUE) by refixing respirational CO₂ without any associated water loss as would occur through stomata with leaf photosynthesis (Cernusak and Marshall 2000, Langenfeld-Heyser 1989, Levy and Jarvis 1998, Pfanz et al. 2002, Wittmann et al. 2006). Another benefit of photosynthesis in branches is that branches may be more tolerant to environmental stress as compared to leaves (Nilsen 1992). While branch chlorenchyma often displays shade acclimation characteristics, corticular photosynthesis can be limited by the ability of the periderm to transmit light, and photosynthesis appears to be dependent on the age of the branches, with younger branches having higher activity levels (Pfanz et al. 2002).

Corticular photosynthesis may be a mechanism that enhances shrub expansion in grass dominated systems. In this study we quantified seasonal variations in corticular photosynthesis across five branch orders for *M. cerifera* on Hog Island, Virginia, USA. Branch order is indicative of branch age, which may lead to variation in corticular photosynthesis. We hypothesized that corticular photosynthesis would contribute to whole

plant carbon gain by reducing the amount of CO₂ lost via respiration and that CO₂ refixation would decrease with increasing branch order as related to decreases in incident light and associated changes in pigmentation. Our objectives were to quantify cortical photosynthesis and corresponding variations in light environments in 1st through 5th order branches, and to determine whether variations in light and photosynthetic characteristics would lead to variations in chlorophyll content and ratios.

Materials and Methods

SITE DESCRIPTION

This study was performed on Hog Island, Virginia, USA. Hog Island (37° 40' N, 75° 40' W) is 8 km from the Eastern Shore peninsula of Virginia and is approximately 1177 ha, 10 km long and 2 km across at the widest point (Semones and Young 1995). Hog Island is one in a chain of more than fifteen barrier islands along the Delmarva peninsula, and it is within the Virginia Coast Reserve, a National Science Foundation Long Term Ecological Research (LTER) site. *Myrica cerifera* is the dominant woody species on Hog Island and occurs in mesic swales (Young et al., *in press*). Measurements were taken during summer and autumn of 2006 and winter and spring of 2007 in a rapidly expanding thicket of *M. cerifera* shrubs less than ten years old and up to 4 m high (Brantley and Young 2007). Minimum and maximum temperatures during field measurements were 23 and 29 °C in summer, 10 and 17 °C in autumn, 2 and 11 °C in winter, and 16 and 27 °C in spring (Krovetz et al. 2006) (Fig. 1).

GAS EXCHANGE MEASUREMENTS

To determine variations in corticular photosynthesis of 1st through 5th order branches of *M. cerifera*, CO₂ efflux under illumination (R_l) as well as CO₂ efflux in the dark (R_d) were determined seasonally. The youngest branches with leaves were considered to be 1st order, the intersection of two 1st order branches resulted in a 2nd order branch progressing to older, thicker branches by order 5. Five samples per branch order each were excised from different *M. cerifera* shrubs with gardening sheers or a small saw and the cut ends were immediately coated with wax to avoid desiccation and to prevent the rapid release of liquid and gas phase CO₂ from the branches (Levy and Jarvis 1998; Teskey and McGuire 2005). The excised branches were measured for length and diameter to determine surface area. The samples were then placed into a portable Li-6200 infrared gas analyzer (Li-Cor, Lincoln, NE) 0.25 L chamber for 5 min in full sun (>1000 µmol m⁻² s⁻¹ photosynthetically active radiation, PAR, 0.4- 0.7 µm) at which point R_l was recorded. The chamber was then placed in a light impermeable sack for 5 min to determine R_d. Corticular photosynthetic rate (*A*) was calculated according to Wittmann et al. (2006) as:

$$A = |R_d - R_l| \quad \text{Eq. 1}$$

Percent refixation was calculated for 1st through 5th order branches using the following equation (Cernusak and Marshall 2000):

$$\% \text{ refixation} = [(R_d - R_l)/R_d] \times 100 \quad \text{Eq. 2}$$

After CO₂ measurement, samples were immediately put on ice and kept in the dark to prevent chlorophyll degradation while being transported back to the laboratory for chlorophyll analysis.

CHLOROPHYLL CONCENTRATIONS

Chlorophyll *a*, chlorophyll *b*, total chlorophyll content, and chlorophyll *a:b* ratios were determined, based on methods recommended by Sestak (1971), seasonally for 1st through 5th order branches in the lab by extracting chlorophyll from the chlorenchyma tissue overnight at 4 °C using an 80% acetone solution. Samples were then ground with an IKA A11 basic analytic mill (IKA Works, Wilmington, NC), filtered, and analyzed using a Spectronic 21 spectrophotometer at 645 and 663 nm wavelengths. Chlorophyll concentrations were calculated using the following equations (Arnon 1949):

$$\text{Chlorophyll } a = 12.7 A_{663} - 2.69 A_{645} \quad \text{Eq. 3}$$

$$\text{Chlorophyll } b = 22.9 A_{645} - 4.68 A_{663} \quad \text{Eq. 4}$$

$$\text{Chlorophyll } (a + b) = 8.02 A_{663} + 20.20 A_{645} \quad \text{Eq. 5}$$

Where A is the absorbance at the specified wavelength.

LIGHT ENVIRONMENT AND BRANCH CHARACTERISTICS

Light attenuation with increasing branch order was quantified to relate the light environment with variations in corticular photosynthesis and photosynthetic pigment concentrations across branch orders and season. The light environment was quantified in the field for ten branches each for 1st through 5th orders using a quantum sensor (model 190S, Li-Cor, Lincoln, NE). The sensor was held perpendicular to the branch and instantaneous PAR was recorded.

Diffusion of gases including CO₂ and O₂ may occur through lenticel pores potentially affecting the internal CO₂ and O₂ concentrations (Langenfeld-Heyser et al. 1996). CO₂ and O₂ concentrations determine whether photosynthesis or respiration occurs (Rachmilevitch et al. 2004), thus, corticular photosynthesis may vary as the number of lenticels varies. Therefore, lenticel density was determined for five branches of each order by counting lenticels of a predetermined area using a dissecting microscope. To account for potential effects of age and periderm thickness, branch diameters were measured on ten branches for each order using dial calipers.

STATISTICS

Two-factor analyses of variance quantified variations in season and branch order (1st through 5th) for the following metrics: CO₂ efflux in the light, CO₂ efflux in the dark, corticular photosynthetic rate, % refixation, incident PAR, total chlorophyll content, chlorophyll *a*, chlorophyll *b*, and chlorophyll *a:b*. One-factor analyses of variance quantified variations in branch diameter and lenticel density across branch orders. In addition, Kolmogorov-Smirnov (KS) and Levene's tests were used to evaluate normality and variance homogeneity, respectively. Sample independence was maintained by using a different shrub for each measurement. For all tests and statistical analyses, $\alpha = 0.05$ and *post-hoc* testing followed Tukey type where appropriate. Statistical analyses were based on recommendations of Zar (1999) and were performed using SPSS 12.0 (SPSS Inc., Chicago, IL).

Results

GAS EXCHANGE MEASUREMENTS

There was a significant effect of branch order ($p \leq 0.001$) as well as season ($p \leq 0.001$) for R_i , and there was an interaction of branch order and season ($p \leq 0.001$). Despite the interaction, R_i generally increased with increasing branch order with the highest values recorded in the summer (Fig. 2). Similarly, R_d also showed a significant effect of both branch order ($p \leq 0.001$) and season ($p \leq 0.001$), and there was a significant interaction of branch order and season ($p = 0.007$). Despite this interaction, R_d generally increased with increasing branch order and values were highest in summer (Fig. 2).

A did not vary significantly across branch orders ($p = 0.829$); however, season did have a significant effect ($p \leq 0.001$). Spring and summer had the highest A and did not differ significantly from each other ($p = 0.573$) (Fig. 2). Values for A for autumn and winter were lowest and also did not differ significantly from each other ($p = 0.998$), but they did differ significantly from those values in spring and summer ($p \leq 0.001$) (Fig. 2). There was no interaction between branch order and season ($p = 0.061$).

Percent of CO_2 refixed varied significantly across branch orders ($p \leq 0.001$) with percent refixation decreasing from 81 ± 11 % in 1st order branches to 31 ± 7 % in 5th order branches (Fig. 3). There was also an effect of season ($p \leq 0.001$) with summer having the lowest refixation, 41 ± 5 %, and spring the highest, 70 ± 6 % (Fig. 3). There was no interaction between branch order and season for percent refixation ($p = 0.616$).

CHLOROPHYLL CONCENTRATIONS

Chlorophyll *a* concentrations varied significantly across both branch order ($p \leq 0.001$) and season ($p \leq 0.001$), and there was a significant interaction ($p = 0.001$). Despite the interaction, mean chlorophyll *a* concentrations ranged from $57 \pm 4 \text{ mg m}^{-2}$ during autumn to $84 \pm 6 \text{ mg m}^{-2}$ during winter and generally increased as branch order increased from $49 \pm 3 \text{ mg m}^{-2}$ in 1st order branches to $100 \pm 6 \text{ mg m}^{-2}$ in 5th order branches (Figure 4). Similarly, chlorophyll *b* varied significantly; both branch order ($p \leq 0.001$) and season ($p \leq 0.001$) were significant and there was an interaction of order and season ($p = 0.001$). Overall, chlorophyll *b* concentrations appeared to increase with increasing branch order; $27 \pm 1 \text{ mg m}^{-2}$ in 1st order branches to $59 \pm 3 \text{ mg m}^{-2}$ in 5th order branches and ranged from $33 \pm 3 \text{ mg m}^{-2}$ in autumn up to $46 \pm 3 \text{ mg m}^{-2}$ in spring (Fig. 4). Total chlorophyll also showed significant branch order ($p \leq 0.001$) and season ($p \leq 0.001$) effects and a significant interaction ($p = 0.001$). Once again concentrations generally increased with increasing branch order going from $77 \pm 4 \text{ mg m}^{-2}$ in 1st order branches to $159 \pm 9 \text{ mg m}^{-2}$ in 5th order branches (Fig. 4). Total chlorophyll concentrations ranged from $92 \pm 6 \text{ mg m}^{-2}$ in autumn to $127 \pm 9 \text{ mg m}^{-2}$ in winter. By comparison, leaf total chlorophyll concentration was ~ 2.5 times greater.

There was an effect of branch order for chlorophyll *a:b* ratios ($p = 0.015$) as well as an effect of season ($p \leq 0.001$). There was also a significant interaction of branch order and season ($p = 0.003$). Winter had a significantly higher chlorophyll *a:b* ratio as compared to all other seasons ($p \leq 0.001$) with a mean of 1.92 ± 0.02 (Fig. 5). Chlorophyll *a:b* ratios decreased significantly from a mean of 1.79 ± 0.04 in 1st order branches to 1.67

± 0.04 in 5th order branches ($p = 0.026$). The chlorophyll $a:b$ ratio for leaves was significantly greater at 2.36 ± 0.18 .

LIGHT ENVIRONMENT AND BRANCH CHARACTERISTICS

The light environment varied significantly with branch order ($p \leq 0.001$) and season ($p \leq 0.001$). Despite the interaction of order and season ($p = 0.045$), PAR typically decreased with increasing branch order ranging from a mean of $899 \pm 75 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 1st order branches to $93 \pm 20 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 5th order branches (Fig. 6). In general, PAR was lowest in summer and highest in winter, $197 \pm 42 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $587 \pm 73 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively (Fig. 6).

Lenticel density differed significantly with branch order ($p \leq 0.001$) and ranged from 35 ± 6 lenticels cm^{-2} in 1st order branches down to 8 ± 1 lenticels cm^{-2} in 5th order branches (Fig. 7). Branch diameter also differed significantly with branch order ($p \leq 0.001$) ranging from 0.26 ± 0.01 cm in 1st order branches up to 1.86 ± 0.12 cm in 5th order branches (Fig. 7).

Discussion

We quantified seasonal corticular photosynthesis in 1st through 5th order branches of a coastal evergreen shrub, *M. cerifera*, to determine whether the refixation of respirational CO_2 may be a mechanism leading to the rapid expansion of this shrub into grass dominated mesic swales. We found that A was the highest in the spring and summer. During the summer, A decreased from 1st order to 5th order branches; the opposite trend

occurred during the spring. Similar to our summer results, Wittmann et al. (2001) found that A decreased from current year twigs of *Fagus sylvatica* to first year twigs, both grown outside in pots under full sunlight conditions. The increase in A for *M. cerifera* during the spring may be due to seasonal variation in metabolic activity of branches.

The percent of CO₂ that was refixed within the branch chlorenchyma was much higher than expected. First order branches during autumn and winter showed the potential for refixation values over 100%, which may indicate that 1st order branches are able to uptake atmospheric CO₂ through the lenticels. Lenticel density was highest for 1st order branches and the density decreased with increasing branch order and diameter.

Langenfeld-Heyser et al. (1996) concluded that CO₂ enters the branch through lenticels. The high density of lenticels in 1st order branches may afford the chlorenchyma with sufficient gas exchange for the use of atmospheric CO₂ in corticular photosynthesis. Levy and Jarvis (1998) measured refixation up to 75% in two Sahelian shrub species, *Guiera senegalensis* and *Combretum micranthum*, and Wittman et al. (2001) had refixation values up to 90% in twigs of *Fagus sylvatica* and *Populus tremula* under both 100% and 20% incident sun-light. Wittmann et al. (2006) detected refixation up to 97% of the respirational CO₂ under a light environment of 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in branches of *Betula pendula*, but there was no net corticular photosynthesis detected. Our data indicated that net corticular photosynthesis was possible in 1st order branches especially during the winter when light levels were highest. In contrast, Coe and McLaughlin (1980) found corticular photosynthesis to be minimal during the winter and probably only slightly reduced the costs of woody tissue respiration in *Cornus florida*, *Acer rubrum*, *Quercus*

alba, and *Liriodendron tulipifera* growing in a hardwood forest in eastern Tennessee, USA.

Percent refixation decreased with increasing branch order and, therefore, decreased with age. This may be a result of the older branches having a thicker outer bark that attenuates the light reaching the chlorenchyma tissue (Pfanzen et al. 2002). Our light measurements indicated that light attenuation occurred with increasing branch order. Fifth order branches experienced a near ten-fold decrease in light as compared to 1st order branches, which may have been the primary limiting factor for CO₂ refixation in higher order branches.

Chlorophyll concentrations increased with increasing branch order, which may indicate that the branches were acclimated to the decreased PAR at higher branch orders. Increased chlorophyll content has been observed in both leaves and twigs in response to low light conditions potentially for the purposes of maximizing light absorption (Wittmann et al. 2001). Total chlorophyll was unexpectedly higher during the winter and spring when light levels were high. Even the highest total chlorophyll content obtained for 5th order branches during the winter was still only 61% of total chlorophyll content of *M. cerifera* leaves.

Chlorophyll *a:b* ratios were highest in the winter and coincided with the high incident light. Similarly, Lewandowska and Jarvis (1977) noted that chlorophyll *a:b* ratios increased in leaves during the winter for *Picea sitchensis* in response to the increase in light resulting from leaf fall of surrounding deciduous trees. Surprisingly, chlorophyll *a:b* ratios from our study did not vary greatly with branch order. While the ratios did decrease

slightly with increasing branch order, the difference was minimal as compared to the difference in total chlorophyll content with branch order.

In shaded environments, the chlorophyll *a:b* ratio typically decreases due to a greater proportion of chlorophyll *b* (Levizou et al. 2004). Under shaded conditions, chlorophyll *b* is preferred due to its greater ability to harvest light compared to chlorophyll *a*, whereas chlorophyll *a* is better equipped to handle excess light energy under high light conditions (Hansen et al. 2002). Wittmann et al. (2001) found that bark chlorophyll *a:b* ratios were comparable to the ratios of shade adapted leaves. We found that chlorophyll *a:b* ratios for *M. cerifera* leaves were significantly higher as compared to branches. Our highest chlorophyll *a:b* ratio for branches collected during winter was still less than for leaves. The leaves of *M. cerifera* are exposed to a higher light environment than branches (Young 1992), which may explain the higher chlorophyll *a:b* ratio. The canopy reduces the amount of light reaching the branches, possibly leading to shade acclimation and a lower chlorophyll *a:b* ratio.

Unlike leaves, the PAR incident on branches must also permeate an outer bark layer to reach the photosynthetically active chlorenchyma layer underneath. Light is transmitted through the periderm and can reach the outer layers of wood or pith (Pfanzen et al. 2002, Wittmann et al. 2001). In one-year-old twigs of *F. sylvatica*, 19% of the light was able to be transmitted through the periderm, whereas 26% was transmitted in twigs of *P. tremula* (Wittmann et al. 2001). In general, older branches have a thicker periderm and thus greater light attenuation (Pfanzen et al. 2002). Therefore, with increasing branch order,

shade acclimation may become more prominent as branch diameter and periderm thickness increase and the PAR reaching the branches decreases.

Functional chlorenchyma tissues provide an advantage to woody plants as long as respirational CO₂ loss is reduced, thereby improving carbon use efficiency (CUE) and avoiding anaerobiosis (Pfanz et al. 2002). In addition to improving CUE, corticular photosynthesis may also increase water use efficiency (WUE) by reducing respirational CO₂ efflux without any additional water loss (Pfanz et al. 2002). Stem or corticular photosynthesis may even be less sensitive than leaf photosynthesis to environmental stresses such as drought (Nilsen and Bao 1990, Nilsen 1992). This may be particularly important to woody plants in water limited environments such as barrier islands (Shao et al. 1995). This study has shown that increased CUE and WUE due to corticular photosynthesis along with an evergreen leaf habit and an association with *Frankia* may all provide *M. cerifera* with a competitive advantage over other species allowing it to successfully invade and become established in grassy swales. We suggest that global warming, increased atmospheric CO₂, and shifts in precipitation patterns associated with climate change will lead to an increase in the importance of corticular photosynthesis as a mechanism facilitating woody plant invasion into grassy areas due to the increase in CUE and WUE up to stand level.

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Figure legends

Figure 1. Minimum, maximum, mean minimum, and mean maximum air temperatures ($^{\circ}\text{C}$) for Hog Island, VA from March 2006 through April 2007. Lines indicate dates on which field measurements were taken for the summer and autumn of 2006 and the winter and spring of 2007. Vertical tick marks represent the first day of the indicated month.

Figure 2. CO_2 efflux in the light (R_l) (top), CO_2 efflux in the dark (R_d) (middle), and cortical photosynthetic rate (A) (bottom) for branch orders 1-5 of *Myrica cerifera* stems during the summer and autumn of 2006 and the winter and spring of 2007 on Hog Island, Virginia. Values represent means \pm standard errors ($n=5$).

Figure 3. Percent of CO_2 refixed as a function of CO_2 efflux in the dark for branch orders 1-5 of *Myrica cerifera* stems during the summer and autumn of 2006 and the winter and spring of 2007 on Hog Island, Virginia. Values represent means \pm standard errors ($n=5$).

Figure 4. Chlorophyll *a* (top), chlorophyll *b* (middle), and total chlorophyll content (bottom) for branch orders 1-5 of *Myrica cerifera* stems during the summer and autumn of 2006 and the winter and spring of 2007 on Hog Island, Virginia. Values represent means \pm standard errors ($n=5$).

Figure 5. Chlorophyll *a:b* ratios for branch orders 1-5 of *Myrica cerifera* stems during the summer and autumn of 2006 and the winter and spring of 2007 on Hog Island, Virginia. Values represent means \pm standard errors (n= 5).

Figure 6. Photosynthetically active radiation (PAR) for branch orders 1-5 of *Myrica cerifera* stems during the summer and autumn of 2006 and the winter and spring of 2007 on Hog Island, Virginia. Values represent means \pm standard errors (n= 5).

Figure 7. Lenticel density (top) and branch diameter (bottom) for branch orders 1-5 of *Myrica cerifera* stems during the summer and autumn of 2006 and the winter and spring of 2007 on Hog Island, Virginia. Values represent means \pm standard errors (n= 5).

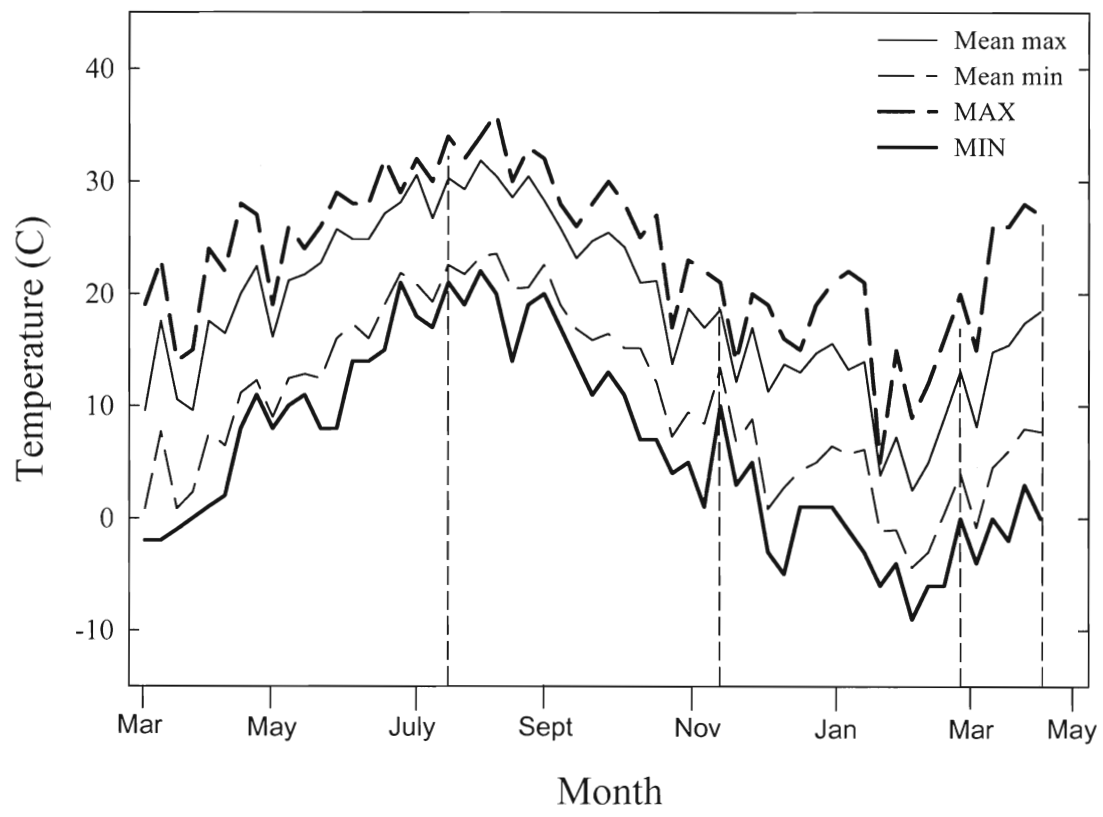


Figure 1.

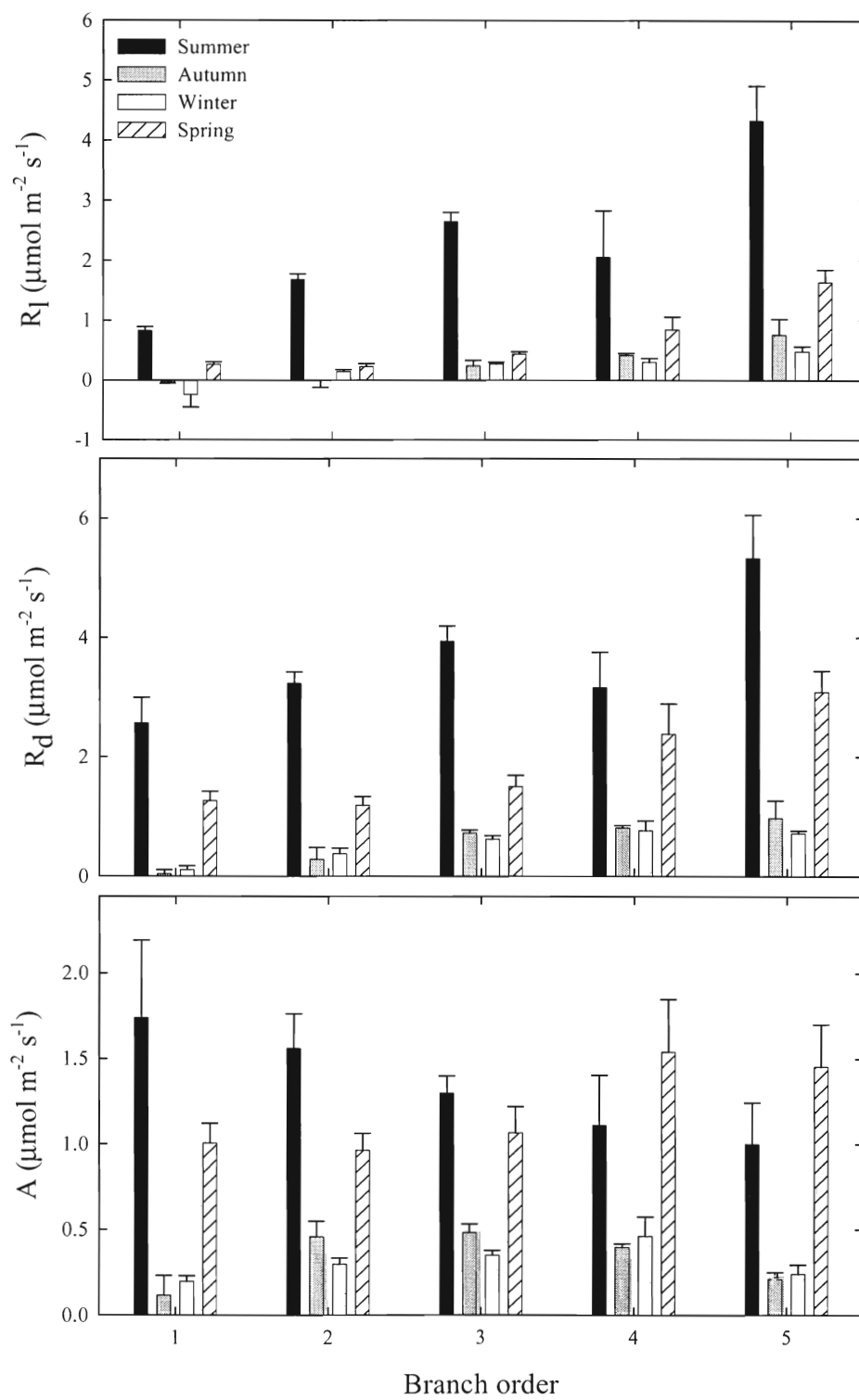


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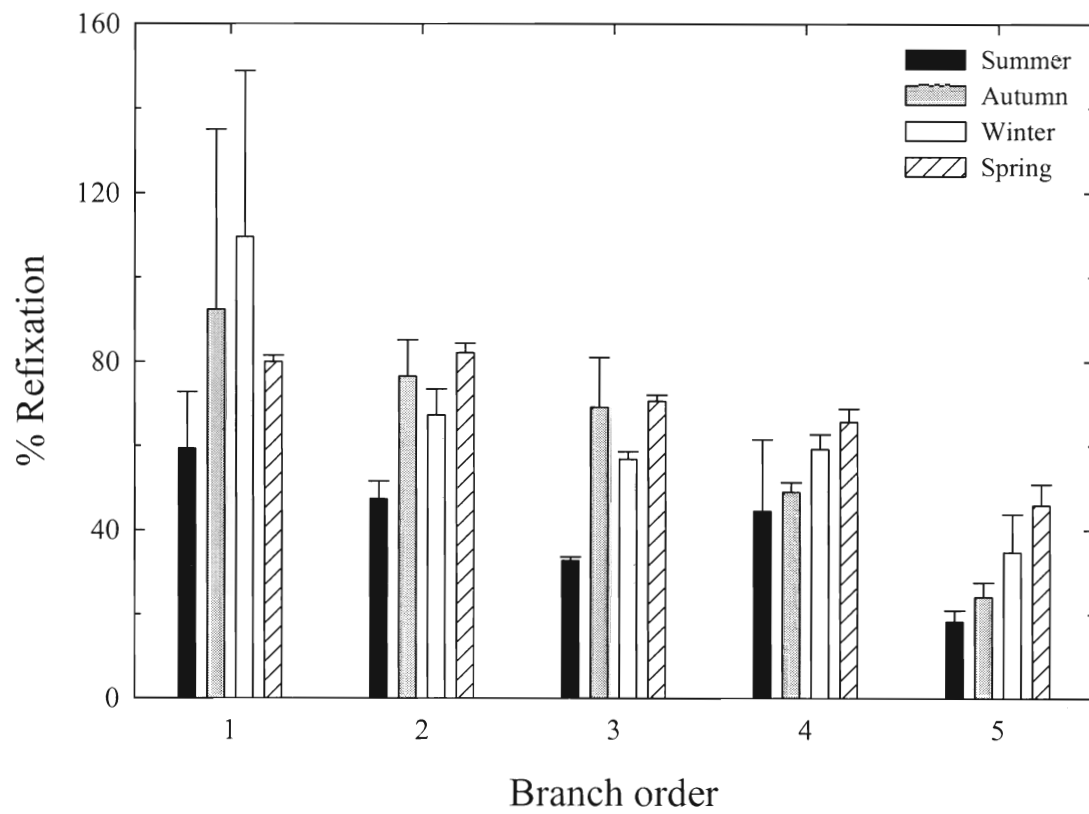


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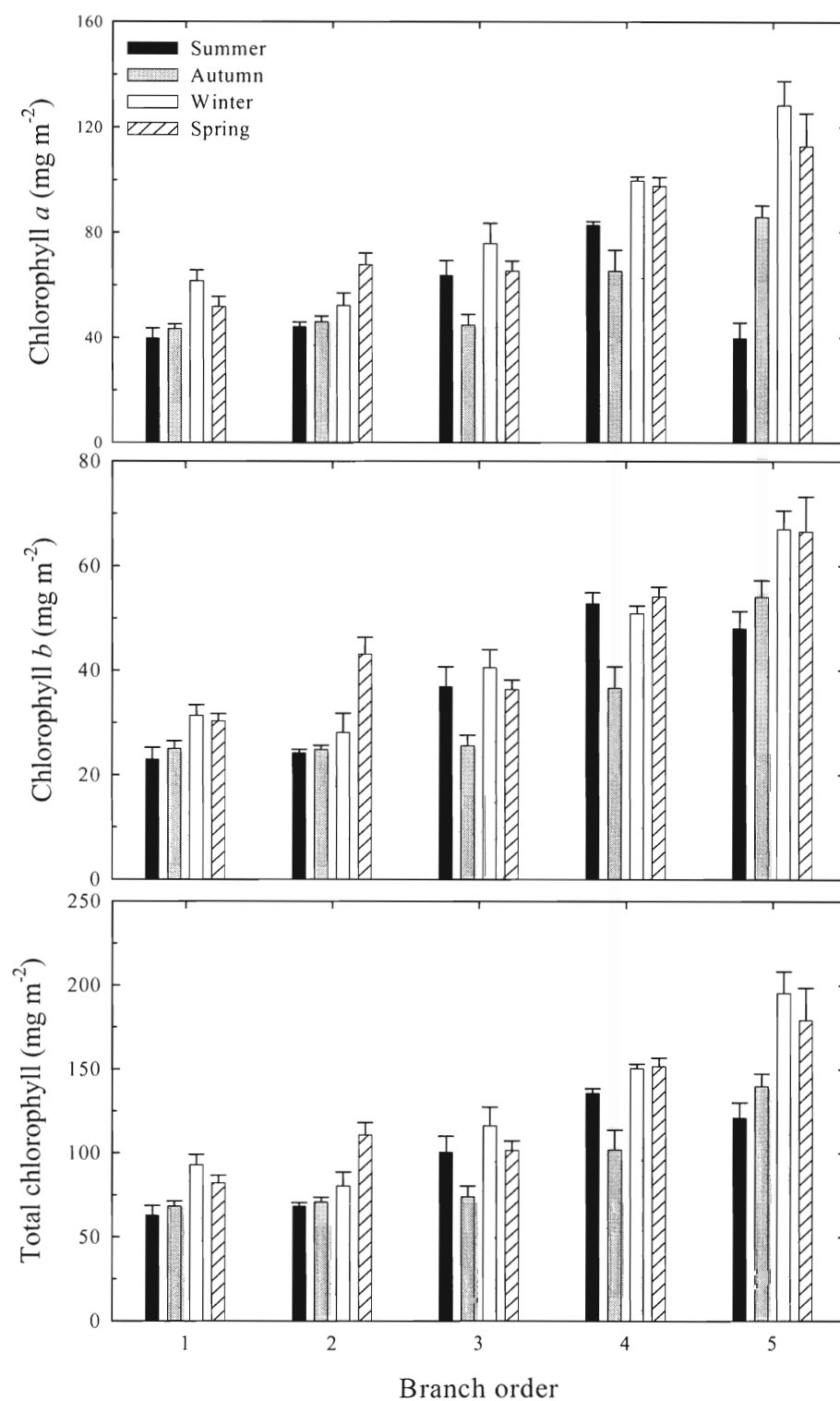


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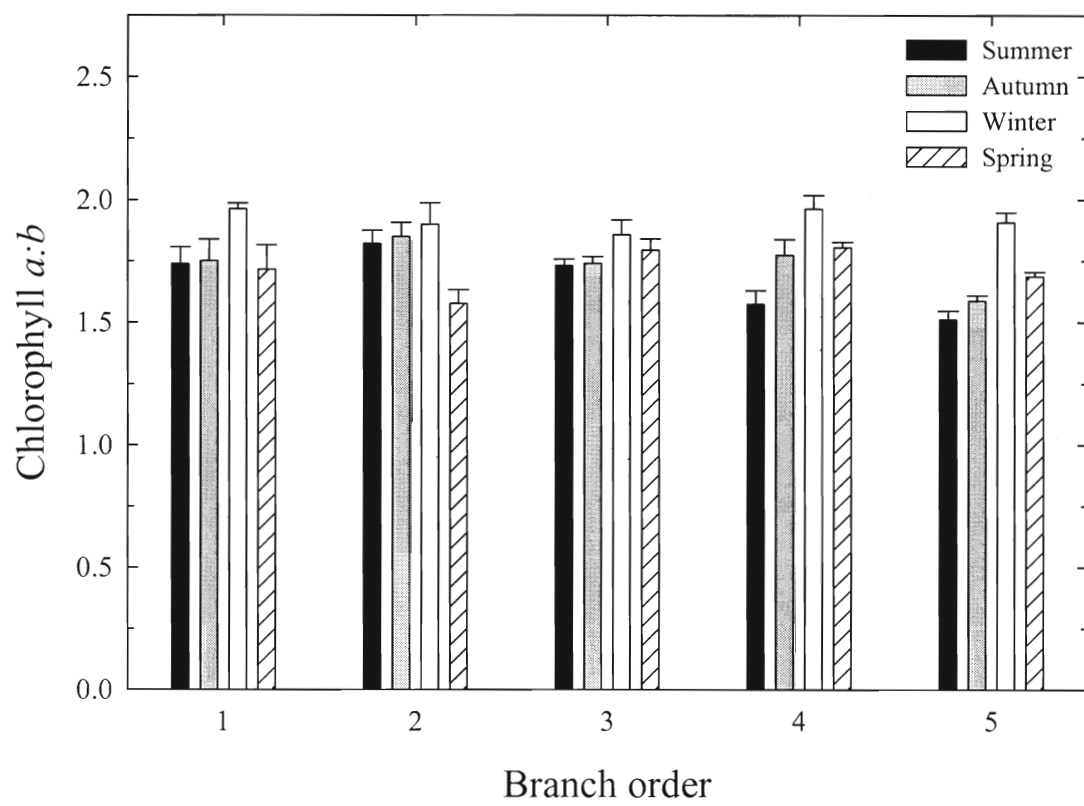


Figure 5.

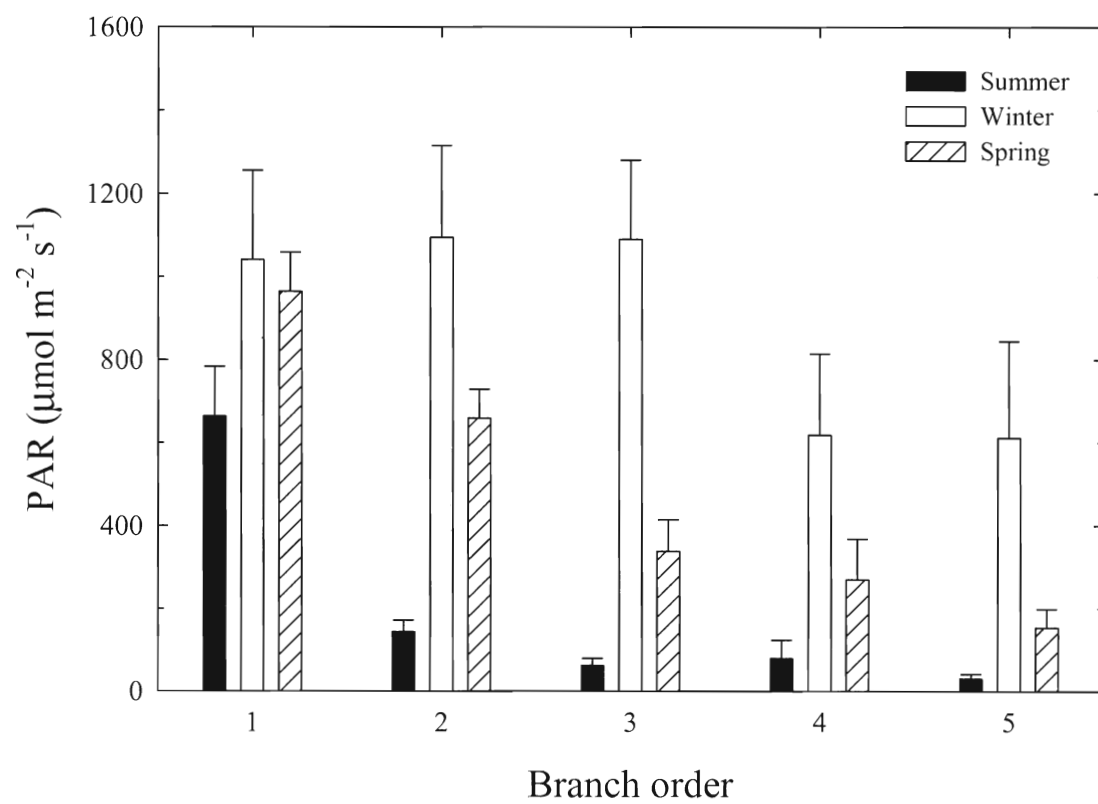


Figure 6.

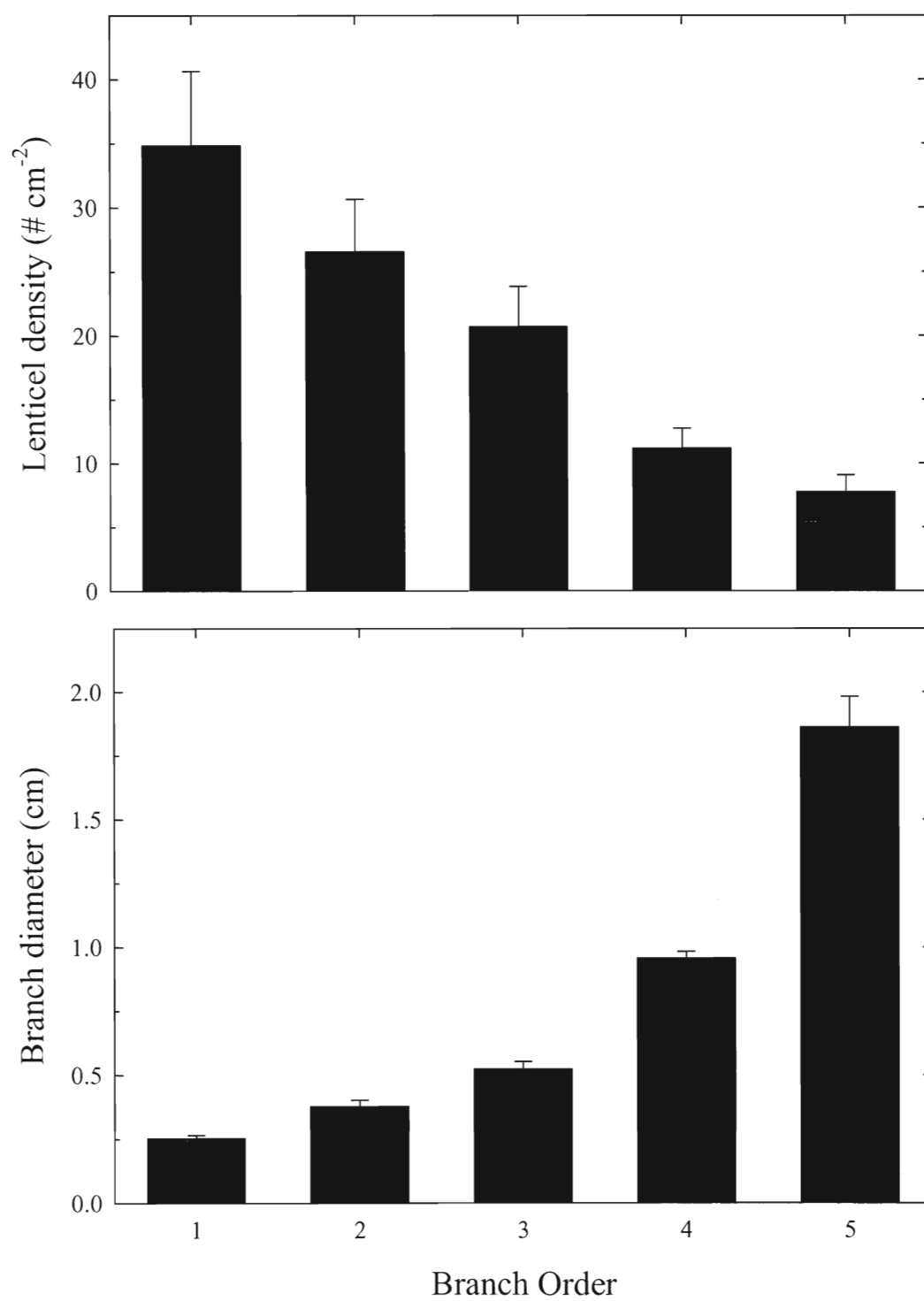


Figure 7.

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