Check for updates

LIMNOLOGY AND OCEANOGRAPHY
Letters

ASLO
Open Access

Limnology and Oceanography Letters 7, 2022, 410–418
© 2022 The Authors. *Limnology and Oceanography Letters* published by Wiley Periodicals LLC on behalf of Association for the Sciences of Limnology and Oceanography.
doi: 10.1002/lol2.10276

LETTER

Variation in seagrass meadow respiration measured by aquatic eddy covariance

Ieva Juska *, *Peter Berg* *
Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia

Scientific Significance Statement

Seagrass meadows are considered "blue carbon" ecosystems and are highly effective at sequestering and storing carbon. Accurate metabolic estimates for seagrass meadows are important for evaluating this role in climate change mitigation. Daily gross primary production for aquatic ecosystems is typically calculated assuming that daytime and nighttime respiration are identical, and respiration does not change over a 24-h period. In this study we examine these assumptions using in situ oxygen fluxes measured by aquatic eddy covariance in a temperate seagrass meadow. Binning 2115 h of hourly oxygen fluxes, we found that respiration varies over a 24-h period and can be described by piecewise linear relationships, demonstrating that the common assumptions in metabolic estimates are not fulfilled. Based on our findings we provide new guidelines for future estimates.

Abstract

Accurate daily metabolic estimates of respiration, gross primary production, and net ecosystem metabolism are necessary to assess ecosystem health and blue carbon contributions of vegetated coastal ecosystems. Using our database of 2115 hourly benthic oxygen (O_2) fluxes measured by aquatic eddy covariance, we examine how respiration for a *Zostera marina* seagrass meadow varies through night and day, and how this affects commonly performed metabolic estimates. Respiration decreased linearly by 29% through the night and a corresponding linear increase in daytime respiration coupled with production described by a standard photosynthesis–irradiance curve accurately predicted measured daytime O_2 fluxes. Many studies have questioned the widely used assumption in metabolic estimates that nighttime and daytime respiration are constant and equal. However, if respiration can be approximated as we found here by linear relationships, standard means for calculating daily metabolic numbers remain valid if estimates are based on full 24-h records of flux data.

Seagrass meadows are highly productive coastal ecosystems that provide many important ecological services, including sequestration and storage of carbon (Hemminga and Duarte 2000). They accumulate organic carbon in their sediments through in situ production as well as by accretion of carbon particulates from the water column. Thus, they act as

*Correspondence: ij7tt@virginia.edu, pb8n@virginia.edu
[Correction added on September 09, 2022, after first online publication: Peter Berg is included as corresponding author.]

Associate editor: James E Cloern

Author Contribution Statement: IJ and PB developed the research question and designed the study. IJ and PB analyzed the data and IJ created the figures. IJ wrote the manuscript, with feedback and input from PB.

Data Availability Statement: Published data and metadata are made available in the Environmental Data Initiative repository and the Virginia Coast Reserve LTER's database. Data can be accessed here: https://doi.org/10.6073/pasta/ff12bdd0b01f0d82d4bb8a6613bc2665.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

23782242, 2022, 5, Downloaded from https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lol2.10276, Wiley Online Library on [21/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

a significant sink of and provide long-term storage for "blue carbon," carbon captured by coastal ecosystems (Nellemann et al. 2009; Mcleod et al. 2011; Greiner et al. 2013). This important ecological service of seagrass meadows has led to substantial restoration efforts as a strategy for climate change mitigation.

To better inform mitigation strategies through carbon accumulation and storage, it is important to understand the dynamic metabolism of seagrass meadows (Berger et al. 2020). To do this, we need accurate assessments of daily values for gross primary production (GPP), respiration (R), and net ecosystem metabolism, which can be estimated from oxygen (O_2) fluxes (Staehr et al. 2012). O_2 fluxes are a good proxy for both photosynthesis and respiration because of the close association between carbon transformation and coupled O_2 production, and between carbon oxidation and O_2 consumption. The ratio between O_2 exchange and CO_2 exchange has been estimated to be approximately 1 (Kirk 1983; Duarte et al. 2010), and is widely used in metabolic studies (Glud 2008; Rheuban et al. 2014*b*; Berger et al. 2020).

Daytime O_2 fluxes for seagrass meadows can show deviations from what is expected based on available light, which is the main control on O_2 fluxes during the day (Ralph et al. 2007). Several studies found that O_2 fluxes in seagrass meadows show a higher net release of O_2 in the morning than in the afternoon at the same light levels (Hanelt 1992; Rheuban et al. 2014*b*; Berg et al. 2017, 2019; Koopmans et al. 2020). Multiple explanations for this have been proposed, including afternoon depletion in water column CO_2 limiting photosynthetic production (Berg et al. 2019), increased afternoon water temperature (Masini and Manning 1997; Rheuban et al. 2014*a*), photoinhibition (Hanelt 1992), and enhanced consumption of highly labile organic compounds produced during photosynthesis causing respiration to vary over the course of a day (Glud 2008; Howarth et al. 2014; Rheuban et al. 2014*b*; Attard and Glud 2020). It is commonly assumed that respiration stays constant throughout the day and night in calculations of daily GPP and R (Hume et al. 2011; Koopmans et al. 2020; Rheuban et al. 2014*a*). Several studies have suggested this assumption may result in incorrect calculations of metabolic numbers (Pace and Prairie 2005; Pringault et al. 2009; Howarth et al. 2014).

Respiration trends have been examined in other systems, with indirect approaches such as inferring respiration from water column O_2 concentration measurements combined with full water column mass balance (Sadro et al. 2014; Mantikci et al. 2020), or isotope ratio measurements through time (Bender and Grande 1987; Tobias et al. 2007; Venkiteswaran et al. 2008). However, these indirect approaches are subject to uncertainties, especially in a dynamic system, caused by air–water gas exchange and vertical and horizontal mixing. In this study we used a more direct approach, the noninvasive aquatic eddy covariance technique (Berg et al. 2003), to examine trends in respiration. Previous aquatic eddy covariance measurements in coral ecosystems have found respiration to decrease throughout the night (Long et al. 2013). Here, we use our extensive database of 2115 hourly benthic O_2 fluxes measured in a dense seagrass meadow at a single site within the Virginia Coast Reserve Long Term Ecological Research site (VCR LTER). This site has been subject to a series of metabolic seagrass studies (Hume et al. 2011; Rheuban et al. 2014*a*,*b*; Berg et al. 2019; Berger et al. 2020). To our knowledge, this is the first study of variation in respiration in a coastal ecosystem using a long-term dataset of metabolic measurements performed under naturally varying environmental conditions.

Methods

The data used in this study (Juska et al. 2022) span 5 years (2014–2019) and compile 161 d of seagrass (*Zostera marina*) metabolism measurements collected at the VCR LTER (Berg et al. 2019; Berger et al. 2020). The VCR LTER is the site of the largest and, to date, most successful seagrass restoration effort in the world. The largest meadow (20 km^2 as of 2018) is located in South Bay (Orth et al. 2020) where the data were collected. South Bay is connected to the Atlantic Ocean by inlets and constrained by barrier islands to the east and the Delmarva Peninsula to the west (Fig. 1). Our site has a mean water depth of 1.2 m, with a tidal range of approximately 1 m. The water in South Bay typically stays significantly warmer than the surrounding oceanic inlets (Berger 2021). *Z. marina* is perennial and seagrass shoot density varies seasonally, growing rapidly from the early spring and through the middle of summer, and undergoing senescence in late summer and continuing through the fall (Duarte 1989; Clausen et al. 2014). In South Bay in June, mean aboveground biomass has been reported to be 50.7 g m^{-2} and mean belowground biomass has been reported to be 55.1 g m^{-2} (Berg et al. 2019). June seagrass shoot density at the center of the meadow in 2018 was 364 ± 13 (mean $\pm$ SE) shoots m^{-2} (Berger et al. 2020).

The measured variables included in this study are O_2 flux, photosynthetically active radiation (PAR) at the top of the seagrass canopy, current velocity, water column O_2 concentration, and temperature. The O_2 flux was measured above the seagrass canopy (at 30 cm above the sediment) using the aquatic eddy covariance technique (Berg et al. 2003), a noninvasive approach for direct O_2 flux measurements under naturally varying in situ conditions. The technique gives fluxes at a high temporal resolution (down to $\sim$ 15 min) for a relatively large area of the benthic surface (typically 10–100 m^2), and thus, integrates well over typical meadow patchiness (Berg et al. 2007; Rheuban and Berg 2013). Older techniques for O_2 flux measurements, such as deployment of benthic in situ chambers, do not fully represent the natural environment as they exclude water movements and exchange processes, and may alter light conditions. Altering these drivers of O_2 flux

23782242, 2022, 5, Downloaded from https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lol2.10276, Wiley Online Library on [21/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

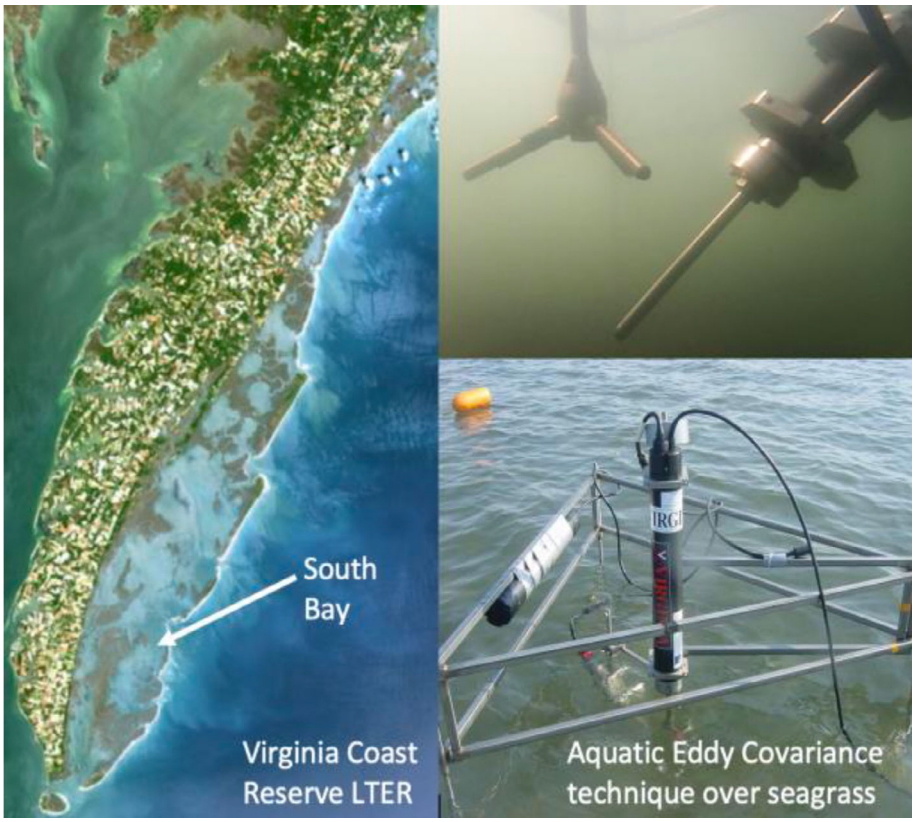

Fig. 1. The data used here were collected at the Virginia Coast Reserve Long term Ecological Research site in the South Bay eelgrass (*Zostera marina*) meadow, using noninvasive aquatic eddy covariance measurements.

can significantly affect metabolic estimates (Martin et al. 2005; Long et al. 2015; Olivé et al. 2016).

In our analysis, we included measurements from late March through late October. Data outside this period were excluded due to the large differences in the periods with daylight. The data were binned into mean hourly values for a full 24-h period, and analyses were performed on the mean data rather than individual days. The site is located in a tidal-driven, shallow bay where current flow and light attenuation change on an hourly basis. Due to the dynamic nature of the system and the strong effect these changing environmental drivers can have on O_2 fluxes (Berger et al. 2020; Berg et al. 2022), hourly data from individual days were highly variable and did not show clear trends in respiration. This led to the use of binned values for trend analysis. Hours were considered to be nighttime hours if PAR values were less than 1% of the maximum daytime PAR, a threshold that has been used in previous metabolic seagrass studies (Hume et al. 2011). This definition gave a well-defined separation between day and night at 20:00 h in the evening and 06:00 h in the morning.

Temperature stress has been shown to occur in temperate *Z. marina* at temperatures above 28°C, where photosynthetic processes are inhibited (Staehr and Borum 2011; Rasmusson et al. 2020). The 28°C threshold was determined in a laboratory study (Staehr and Borum 2011). Research conducted in situ at the VCR LTER has found the threshold for *Z. marina* to be 28.6°C, close to the 28°C value (Berger 2021). To avoid bias in our analyses caused by such effects, O_2 flux data associated with daytime temperatures above 28°C were excluded. This left 2115 h of data for analysis, distributed as 1029 daytime hours and 1086 nighttime hours.

While daytime O_2 fluxes reflect the net result of photosynthetic processes and respiration, nighttime fluxes represent exclusively respiratory processes in the seagrass meadow. To identify trends in respiration, hourly O_2 flux measurements during the night were examined using a least-squares linear regression analysis of the binned values of fluxes with "time after dusk" as the independent variable. A two-sample *t*-test assuming unequal variances (alpha = 0.05, df = 197) was performed comparing O_2 flux measurements during the first hour of night and during the last hour of night. Nighttime hourly means for three other variables that could potentially impact O_2 flux variability were also examined: current velocity, O_2 concentration, and water temperature.

For current velocity, which has been shown to stimulate O_2 fluxes in seagrass meadows (Hume et al. 2011; Long et al. 2015), a two-sample t-test assuming unequal variances (alpha = 0.05, df = 210) was performed comparing velocity

23782242, 2022, 5, Downloaded from https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lol2.10276, Wiley Online Library on [21/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

measurements during the first hour of night and during the last hour of night. Mean hourly O_2 concentration values for the first and last hours of night were examined, and the change in O_2 concentration over the night was evaluated. The O_2 concentrations were assessed for their likelihood to impact respiration. To evaluate the role of temperature, which has been shown to impact respiration (Staehr and Borum 2011), a first-order Q10 model calculation was performed. This classic model (Berry and Raison 1979), which expresses how much respiration will increase if the temperature increases by 10°C, was used to calculate the expected change in respiration through the night using a Q10 value for respiration in *Z. marina* meadows of 2.4 (Marsh et al. 1986).

The linear decrease in nighttime respiration and an assumed linear increase in daytime respiration constituted a 24-h respiration model. Daytime production values were calculated as the difference between measured hourly daytime fluxes and assumed daytime respiration. A widely used standard photosynthesis–irradiance (P-I) curve (Webb et al. 1974) was then fitted to the production values. The respiration model combined with the P-I curve produced a 24-h O_2 flux model based on hour of day and PAR. Residuals were calculated for the modeled hourly O_2 fluxes and used to evaluate the model. R^2 values for the P-I curve and the 24-h O_2 flux model represent the results of a linear regression between expected and measured values for each fitting.

Results

The mean O_2 flux for the first hour of night was significantly different than the mean O_2 flux for the last hour of night ($t = -4.249$; $p = 0.0000332$). A linear fitting to the mean nighttime hourly O_2 fluxes showed a clear trend (slope = 5.11 mmol m^{-2} d^{-1} h^{-1}; $R^2 = 0.946$, $p = 2.37 \times 10^{-6}$) throughout the night (Fig. 2A). A very similar trend (slope = 5.09 mmol m^{-2} d^{-1} h^{-1}; $R^2 = 0.027$, $p = 4.09 \times 10^{-8}$) was obtained when fitting the individual hourly O_2 fluxes (not shown) that comprised the binned data. These fits revealed that respiration in the meadow decreased by 29% through the night. The mean hourly velocity shows some variation after dusk, slightly increasing during the middle of the night (Fig. 2B). However, during the first hour after

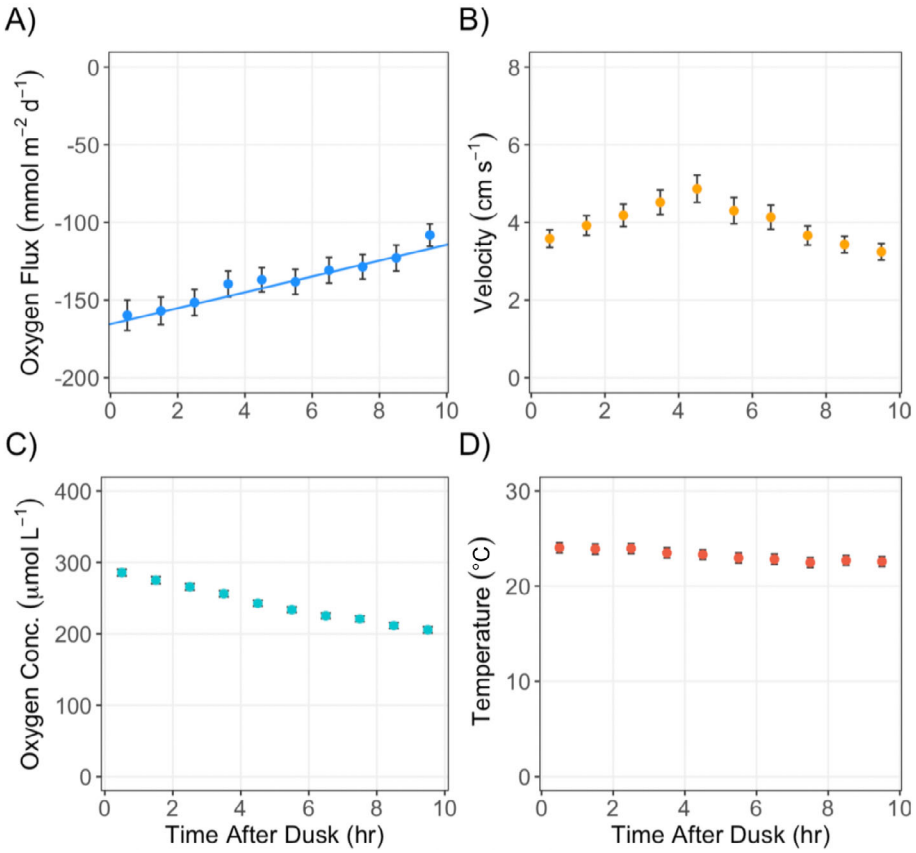

Fig. 2. Average nighttime measurements of key variables from 1086 h of nighttime data plotted against time after dusk (n ranges from 102 to 113 for each hour and is the same across all variables). The first hour after dusk represents measurements between 20:00 h and 21:00 h and the last hour before dawn represents measurements between 05:00 h and 06:00 h. (**A**) The trend in the mean O_2 flux ($n = 10$, $R^2 = 0.95$, $p = 2.37 \times 10^{-6}$) and the mean measurements for each hour ± SE. (**B**) Mean measurements of current velocity for each hour after dusk ± SE. (**C**) Mean measurements of O_2 concentration for each hour after dusk ± SE. (**D**) Mean measurements of water temperature for each hour after dusk ± SE.

23782242, 2022, 5, Downloaded from https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lol2.10276, Wiley Online Library on [21/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

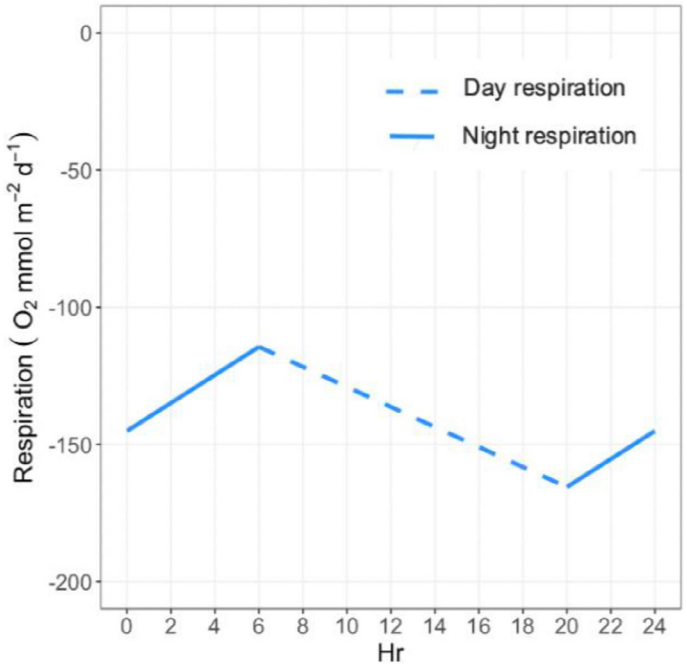

Fig. 3. Respiration trend throughout the full 24-h period, including the linear trend for respiration during the nighttime hours (20:00–06:00; same as in Fig. 2A) and the theoretical daytime respiration.

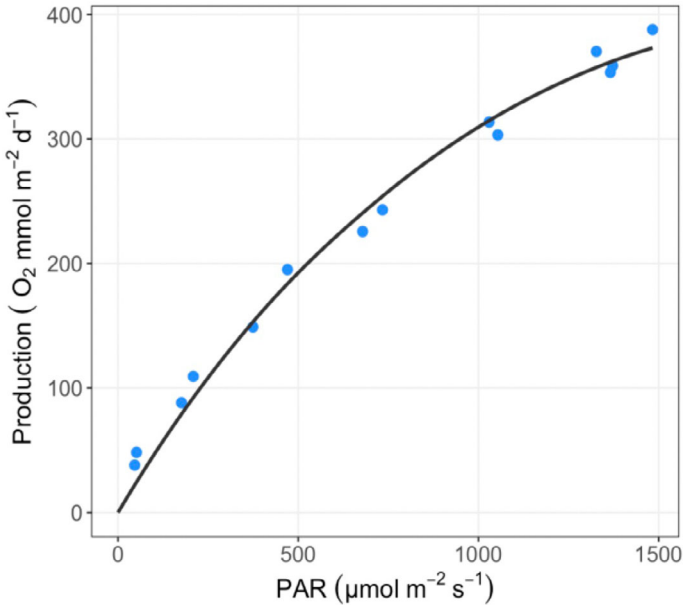

Fig. 4. Photosynthesis–irradiance (PI) curve with production values ($n = 14$) found from 1029 of hourly O_2 flux measurements. Production values are found by subtracting the theoretical daytime respiration (Fig. 3) from the mean O_2 flux. Comparing the measured and predicted PI curve production values using linear regression gives a slope of 1.04 and an R^2 of 0.991.

dusk and the last hour before dawn the current velocities were not statistically different ($t = 1.089$; $p = 0.14$), and thus, were evaluated not to impact respiration significantly. Water column O_2 concentration decreased after dusk (Fig. 2C) as benthic and water column respiration consumed O_2, amounting to a 28% decline over the night. However, the O_2 level never fell below 200 μmol L^{-1} (see Discussion). Water column temperature (Fig. 2D) declined throughout the night by 11%. The observed temperature change of 1.5°C, based on a Q10 value of 2.4, would only decrease metabolism by 2.0%, far from the identified 29% decline through the night.

A piecewise linear description of nighttime and daytime respiration (Fig. 3) combined with a widely used standard P-I curve (Fig. 4) for production ($R^2 = 0.991$) generated a model for hourly O_2 fluxes through the full 24-h period (Fig. 5). This model approximation of the measured O_2 fluxes had an R^2 of 0.993 for a full 24-h period and an R^2 of 0.989 for just daytime values. The hourly residuals had small discrepancies during the early morning and the late evening, but beyond that showed no general trend in variation over the course of the day. In the measured values for O_2 flux and PAR there is a slight decline during the middle of the day (Fig. 5), likely due to pop-up storm formation that often occurs in the early afternoon at the site.

Discussion

Past studies have questioned key assumptions behind the conventional way metabolic numbers for aquatic ecosystems are calculated; that nighttime and daytime respiration are constant and equal (Pringault et al. 2009; Howarth et al. 2014; Sadro et al. 2014; Mantikci et al. 2020). If these assumptions do not hold, errors will arise when using only a few hours of nighttime respiration measurements to represent respiration for a 24-h period. The linear decrease in respiration by 29% through the night identified here for a temperate seagrass meadow (Fig. 2A) showed that this concern is warranted.

Water column temperature and current velocity in our study did not show variation that could explain this significant decline in nighttime respiration. Although there is a small increase in velocity during the middle of the night, it likely only stimulates respiration slightly based on a previous study that investigated this dependency in the same meadow (Hume et al. 2011). Water column O_2 concentrations decreased throughout the night by 28%. It is possible that aerobic respiration in the sediment would decrease as bottom water O_2 concentration declined (Thamdrup et al. 1998; Lehmann et al. 2009). However, the sedimentary O_2 uptake at this site was determined to be a small component (~ 10%) of total O_2 fluxes in the meadow (Rheuban et al. 2014*a*). In addition, metabolic activity in other seagrass ecosystems has been shown to be dominated by the plants themselves (Søndergaard 1979; Colmer and Pedersen 2008; Duarte et al. 2014). The mean hourly O_2 concentration stayed well above what has been suggested to be respiration-limiting in seagrass meadows (Borum et al. 2005; Rasmusson et al. 2020).

23782242, 2022, 5, Downloaded from https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lol2.10276, Wiley Online Library on [21/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

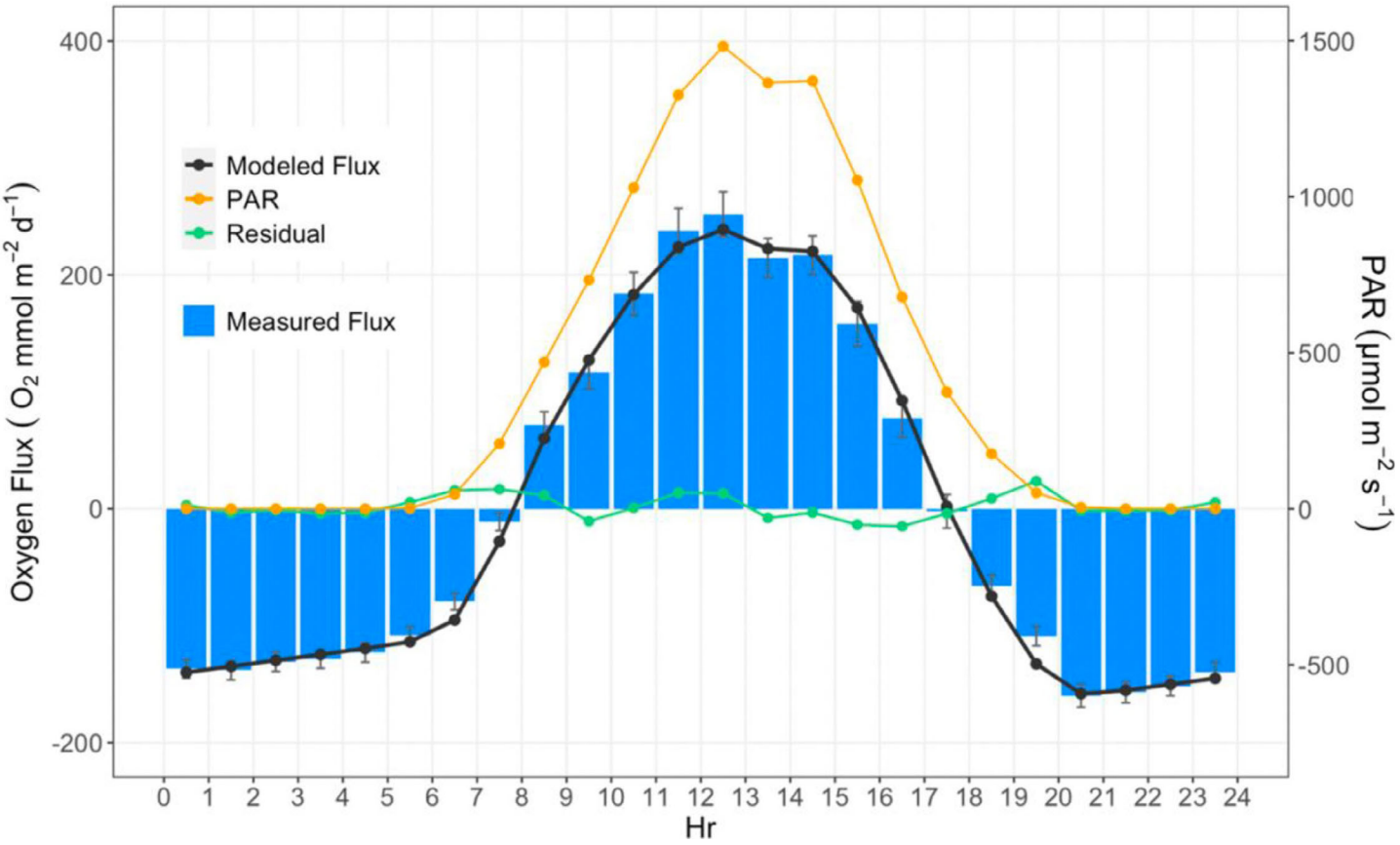

Fig. 5. A model for O2 flux over the full 24-h period based on PAR (Fig. 4) and the piecewise linear variation in respiration (Fig. 3). Comparing the measured and modeled O_2 flux values using linear regression gives a slope of 1.01 and an R^2 of 0.993 for the full 24-h period, and a slope of 1.06 and an R^2 of 0.989 for just daytime values.

For the small component of respiration associated with the sediment, studies have suggested that at high O_2 concentration levels the uptake largely follows zero-order kinetics (Glud et al. 2003; Glud 2008). A decline in O_2 concentration would reduce the direct aerobic respiration, but would largely be compensated for by an increase in oxidation of reduced products of anaerobic decay present beneath the oxic zone. As a result, we conclude that the observed decrease in O_2 concentration only explains a small fraction of the 29% decline in seagrass meadow respiration throughout the night (Fig. 2).

Consequently, we find it most likely that variation in respiration over the 24-h period (Fig. 3) is primarily caused by highly labile compounds produced by photosynthetic processes that accumulate as the day progresses and are consumed during the night; an explanation that is supported by several studies. These compounds can be found on the surfaces of seagrass tissues in the form of dissolved organic carbon (DOC) exudates, which have been shown in laboratory experiments to stimulate respiration (Moriarty et al. 1986) and to decrease in concentration on seagrass leaves after the onset of darkness (Penhale and Smith 1977). They have also been shown to stimulate microbial activity in the root zone of seagrasses (Gribsholt and Kristensen 2002; Aoki and McGlathery 2018) and are quickly consumed by epiphytic bacteria when exuded from seagrass leaf tissue (Kirchman et al. 1984). This explanation is further supported by the fact that the piecewise linear description of nighttime and daytime respiration (Fig. 3) combined with a widely used P-I curve for daytime production generated a 24-h O_2 flux model that accurately described the measured hourly fluxes ($R^2 = 0.993$). The model has a comparable predictive power for the daytime fluxes alone ($R^2 = 0.989$) (Fig. 5). The modeled flux was able to better predict the smaller measured fluxes in the afternoon at the same light levels compared to the observed morning measurements. Our findings provide the first evidence, based on extensive metabolic aquatic eddy covariance measurements under naturally varying conditions, for substantial variation in seagrass respiration which is likely due to the production and consumption of highly labile compounds over the diel cycle; a dynamic mechanism that has been hypothesized in previous studies (Howarth et al. 2014; Rheuban et al. 2014*b*; Attard and Glud 2020).

23782242, 2022, 5, Downloaded from https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lol2.10276, Wiley Online Library on [21/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

The documented variation in respiration confirms that the widely used assumption in conventional calculations of daily GPP and R, that respiration stays constant during day and night, is not fulfilled (Figs. 2A and 3). However, if respiration varies linearly through night and day, as found to be a good approximation here and likely applicable to other phototrophic aquatic ecosystems, the separately integrated nighttime and daytime respiration are equal, which implies that the conventional means for calculating daily R and GPP still hold. However, it is important to have sets of measurements that include data throughout the night to get an accurate mean of nighttime respiration. Using, for example, sampling periods that only include a few evening night hours would result in a significant overestimation of daily R.

As a concluding remark, our study exemplifies the value of long-term research. Our metabolic findings would not have been possible without the long-term dataset consisting of over 2100 h of aquatic eddy covariance data. The highly dynamic nature of seagrass metabolism makes it difficult to see trends in parameters such as respiration. Future studies to further refine our understanding of respiration for seagrass meadows should preferably include quantifications of above- and below-ground DOC exudates in tandem with O_2 flux measurements. A more complete picture of seagrass metabolism and its drivers are critically important to correctly assess the role these threatened ecosystems play in climate change mitigation through coastal blue carbon sequestration and storage.

References

Aoki, L., and K. McGlathery. 2018. Restoration enhances denitrification and DNRA in subsurface sediments of *Zostera marina* seagrass meadows. Mar. Ecol. Prog. Ser. **602**: 87–102. doi:10.3354/meps12678

Attard, K. M., and R. N. Glud. 2020. Technical note: Estimating light-use efficiency of benthic habitats using underwater O_2 eddy covariance. Biogeosciences **17**: 4343–4353. doi:10.5194/bg-2020-140

Bender, M. L., and K. D. Grande. 1987. Production, respiration, and the isotope geochemistry of O_2 in the upper water column. Glob. Biogeochem. Cycles **1**: 49–59. doi:10.1029/GB001i001p00049

Berg, P., H. Røy, F. Janssen, V. Meyer, B. Jørgensen, M. Huettel, and D. de Beer. 2003. Oxygen uptake by aquatic sediments measured with a novel non-invasive eddy-correlation technique. Mar. Ecol. Prog. Ser. **261**: 75–83. doi:10.3354/meps261075

Berg, P., H. Røy, and P. L. Wiberg. 2007. Eddy correlation flux measurements: The sediment surface area that contributes to the flux. Limnol. Oceanogr. **52**: 1672–1684. doi:10.4319/lo.2007.52.4.1672

Berg, P., M. L. Delgard, R. N. Glud, M. Huettel, C. E. Reimers, and M. L. Pace. 2017. Non-invasive flux measurements at the benthic interface: The aquatic Eddy covariance technique. Limnol. Oceanogr.: e-Lectures **7**: 1–50. doi:10.1002/loe2.10005

Berg, P., M. L. Delgard, P. Polsenaere, K. J. McGlathery, S. C. Doney, and A. C. Berger. 2019. Dynamics of benthic metabolism, O_2, and pCO_2 in a temperate seagrass meadow. Limnol. Oceanogr. **64**: 2586–2604. doi:10.1002/lno.11236

Berg, P., M. Huettel, R. N. Glud, C. E. Reimers, and K. M. Attard. 2022. Aquatic eddy covariance: The method and its contributions to defining oxygen and carbon fluxes in marine environments. Ann Rev Mar Sci **14**: 431–455. doi:10.1146/annurev-marine-042121-012329

Berger, A. C. 2021. Long-term aquatic eddy covariance measurements of seagrass metabolism and ecosystem response to warming oceans. Published dissertation. Univ. of Virginia.

Berger, A. C., P. Berg, K. J. McGlathery, and M. L. Delgard. 2020. Long-term trends and resilience of seagrass metabolism: A decadal aquatic eddy covariance study. Limnol. Oceanogr. **65**: 1423–1438. doi:10.1002/lno.11397

Berry, J. A., and J. K. Raison. 1979. Responses of macrophytes to temperature, p. 277–338. *In* O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler [eds.], *Responses to the physical environment*. Springer-Verlag. doi:10.1007/978-3-642-68090-8_11

Borum, J., O. Pedersen, T. M. Greve, T. A. Frankovich, J. C. Zieman, J. W. Fourqurean, and C. J. Madden. 2005. The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass, *Thalassia testudinum*. J. Ecol. **93**: 148–158. doi:10.1111/j.1365-2745.2004.00943.x

Clausen, K., D. Krause-Jensen, B. Olesen, and N. Marbà. 2014. Seasonality of eelgrass biomass across gradients in temperature and latitude. Mar. Ecol. Prog. Ser. **506**: 71–85. doi:10.3354/meps10800

Colmer, T. D., and O. Pedersen. 2008. Underwater photosynthesis and respiration in leaves of submerged wetland plants: Gas films improve CO_2 and O_2 exchange. New Phytol. **177**: 918–926. doi:10.1111/j.1469-8137.2007.02318.x

Duarte, C. M. 1989. Temporal biomass variability and production/biomass relationships of seagrass communities. Mar. Ecol. Prog. Ser. **51**: 269–276. doi:10.3354/MEPS051269

Duarte, C. M., N. Marbà, E. Gacia, J. W. Fourqurean, J. Beggins, C. Barrón, and E. T. Apostolaki. 2010. Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. Glob. Biogeochem. Cycles **24**: GB4032. doi:10.1029/2010GB003793

Duarte, B., D. Santos, H. Silva, J. C. Marques, I. Caçador, and N. Sleimi. 2014. Light–dark O_2 dynamics in submerged leaves of C_3 and C_4 halophytes under increased dissolved CO_2: Clues for saltmarsh response to climate change. AoB Plants **6**: plu067. doi:10.1093/aobpla/plu067

Glud, R. N. 2008. Oxygen dynamics of marine sediments. Mar. Biol. Res. **4**: 243–289. doi:10.1080/17451000801888726

23782242, 2022, 5, Downloaded from https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lol2.10276, Wiley Online Library on [21/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Glud, R. N., J. K. Gundersen, H. Røy, and B. B. Jørgensen. 2003. Seasonal dynamics of benthic O_2 uptake in a semi-enclosed bay: Importance of diffusion and faunal activity. Limnol. Oceanogr. **48**: 1265–1276. doi:10.4319/lo.2003.48.3.1265

Greiner, J. T., K. J. McGlathery, J. Gunnell, and B. A. McKee. 2013. Seagrass restoration enhances "blue carbon" sequestration in coastal waters. PLoS ONE **8**: e72469. doi:10.1371/journal.pone.0072469

Gribsholt, B., and E. Kristensen. 2002. Impact of sampling methods on sulfate reduction rates and dissolved organic carbon (DOC) concentrations in vegetated salt marsh sediments. Wetlands Ecol. Manag. **10**: 371–379. doi:10.1023/A:1020940314010

Hanelt, D. 1992. Photoinhibition of photosynthesis in marine macrophytes of the South China Sea. Mar. Ecol. Prog. Ser. **82**: 199–206. doi:10.3354/MEPS082199

Hemminga, M. A., and C. M. Duarte. 2000, *Seagrass ecology*. Cambridge Univ. Press.

Howarth, R. W., M. Hayn, R. M. Marino, N. Ganju, K. Foreman, K. McGlathery, A. E. Giblin, P. Berg, and J. D. Walker. 2014. Metabolism of a nitrogen-enriched coastal marine lagoon during the summertime. Biogeochemistry **118**: 1–20. doi:10.1007/s10533-013-9901-x

Hume, A. C., P. Berg, and K. J. McGlathery. 2011. Dissolved oxygen fluxes and ecosystem metabolism in an eelgrass (*Zostera marina*) meadow measured with the eddy correlation technique. Limnol. Oceanogr. **56**: 86–96. doi:10.4319/lo.2011.56.1.0086

Juska, I., M. Delgard, A. Berger, and P. Berg. 2022. Mean seagrass meadow metabolism by time of day in Virginia, USA ver 1. Environmental Data Initiative. 10.6073/pasta/ff12bdd0b01f0d82d4bb8a6613bc2665

Kirchman, D., L. Mazzella, R. Alberte, and R. Mitchell. 1984. Epiphytic bacterial production on *Zostera marina*. Mar. Ecol. Prog. Ser. **15**: 117–123. doi:10.3354/meps015117

Kirk, J. T. O. 1983, *Light and photosynthesis in aquatic ecosystems*. Cambridge Univ. Press.

Koopmans, D., M. Holtappels, A. Chennu, M. Weber, and D. de Beer. 2020. High net primary production of Mediterranean seagrass (*Posidonia oceanica*) meadows determined with aquatic eddy covariance. Front. Mar. Sci. **7**: 118. doi:10.3389/fmars.2020.00118

Lehmann, M. F., B. Barnett, Y. Gélinas, D. Gilbert, R. J. Maranger, A. Mucci, B. Sundby, and B. Thibodeau. 2009. Aerobic respiration and hypoxia in the lower St. Lawrence estuary: Stable isotope ratios of dissolved oxygen constrain oxygen sink partitioning. Limnol. Oceanogr. **54**: 2157–2169. doi:10.4319/lo.2009.54.6.2157

Long, M. H., P. Berg, D. de Beer, and J. C. Zieman. 2013. In situ coral reef oxygen metabolism: An eddy correlation study. PLoS ONE **8**: e58581. doi:10.1371/journal.pone.0058581

Long, M., P. Berg, K. McGlathery, and J. Zieman. 2015. Sub-tropical seagrass ecosystem metabolism measured by eddy covariance. Mar. Ecol. Prog. Ser. **529**: 75–90. doi:10.3354/meps11314

Mantikci, M., P. A. Staehr, J. L. S. Hansen, and S. Markager. 2020. Patterns of dark respiration in aquatic systems. Mar. Freshw. Res. **71**: 432–442. doi:10.1071/MF18221

Marsh, J. A., W. C. Dennison, and R. S. Alberte. 1986. Effects of temperature on photosynthesis and respiration in eelgrass (*Zostera marina*). J. Exp. Mar. Biol. Ecol. **101**: 257–267. doi:10.1016/0022-0981(86)90267-4

Martin, S., and others. 2005. Comparison of *Zostera marina* and maerl community metabolism. Aquat. Bot. **83**: 161–174. doi:10.1016/j.aquabot.2005.06.002

Masini, R. J., and C. R. Manning. 1997. The photosynthetic responses to irradiance and temperature of four meadow-forming seagrasses. Aquat. Bot. **58**: 21–36. doi:10.1016/S0304-3770(97)00008-9

Mcleod, E., and others. 2011. A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. Front. Ecol. Environ. **9**: 552–560. doi:10.1890/110004

Moriarty, D. J. W., R. L. Iverson, and P. C. Pollard. 1986. Exudation of organic carbon by the seagrass *Halodule wrightii* Ashers. And its effect on bacterial growth in the sediment. J. Exp. Mar. Biol. Ecol. **96**: 115–126. doi:10.1016/0022-0981(86)90237-6

Nellemann, C., E. Corcoran, C. M. Duarte, L. Valdés, C. De Young, L. Fonseca, and G. Grimsditch [eds.]. 2009, *Blue carbon. A rapid response assessment. United Nations environment programme, GRID-Arendal*. Birkeland Trykkeri AS.

Olivé, I., J. Silva, M. M. Costa, and R. Santos. 2016. Estimating seagrass community metabolism using benthic chambers: The effect of incubation time. Estuaries Coasts **39**: 138–144. doi:10.1007/s12237-015-9973-z

Orth, R. J., and others. 2020. Restoration of seagrass habitat leads to rapid recovery of coastal ecosystem services. Sci. Adv. **6**: eabc6434. doi:10.1126/sciadv.abc6434

Pace, M., and Y. L. Prairie. 2005. Respiration in lakes, 103-121. P. A. del Giorgio and P. J. B. Williams, *Respiration in aquatic ecosystems*. Oxford Univ. Press. 10.1093/acprof:oso/9780198527084.003.0007

Penhale, P. A., and W. O. Smith. 1977. Excretion of dissolved organic carbon by eelgrass (*Zostera marina*) and its epiphytes: Eelgrass-epiphyte excretion. Limnol. Oceanogr. **22**: 400–407. doi:10.4319/lo.1977.22.3.0400

Pringault, O., S. Tesson, and E. Rochelle-Newall. 2009. Respiration in the light and bacterio-phytoplankton coupling in a coastal environment. Microb. Ecol. **57**: 321–334. doi:10.1007/s00248-008-9422-7

Ralph, P. J., M. J. Durako, S. Enríquez, C. J. Collier, and M. A. Doblin. 2007. Impact of light limitation on seagrasses. J. Exp. Mar. Biol. Ecol. **350**: 176–193. doi:10.1016/j.jembe.2007.06.017

23782242, 2022, 5, Downloaded from https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lol2.10276, Wiley Online Library on [21/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Rasmusson, L. M., P. Buapet, R. George, M. Gullström, P. C. B. Gunnarsson, and M. Björk. 2020. Effects of temperature and hypoxia on respiration, photorespiration, and photosynthesis of seagrass leaves from contrasting temperature regimes. ICES J. Mar. Sci. **77**: 2056–2065. doi:10.1093/icesjms/fsaa093

Rheuban, J., and P. Berg. 2013. The effects of spatial and temporal variability at the sediment surface on aquatic eddy correlation flux measurements. Limnol. Oceanogr.: Methods **11**: 351–359.

Rheuban, J., P. Berg, and K. J. McGlathery. 2014*a*. Ecosystem metabolism along a colonization gradient of eelgrass (*Zostera marina*) measured by eddy correlation. Limnol. Oceanogr. **59**: 1376–1387. doi:10.4319/lo.2014.59.4.1376

Rheuban, J., P. Berg, and K. McGlathery. 2014*b*. Multiple timescale processes drive ecosystem metabolism in eelgrass (*Zostera marina*) meadows. Mar. Ecol. Prog. Ser. **507**: 1–13. doi:10.3354/meps10843

Sadro, S., G. W. Holtgrieve, C. T. Solomon, and G. R. Koch. 2014. Widespread variability in overnight patterns of ecosystem respiration linked to gradients in dissolved organic matter, residence time, and productivity in a global set of lakes. Limnol. Oceanogr. **59**: 1666–1678. doi:10.4319/lo.2014.59.5.1666

Søndergaard, M. 1979. Light and dark respiration and the effect of the lacunal system on refixation of CO_2 in submerged aquatic plants. Aquat. Bot. **6**: 269–283. doi:10.1016/0304-3770(79)90065-2

Staehr, P. A., and J. Borum. 2011. Seasonal acclimation in metabolism reduces light requirements of eelgrass (*Zostera marina*). J. Exp. Mar. Biol. Ecol. **407**: 139–146. doi:10.1016/j.jembe.2011.05.031

Staehr, P. A., J. M. Testa, W. M. Kemp, J. J. Cole, K. Sand-Jensen, and S. V. Smith. 2012. The metabolism of aquatic ecosystems: History, applications, and future challenges. Aquat. Sci. **74**: 15–29. doi:10.1007/s00027-011-0199-2

Thamdrup, B., J. W. Hansen, and B. B. Jorgensen. 1998. Temperature dependence of aerobic respiration in a coastal sediment. FEMS Microbiol. Ecol. **25**: 189–200. doi:10.1111/j.1574-6941.1998.tb00472.x

Tobias, C. R., J. K. Böhlke, and J. W. Harvey. 2007. The oxygen-18 isotope approach for measuring aquatic metabolism in high productivity waters. Limnol. Oceanogr. **52**: 1439–1453. doi:10.4319/lo.2007.52.4.1439

Venkiteswaran, J. J., S. L. Schiff, and L. I. Wassenaar. 2008. Aquatic metabolism and ecosystem health assessment using dissolved O_2 stable isotope diel curves. Ecol. Appl. **18**: 965–982. doi:10.1890/07-0491.1

Webb, W. L., M. Newton, and D. Starr. 1974. Carbon dioxide exchange of *Alnus rubra*. Oecologia **17**: 281–291. doi:10.1007/BF00345747

Acknowledgments

Support for this study was provided by the University of Virginia and the National Science Foundation (NSF) through the following grants: the Virginia Coast Reserve Long-Term Ecological Research Program (DEB-0621014, DEB-1237733, and DEB-1832221), to Peter Berg from the Chemical Oceanography Program (OCE-1061364 and OCE-1824144) and the Ocean Technology and Interdisciplinary Coordination Program (OCE-1824144 and OCE-2223204). We would like to thank the staff at the UVA Coastal Research Center for their support and acknowledge all of those who contributed to the collection of this data.

Submitted 08 September 2021
Revised 24 July 2022
Accepted 24 July 2022

23782242, 2022, 5, Downloaded from https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lol2.10276, Wiley Online Library on [21/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License