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Corticular photosynthesis: A mechanism to enhance shrub expansion in coastal environments

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Abstract

Myrica cerifera L. (Myricaceae), the dominant woody species on many barrier islands along the southeastern coast of the United States, is expanding into grass-dominated, mesic, interdunal depressions where it forms dense thickets. Expansion may be attributed to a symbiotic nitrogen fixation with the bacterium *Frankia*, an evergreen leaf habit and, possibly, corticular photosynthesis (CP, *i.e.* refixation of respired CO_2, %ref). We quantified seasonal variations in CP characteristics in first through fifth order branches of *M. cerifera* to determine the extent and relevance of CP to shrub expansion in coastal environments. Maximum mean %ref was 110±39 % of CO_2 efflux in the dark (R_D) in first order branches during winter. Minimum %ref was 18±3 % in fifth order branches during summer. Variations in %ref paralleled changes in incident photosynthetic photon flux density (PPFD). As incident PPFD attenuated with increasing branch order, %ref decreased. A less dense canopy in winter led to increased PPFD and increases in %ref. Total chlorophyll (Chl) content and Chl *a/b* ratios were consistent with shade acclimation as branch order increased. CP may be a mechanism to enhance *M. cerifera* shrub expansion because of the potential increase in whole plant carbon use efficiency and water use efficiency attributed to refixation of respired CO_2.

Additional key words: attenuation; barrier islands; chlorophyll; CO_2 refixation; gross photosynthesis; respiration; shrub expansion.

Introduction

Woody plant encroachment is occurring in many ecological systems worldwide including tall grass prairies (Briggs *et al.* 2005), savannas (Archer *et al.* 1995), and the arctic (Sturm *et al.* 2005). Expansion of shrubs into these systems has been attributed to changes in disturbance and resource abundance caused by shifts in climate, livestock grazing patterns, agricultural use, and fire regimes (Archer *et al.* 1995, Briggs *et al.* 2005). Coastal systems and barrier islands in particular may be sensitive to effects of climate change and for this reason are ideal for the study of shrub expansion (Young *et al.* 2007). For example, Hog Island, an Atlantic coast barrier island, has experienced rapid shrub expansion of *Myrica cerifera* L. (Myricaceae) into grass dominated swales (*i.e.* mesic, interdunal depressions). As a result, *M. cerifera* has become the dominant woody shrub on many barrier islands along the southeastern coast of North America (Young 1992, Young *et al.* 1995). Other *Myrica* species, such as *M. rubra*, are cultivated in southeastern China (Guo *et al.* 2006) and their photosynthetic metabolism is intensively studied. Despite the 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 an evergreen leaf habit, a symbiotic association with the nitrogen-fixing bacterium *Frankia* (Young *et al.* 1992), and possibly corticular photosynthesis (CP).

Branch, or corticular, photosynthesis is characterized by refixation of CO_2 from respiring living cells of xylem parenchyma, cambium, and phloem (Levy and Jarvis 1998, Aschan and Pfanz 2003), and it occurs in chlorenchyma tissue located beneath the periderm (Wittmann *et al.* 2001, Pfanz *et al.* 2002, Manetas 2004a,b). Periderm is permeable to radiant energy but highly resistant to diffusion of gas (Damesin 2003, Manetas 2004a,b).

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Abbreviations: CP – corticular photosynthesis; CUE – carbon use efficiency; P_G – gross photosynthesis; PPFD – photosynthetic photon flux density; R_D – CO_2 efflux in the dark; R_L – CO_2 efflux under irradiation; WUE – water use efficiency.

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This leads to a build-up of CO_2 in chlorenchyma tissue just beneath the periderm (Cernusak and Marshall 2000, Pfanz *et al.* 2002). High CO_2 concentrations effectively eliminate photorespiration and enhance photosynthetic potential within branches (Damesin 2003, Rachmilevitch *et al.* 2004, Wittmann *et al.* 2006).

While CP rarely results in a net carbon gain at the tissue level, it may improve whole plant carbon use efficiency (CUE) and water use efficiency (WUE) by refixing respired CO_2 without any associated water (Langenfeld-Heyser 1989, Levy and Jarvis 1998, Cernusak and Marshall 2000, Pfanz *et al.* 2002, Wittmann *et al.* 2006). For *M. cerifera*, a higher photosynthetic rate in younger branches may contribute to rapid shoot growth during spring and summer months leading to low irradiance inhibition of other species near the edge of *M. cerifera* thickets. Expanding, monospecific stands of *M. cerifera* may in part be a result of this rapid shoot growth.

CP may be a mechanism that enhances shrub expansion in grass dominated systems because of increased CUE and WUE, and rapid shoot growth during spring and summer. In this study we quantified seasonal variations in CP across five branch orders for *M. cerifera* on Hog Island, Virginia, USA. We hypothesized that CP may contribute to whole plant carbon gain by reducing the amount of CO_2 lost *via* respiration and that CO_2 refixation would decrease with increasing branch order as related to decreases in incident PPFD and associated changes in pigmentation. Our objectives were to quantify CP and corresponding variations in irradiance in first through fifth order branches, and to determine whether variations in photosynthetic characteristics and chlorophyll (Chl) contents are related to variations in PPFD among branch orders throughout the year.

Materials and methods

Site: 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 750 ha, 10 km long, and 2.5 km across at the widest point (Young *et al.* 2007). Hog Island is one in a chain of more than fifteen barrier islands along the coast of Virginia, USA, and it is within the Virginia Coast Reserve, a National Science Foundation Long Term Ecological Research (LTER) site. *M. cerifera* is the dominant woody species on Hog Island and occurs in mesic swales (Young *et al.* 2007). Data were collected between July of 2006 and November 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).

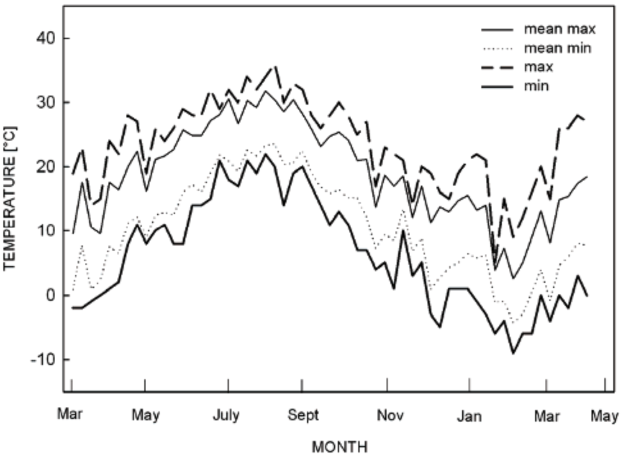

Fig. 1. Minimum, maximum, mean minimum, and mean maximum air temperatures [°C] for Hog Island, VA from March 2006 through April 2007. *Lines* indicate dates on which field measurements were taken for summer and autumn of 2006 and winter and spring of 2007. *Vertical tick marks* represent the first day of the indicated month.

Gas exchange: To determine variations in CP of first through fifth order branches of *M. cerifera*, CO_2 efflux under irradiance (R_L) as well as CO_2 efflux in the dark (R_D) were determined seasonally. The youngest branches with leaves were considered to be first order, the intersection of two first order branches resulted in a second order branch progressing to older, thicker branches by order 5. There are a maximum of three years difference between first and fifth order branches. Five samples per branch order each were excised from different *M. cerifera* shrubs with gardening shears or a small saw and cut ends were immediately coated with wax to avoid desiccation and to prevent rapid release of liquid and gas phase CO_2 from branches (Levy and Jarvis 1998, Teskey and McGuire 2005). Excised branches were measured for length and diameter to determine surface area. Samples were then placed into a portable infrared gas analyzer (*Li-6200*, *Li-Cor*, Lincoln, Nebr, USA) 250 cm^3 chamber for 5 min in full sun (>1 000 μmol m^{-2} s^{-1} photosynthetic photon flux density, PPFD, 0.4–0.7 μm) at which point R_L was recorded. The chamber was then placed in an opaque sack for 5 min to determine R_D. Gross photosynthesis (P_G) was calculated according to Cernusak and Marshall (2000) as: $P_G = R_D - R_L$. Percent refixation (%ref) was calculated for first through fifth order branches using the following equation (Cernusak and Marshall 2000): $\%ref = [(R_D - R_L)/R_D] \times 100$. After CO_2 measurement, samples were immediately put on ice and kept in the dark to prevent Chl degradation while being transported back to the laboratory for Chl analysis.

Photosynthetic chemical reactions discriminate against ^{13}C, so CP may result in a more negative $\delta^{13}C$ value as compared to the $\delta^{13}C$ value of atmospheric CO_2

because of discrimination during re-assimilation of respired CO_2 within branches (Cernusak *et al.* 2001). For this reason, differences between $\delta^{13}C$ values of leaves and various tissues within branches may be another indication that respired CO_2 is being recycled within branches. $\delta^{13}C$ values for five ground samples each of wood, chlorenchyma, and bark tissues of third order branches and five leaves were measured using a continuous flow isotope ratio mass spectrometer (*Hydra 20/20*, *Europa Scientific*, Cambridge, UK) at the Stable Isotope Facility at the University of California, Davis.

Chl contents were determined, based on methods recommended by Šesták (1971), seasonally for first through fifth order branches in the laboratory by extracting Chl from chlorenchyma tissue overnight at 4 °C immersed in an 80 % acetone solution. Samples were then ground with a basic analytic mill (*A11*, *IKA Works*, Wilmington, NC, USA), filtered, and analyzed using a spectrophotometer (*Spectronic 21*, *Thermo Electron Corporation*, Waltham, Mass, USA) at 645 and 663 nm wavelengths. Chl concentrations were calculated using equations of Arnon (1949).

PPFD and branch characteristics: Attenuation with increasing branch order was measured to relate incident PPFD with variations in CP and photosynthetic pigment contents across branch orders and season. PPFD was quantified in the field for ten branches each for first through fifth orders using a quantum sensor (*190S*, *Li-Cor*, Lincoln, Nebr, USA). The sensor was held perpendicular to the branch and incident PPFD was recorded; measurements were taken between 11:00 and 13:00 h on clear days.

Diffusion of gases including CO_2 and O_2 may occur through lenticel pores potentially affecting internal CO_2 and O_2 concentrations (Langenfeld-Heyser *et al.* 1996). - CO_2 and O_2 concentrations determine whether photosynthesis or respiration occurs (Rachmilevitch *et al.* 2004), thus, CP may vary as 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.

Results

Gas exchange: There was a significant effect of branch order ($p \leq 0.001$) and season ($p \leq 0.001$) for R_L, as well as an interaction ($p \leq 0.001$). Despite interaction, R_L generally increased with increasing branch order with highest values recorded in 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 an interaction ($p=0.007$). Despite this interaction, R_D generally increased with increasing branch order and values were highest in summer (Fig. 2).

P_G did not vary significantly across branch orders ($p=0.829$); however, season did have a significant effect ($p \leq 0.001$). P_G was highest in spring and summer and did not differ significantly between these seasons ($p=0.573$) (Fig. 2). Values for P_G 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 both 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 %ref decreasing from 81±11 % in first order branches to 31±7 % in fifth order branches (Fig. 3). There was also an effect of season ($p \leq 0.001$) with summer having lowest %ref, 41±5 %, and spring the highest, 70±6 % (Fig. 3). There was no interaction between branch order and season for %ref ($p=0.616$).

Third order $\delta^{13}C$ values for branch tissues varied significantly ($p \leq 0.001$). Bark $\delta^{13}C$ values were significantly more negative than both chlorenchyma ($p=0.037$) and wood ($p \leq 0.001$). Chlorenchyma $\delta^{13}C$ values were significantly more negative than wood ($p=0.023$). Finally, while leaf $\delta^{13}C$ values did not vary significantly from wood values ($p=0.053$) or chlorenchyma values ($p=0.945$), leaf $\delta^{13}C$ values were significantly higher than bark values ($p=0.007$) (Fig. 4).

Chl *a* contents varied significantly across both branch order ($p \leq 0.001$) and season ($p \leq 0.001$), and there was an interaction ($p=0.001$). Despite interaction, mean Chl *a* content ranged from 57±4 mg m^{-2} during autumn to 84±6 mg m^{-2} during winter and generally increased as branch order increased from 49±3 mg m^{-2} in first order branches to 100±6 mg m^{-2} in fifth order branches (Fig. 5). Similarly, for Chl *b* both branch order ($p \leq 0.001$) and season ($p \leq 0.001$) were significant and there was an interaction ($p=0.001$). Overall, Chl *b* contents increased with increasing branch order; 27±1 mg m^{-2} in first order branches to 59±3 mg m^{-2} in fifth order branches and ranged from 33±3 mg m^{-2} in autumn to 46±3 mg m^{-2} in spring (Fig. 5). Total Chl content also showed significant branch order (p≤0.001) and season ($p \leq 0.001$) effects and a significant interaction ($p=0.001$). Once again contents generally increased with increasing branch order going from 77±4 mg m^{-2} in first order branches to 159±9 mg m^{-2} in fifth order branches (Fig. 5). Total Chl contemts ranged from 92±6 mg m^{-2} in autumn to 127±9 mg m^{-2} in winter. By comparison, leaf total Chl content was ~2.5 times greater.

There was an effect of branch order for Chl *a/b* ratios ($p=0.015$) as well as an effect of season ($p \leq 0.001$) and an

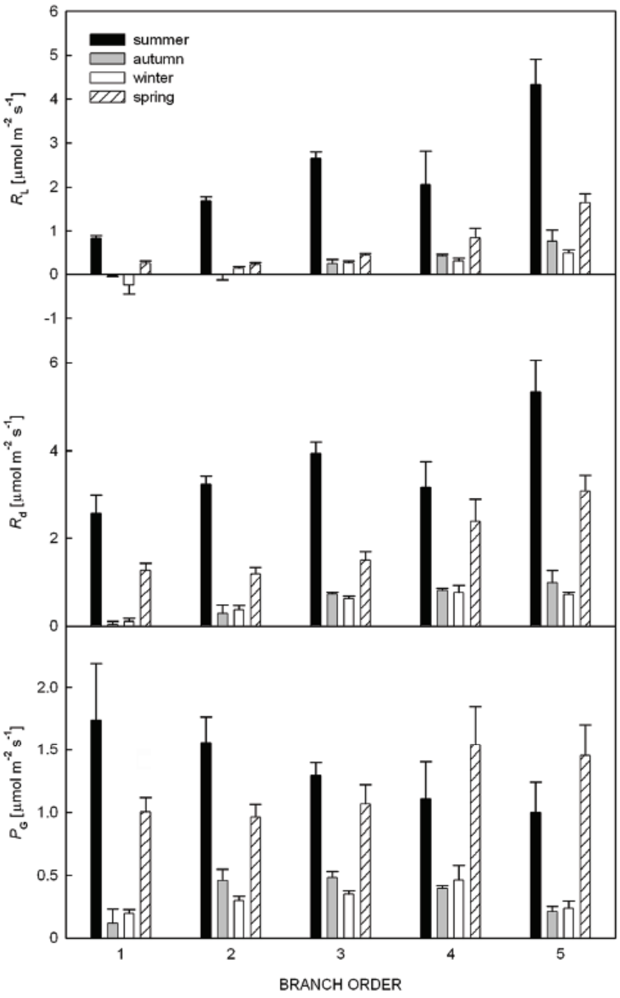

Fig. 2. CO_2 efflux under irradiation (R_L) (*top*) or in the dark (R_D) (*middle*), and gross photosynthesis, P_G (*bottom*) for branch orders 1−5 of *Myrica cerifera* during summer and autumn of 2006 and winter and spring of 2007 on Hog Island, Virginia. Means ± SE (n = 5).

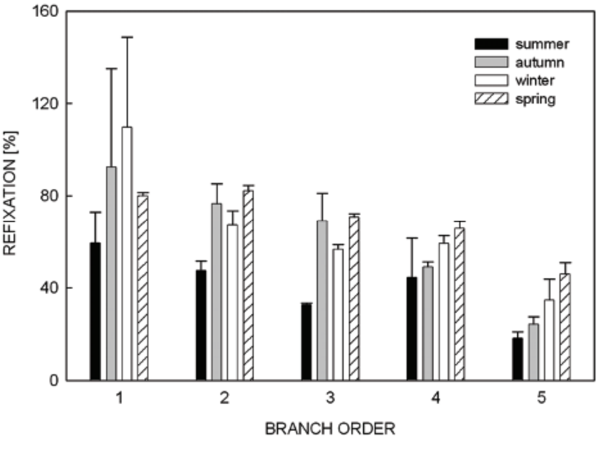

Fig. 3. Percent of CO_2 refixed as a function of CO_2 efflux in the dark for branch orders 1−5 of *Myrica cerifera* during summer and autumn of 2006 and winter and spring of 2007 on Hog Island, Virginia. Means ± SE (n = 5).

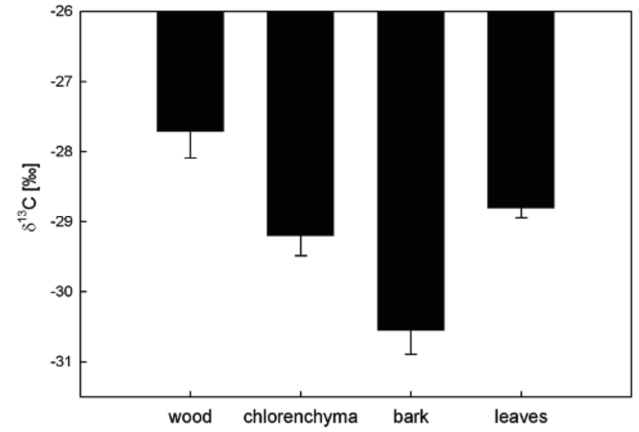

Fig. 4. $\delta^{13}C$ for wood, chlorenchyma, bark, and leaf tissues of third order branches of *Myrica cerifera*. Means ± SE (n = 5).

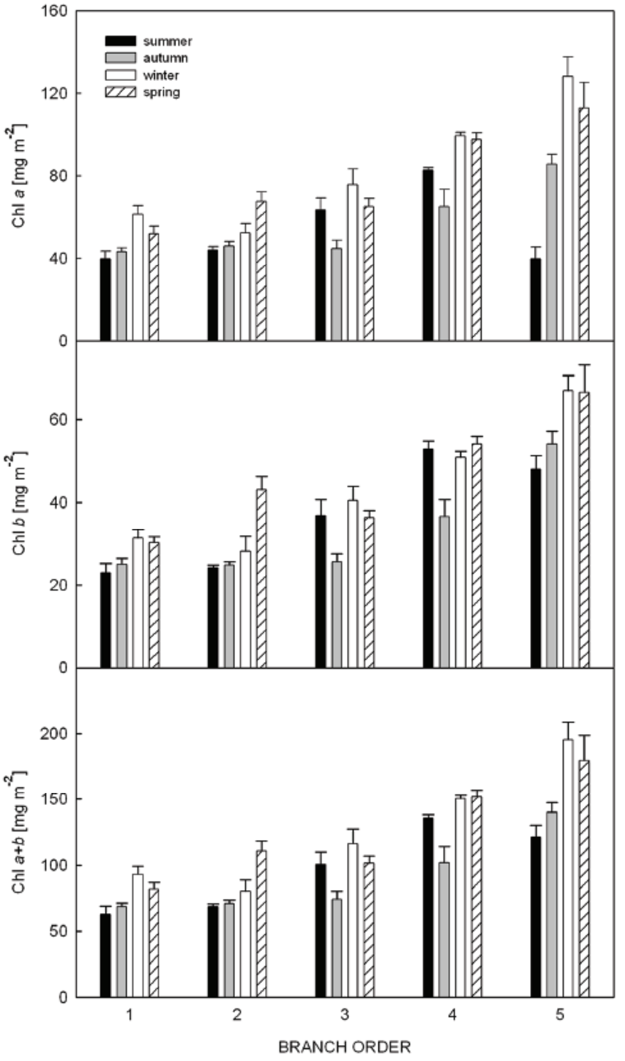

Fig. 5. Chlorophyll (Chl) *a* (*top*), Chl *b* (*middle*), and total Chl content (*bottom*) for branch orders 1−5 of *Myrica cerifera* during summer and autumn of 2006 and winter and spring of 2007 on Hog Island, Virginia. Means ± SE (n = 5).

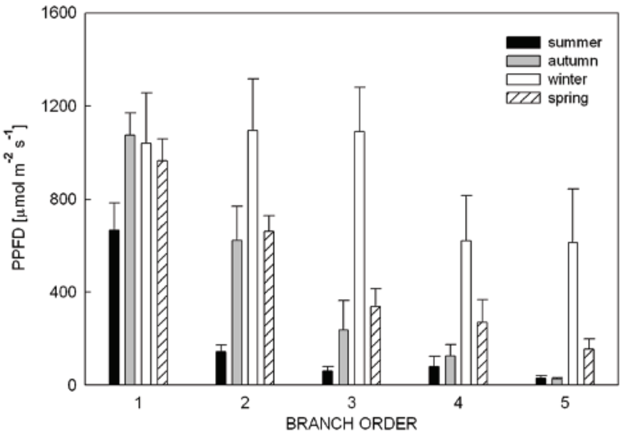

Fig. 6. Incident photosynthetic photon flux density (PPFD) for branch orders 1−5 of *Myrica cerifera* during summer and autumn of 2006 and winter and spring of 2007 on Hog Island, Virginia. Means ± SE (n = 5).

interaction (p=0.003). Winter had a significantly higher Chl *a*/*b* ratio (1.92±0.02) as compared to all other seasons (mean = 1.76±0.02; p≤0.001). Chl *a*/*b* ratios decreased significantly from a mean of 1.79±0.04 in first order branches to 1.67±0.04 in fifth order branches (p=0.026). Chl *a/b* ratio for leaves was significantly greater at 2.36±0.18.

Incident PPFD and branch characteristics: PPFD varied significantly with branch order (p≤0.001) and season (p≤0.001). Despite interaction of order and season (p=0.065), incident PPFD typically decreased with increasing branch order ranging from a mean of 943±62 μmol m^{-2} s^{-1} in first order branches to 76±16 μmol m^{-2} s^{-1} in fifth order branches (Fig. 6). In general, PPFD was lowest in summer and highest in winter, 197±42 and 587±73 μmol m^{-2} s^{-1}, respectively (Fig. 6).

Lenticel density differed significantly with branch order (p≤0.001) and ranged from 35±6 lenticels per cm^2 in first order branches down to 8±1 lenticels per cm^2 in fifth order branches (Fig. 7). Branch diameter also differed significantly with branch order (p≤0.001) ranging from 0.26±0.01 cm in first order branches to 1.86±0.12 cm in fifth order branches (Fig. 7).

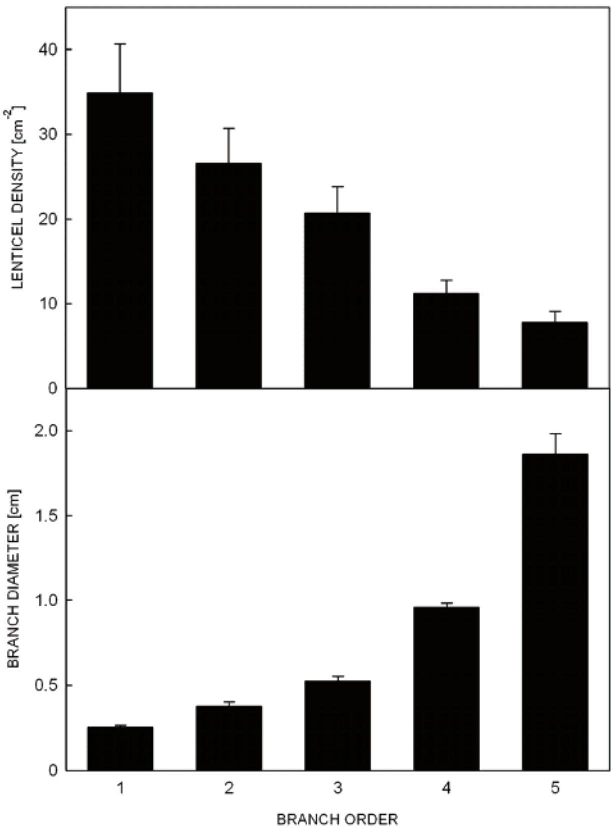

Fig. 7. Lenticel density (*top*) and branch diameter (*bottom*) for branch orders 1−5 of *Myrica cerifera* during summer and autumn of 2006 and winter and spring of 2007 on Hog Island, Virginia. Means ± SE (n = 5).

Discussion

We quantified seasonal CP in first through fifth order branches of *M. cerifera* to determine whether refixation of respired CO_2 may be a contributing mechanism to rapid expansion of this shrub into grass dominated mesic swales. Percent of CO_2 refixed within 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 first order branches are able to assimilate atmospheric CO_2 through lenticels.

Lenticel density was highest for first order branches and density decreased with increasing branch order and diameter. Langenfeld-Heyser *et al.* (1996) concluded that CO_2 enters the branch through lenticels. High lenticel density in first order branches may afford chlorenchyma with sufficient gas exchange for use of atmospheric CO_2 in CP. Other studies have reported refixation from 75 to 97 % of respired CO_2 (Levy and Jarvis 1998, Wittman *et al.* 2001, 2006). Our data indicated that net CP was possible in first order branches especially during winter when irradiances were highest. In contrast, Coe and McLaughlin (1980) found CP to be minimal for Tennessee, USA deciduous trees during winter and only slightly reduced costs of woody tissue respiration.

In contrast to first order branches, higher order branches had much lower %ref and were not capable of net photosynthesis. One explanation for this decrease in refixation with branch order may be the incident PPFD within the shrub thicket. Our measurements indicated that incident PPFD attenuation occurred with increasing branch order. Fifth order branches experienced a near tenfold decrease in incident PPFD as compared to first order branches, which may have been the primary limiting factor for CO_2 refixation in higher order branches.

Further evidence that refixation occurred in branches was provided by our third order $\delta^{13}C$ results. Wood had the highest $\delta^{13}C$ values which were similar to values obtained for leaves. This may be an indication that wood is formed using stored photosynthates from leaf photosynthesis (see Cernusak *et al.* 2001). The tissue to the outside of the wood, the chlorenchyma, was significantly more negative than wood but did not differ from leaf $\delta^{13}C$ values, perhaps carbon within chlorenchyma is the product of both leaf photosynthesis and refixation (Nilsen and Sharifi 1997). Respired CO_2 within branches can either diffuse out of the branch or be recycled *via* refixation (Cernusak *et al.* 2001). Since photosynthesis discriminates against ^{13}C (O'Leary 1988), it follows that respired CO_2 within branches has a more negative $\delta^{13}C$ value than atmospheric CO_2. When this more negative respired CO_2 is refixed, ^{13}C is discriminated against yet again during CP and so photosynthates from refixation should be more negative than those even from leaf photosynthesis. Bark had the lowest $\delta^{13}C$ values which were significantly more negative than leaves, chlorenchyma, and wood; therefore, we speculate that the carbon in bark of third order branches is derived almost entirely from refixation and not from assimilated atmospheric CO_2 *via* leaves or lenticels. In contrast, we would expect bark of first order branches to have $\delta^{13}C$ values similar to those of leaves since our results suggest that first order branches are capable of net photosynthesis and therefore assimilate atmospheric CO_2 *via* lenticels. Nilsen and Sharifi (1997) obtained results similar to our third order $\delta^{13}C$ values with woody legumes; $\delta^{13}C$ of wood was less negative than bark for all species. They proposed that variations in biochemical composition of branch tissues may be an alternative explanation for differences in $\delta^{13}C$ values of these tissues. However, results obtained by Cernusak *et al.* (2001) regarding $\delta^{13}C$ within branches suggest that refixed carbon quickly becomes available for use during respiration and tissue synthesis.

While refixation peaked during cooler months, we found that P_G was highest in spring and summer. During summer, P_G decreased from first order to fifth order branches; the opposite trend occurred during spring. Similar to our summer results, Wittmann *et al.* (2001) found that P_G decreased from current year twigs of *Fagus sylvatica* to one-year-old twigs, both grown outside in pots under full sunlight. Increased P_G for *M. cerifera* during spring may be caused by seasonal variation in metabolic activity of branches and relatively high incident PPFD.

Unlike leaves, incident PPFD on branches must also permeate an outer bark layer to reach the photosynthetically active chlorenchyma layer underneath. Irradiance is transmitted through the periderm and can reach the outer layers of wood or pith (Wittmann *et al.* 2001, Pfanz *et al.* 2002). In one-year-old twigs of *Fagus sylvatica,* 19 % of incident PPFD was transmitted through the periderm, whereas 26 % was transmitted in twigs of *Populus tremula* (Wittmann *et al.* 2001). In general, older branches have a thicker periderm and thus greater attenuation (Pfanz *et al.* 2002). We found that %ref decreased with increasing branch order and, therefore, decreased with age which may be a result of older branches having a thicker periderm that attenuates irradiance reaching chlorenchyma tissue (Pfanz *et al.* 2002). Therefore, with increasing branch order, shade acclimation may become more prominent as branch diameter and periderm thickness increase and PPFD reaching branches decreases.

Chl contents increased with increasing branch order (for further information *see* Šesták 1985), which may indicate that branches were acclimated to the decreased PPFD at higher branch orders. Increased Chl content has been observed in both leaves and twigs in response to low irradiances potentially for the purpose of maximizing PPFD absorption (Wittmann *et al.* 2001). Total Chl content was unexpectedly higher during winter and spring when PPFD was high. In comparison, Chl *a/b* ratios were highest in winter and coincided with high incident PPFD. Similarly, Lewandowska and Jarvis (1977) noted that Chl *a/b* increased in leaves during winter for *Picea sitchensis* in response to increased PPFD resulting from leaf fall of surrounding deciduous trees.

Functional Chl containing chlorenchyma tissues, which are found in branches of most woody plants, are advantageous as long as respired CO_2 loss is reduced, thereby improving CUE and avoiding anaerobisis (Pfanz *et al.* 2002). In addition to improving CUE, CP may also increase WUE by reducing respired CO_2 (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). For *M. cerifera*, an implied increase in CUE and WUE from CP along with an evergreen leaf habit and an association with *Frankia* may enable successful invasion and expansion in grassy swales. We suggest that global warming and shifts in precipitation patterns associated with climate change will lead to an increase in importance of CP as a mechanism facilitating woody plant invasion into grass dominated systems due to increased CUE and WUE up to stand level.

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