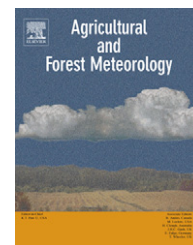


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Why is marsh productivity so high? New insights from eddy covariance and biomass measurements in a *Typha* marsh

Adrian V. Rocha^{*}, Michael L. Goulden

Department of Earth System Science, University of California, Irvine, CA 92697-3100, USA

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ABSTRACT

Researchers have a poor understanding of the mechanisms that allow freshwater marshes to achieve rates of net primary production (NPP) that are higher than those reported for most other types of ecosystems. We used an 8-year record of the gross primary production (GPP) and NPP at the San Joaquin Freshwater Marsh (SJFM) in Southern California to determine the relative importance of GPP and carbon use efficiency (CUE; the ratio of total NPP to GPP calculated as NPP GPP^{-1}) in determining marsh NPP. GPP was calculated from continuous eddy covariance measurements and NPP was calculated from annual harvests. The NPP at the SJFM was typical of highly productive freshwater marshes, while the GPP was similar to that reported for other ecosystem types, including some with comparatively low NPPs. NPP was weakly related to GPP in the same year, and was better correlated with the GPP summed from late in the previous year's growing season to early in the current growing season. This lag was attributed to carbohydrate reserves, which supplement carbon for new leaf growth in the early growing season of the current year. The CUE at the SJFM for the 8-year period was 0.61 ± 0.05 . This CUE is larger than that reported for tropical, temperate, and boreal ecosystems, and indicates that high marsh NPP is attributable to a high CUE and not a high GPP. This study underscores the importance of autotrophic respiration and carbon allocation in determining marsh NPP.

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1. Introduction

Freshwater marshes, also known as reed swamps or reed beds, have among the highest rates of net primary production (NPP) reported for terrestrial ecosystems (Westlake, 1963; Whitaker, 1975; Keefe, 1972; Bradbury and Grace, 1983; Mitsch and Gosselink, 1993; Valiela, 1995; Keddy, 2000). Marsh NPP can be as high as that of tropical forests and intensive agricultural ecosystems, but the physiological mechanisms that drive high wetland production are poorly understood. Ecosystem NPP represents the balance between carbon uptake by photosynthesis (gross primary production, GPP) and carbon loss by autotrophic respiration (R_a). There are two likely, non-mutually exclusive explanations for the reports of high

productivity by marshes. First, freshwater marshes may have high GPP, which directly leads to high rates of NPP. Alternatively, freshwater marshes may have a high carbon use efficiency (CUE), which allow for high rates of NPP even though GPP is not atypical.

Marsh vegetation and environments have unique attributes that may favor high GPP. These traits include abundant resources, such as nutrients and water (Keefe, 1972; Bradbury and Grace, 1983), and plant canopies with vertically orientated leaves (Jervis, 1969; Longstreth, 1989). Wetlands accumulate nutrients (Bowden, 1987; Childers, 2006), such as nitrogen and phosphorus, which are positively related to leaf photosynthetic capacity (Wright et al., 2004). Carbon gain comes at the expense of water loss, and the high water table associated

^{*} Corresponding author. Current address: Marine Biological Laboratory, 7 MBL Street, Woods Hole, MA 02345, USA. Tel.: +1 949 824 9273. E-mail address: arocha@mbl.edu (A.V. Rocha).

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with wetlands decreases the chance of water stress, which can reduce leaf photosynthetic capacity, induce leaf senescence, and decrease the length of the growing season (Morgan, 1984). Marshes are dominated by species with vertical leaf orientation, such as Cattail (*Typha* spp.) and Bullrush (*Scirpus* spp.). Canopies with vertically oriented leaves allow for greater light penetration into the canopy, and are less prone to self-shading than canopies with horizontally oriented leaves (Sheehy and Cooper, 1973). These factors would lead one to hypothesize that marshes create environments that are suited to maximize GPP. However, our ability to test this hypothesis is limited by the lack of marsh GPP measurements.

Although GPP determines the amount of carbon fixed by the canopy, plant growth (i.e. NPP) is ultimately controlled by the conversion efficiency of photosynthate to plant biomass (Amthor, 1989). This conversion efficiency is known as the Carbon Use Efficiency, and is thought to be largely controlled by plant respiration (Van Iersel, 2003). The regulation of respiration by photosynthetically derived sugars and the coupling of respiration to photosynthesis at long timescales (Dewar et al., 1998) have led some to hypothesize that CUE is constant across ecosystems (Waring et al., 1998; Gifford, 2003). However, methodological limitations associated with deriving CUE (Medlyn and Dewar, 1999), the lack of CUE data from a variety of ecosystem types, and a limited understanding of the physiological mechanisms that drive a constant CUE have led others to question the idea that CUE is constant (Amthor, 2000; DeLucia et al., 2007). Moreover, it remains to be determined how CUE could remain constant when carbon allocation to leaves, roots, and stems differs between ecosystems, and the respiratory cost of maintaining and constructing these different plant tissues varies widely (Penning de Vries et al., 1974; Poorter and Villar, 1997; Chapin, 1989).

Marsh vegetation and environments have several features that may lower the respiratory requirements of the plants and lead to a high CUE relative to other terrestrial systems. Marsh sediments are reduced and contain high amounts of ammonium relative to nitrite and nitrate (Bowden, 1987). Constructing plant tissues with ammonium rather than nitrate can reduce plant respiratory costs by 13% because ammonium does not have to be reduced for incorporation into amino acids, as is the case with nitrate (Poorter and Villar, 1997). Wetland macrophytes allocate a disproportionate portion of their carbon to leaves rather than stems or roots (Gustafson, 1976; Lorenzen et al., 2001), and CUE has been shown to increase with increased investment in leaves relative to roots (DeLucia et al., 2007). Anaerobic conditions created by waterlogged soils are unfavorable habitats for mycorrhizae (Peat and Fitter, 1993). Since mycorrhizae can decrease plant productivity and increase photosynthetic rates (Dunham et al., 2003), the lack of mycorrhizae in wetlands may result in an increased CUE.

We used 8 years of eddy covariance data and peak biomass harvests, and 2 years of belowground biomass harvests, in a Southern California marsh to determine the relative importance of GPP and CUE in determining marsh NPP. The eddy covariance method provides a measure of the net ecosystem exchange of CO₂ (NEE), which can be used to determine whole ecosystem GPP. Recent studies have paired eddy covariance

observations with simultaneous measurements of primary production to understand the relationship between carbon uptake and plant growth (Arneeth et al., 1998; Curtis et al., 2002; Rocha et al., 2006; Gough et al., 2008). Our goal was to use this strategy to determine the physiological mechanisms that allow marshes to attain high NPP. In this study, we consider carbon fluxes (GPP) and carbon allocation as the direct controllers of NPP, while nutrients and water availability are considered indirect controls that impact NPP by altering GPP or CUE.

2. Methods

2.1. Site description

The study was conducted at the San Joaquin Freshwater Marsh (SJFM) reserve located in the University of California's Irvine campus in coastal Orange County (33°39'44.4"N, 117°51'6.1"W) (see Goulden et al., 2007; Rocha and Goulden, *in press* for details). The site was dominated by Cattail (*Typha latifolia* L.) and water levels were managed for research and wildlife habitat. The SJFM was flooded annually to a depth of ~1 m in the winter of most years, after which water levels gradually declined through evapotranspiration or subsurface drainage (Rocha, 2008). The lone exception to this pattern in the last 10 years occurred in 2004, when the marsh remained dry year-round because of concern about the West-Nile virus and a management decision to reduce mosquito habitat.

2.2. Calculating GPP from eddy covariance observations

NEE was measured using the eddy covariance method (see Goulden et al., 2007; Rocha and Goulden, *in press* for details). Quality of the eddy covariance data was dependent on several conditions, including adequate turbulent mixing ($u_* > 0.20 \text{ m s}^{-1}$), instrument functioning, and adequate sampling of the ecosystem due to wind direction. Data that did not meet these conditions were excluded from the analysis, and data gaps filled subsequently. Analysis of the energy budget closure at the SJFM indicated the raw turbulent energy flux measurements underestimated the true energy flux by ~20% (Goulden et al., 2007). This percentage of unaccounted flux is similar to that observed in many other eddy covariance studies, and is presumably caused by transport in low-frequency circulations that are underestimated by a 30-min averaging interval (Mahrt, 1998; Twine et al., 2000). The 20% underestimation of energy flux is generally interpreted as an indication that the CO₂ flux is similarly underestimated by 20%, so CO₂ fluxes were increased by 20% to account for this underestimation (Twine et al., 2000).

Gross primary production was calculated from eddy covariance derived daytime growing season NEE by separately considering the day and night observations (Goulden et al., 1997). NEE represents the sum of two component fluxes: GPP and total ecosystem respiration (R). At night, GPP is zero and NEE (NEE_{night}) is equal to total ecosystem respiration ($NEE_{\text{night}} = R$). The difference between NEE_{day} and NEE_{night} can be used to calculate GPP provided that a realistic approach is

adopted for extrapolating nocturnal respiration (Modeled NEE_{night}) to daytime periods (Eq. (1)):

$$NEE = R + GPP = \text{Modeled } NEE_{\text{night}} + GPP \quad (1)$$

There is no standardized approach to modeling daytime respiration, and researchers have used a variety of approaches (Richardson et al., 2006). Some approaches may overestimate daytime respiration and GPP because the respiration model is parameterized with cool nocturnal temperatures and extrapolated to warmer daytime temperatures; other approaches may underestimate respiration and GPP because the empirical model poorly represents the diel and seasonal changes in respiration.

We calculated GPP using several approaches to test for methodological sensitivity. We used four empirical models of ecosystem respiration (simple (Rocha and Goulden, in press), linear, Q_{10} , and the restricted form of Lloyd and Taylor; see Table 1 in Richardson et al., 2006 for details) with air temperature to calculate GPP from NEE_{day} . The simple model used average NEE_{night} to calculate daytime respiration, while the linear model used an empirical relationship between NEE_{night} and air temperature to model daytime respiration. The Q_{10} and restricted form of Lloyd and Taylor are empirical exponential models that use air temperature to calculate ecosystem respiration during the day. We also tested the sensitivity of GPP to integration time by using integration times of 15 and 25 days. Respiration models were chosen because they represented a broad range of commonly used respiration model functions to derive GPP from NEE.

Annual GPP was calculated by subtracting modeled total ecosystem respiration from NEE_{day} and integrating GPP over the course of a year. Small gaps were filled using a Michaelis–Menten hyperbolic regression between GPP and solar radiation (<20 days long). A longer gap in 2000 was filled by combining the Michaelis–Menten equation with an estimate of leaf phenology based on the empirical relationship between NEE and reflected radiation. On the whole, 15% of the GPP data were filled, which is typical for a long-term eddy covariance record. These analyses yielded 12 estimates of GPP per year for a total of 108 estimates of GPP for the 1999–2007 record. These estimates were used to calculate the uncertainty in GPP.

2.3. Peak biomass observations

We sampled living plants from 1999 to 2007 within thirty 0.25 m² quadrats along a 91.5-m transect that radiated to the southwest of the eddy covariance tower during September (the month of peak biomass). Plants were pulled from the ground, clipped below the crown to remove rhizomes and roots, taken to the lab, oven dried at 65 °C for 2–3 days and weighed. We partitioned growth into leaves, stems, inflorescences, and the crown base. We conducted additional harvests in November 2006 and 2007 in eight 1 m² plots to determine the proportional allocation to aboveground and belowground biomass. Belowground organs (crown bases, rhizomes, and coarse roots) were excavated and separated according to organ type and age. Belowground biomass produced in a given year was identified by texture and color (Jervis, 1969; Gustafson, 1976). Sorted material was oven dried at 65 °C for 2–3 days and weighed.

2.4. Calculating NPP from biomass observations

NPP was calculated from observations of peak biomass. We used the growth of leaves, stems and inflorescences as a measure of aboveground net primary production (ANPP) because aboveground components of *Typha* (i.e. leaves, stems, inflorescences) are produced and senesce every year. Crown bases are also produced every year, and these were harvested and counted as a portion of belowground NPP (BNPP). Coarse root and rhizome production was not measured every year, and we used the average allocation ratios between the crown base and the rhizomes and roots during 2006 and 2007 to estimate the remaining BNPP components during the other years.

The plants at the SJFM are herbaceous perennials that store starch reserves over winter and subsequently use this starch for leaf growth during spring. Carbohydrate storage can complicate the determination of NPP because growth can include carbon that was fixed in a previous year (Gustafson, 1976; Roxburgh et al., 2005). Consequently, we calculated a conservative NPP by correcting NPP estimates for potential double counting of the starch reserve (S_R). S_R in harvested plants was calculated as 50% of the previous year's BNPP, and was based on two independent studies that showed that the end of season starch pool in *Typha* comprises 45–47% of crown, root, and rhizome weight (Gustafson, 1976; Kausch et al., 1981). S_R in 2005 (i.e. the year after the dry down) was estimated from BNPP in 2003. S_R in 1999 was estimated by the average ratio of corrected to uncorrected NPP during the flooded years. This conservative approach to calculating NPP assumes that all of the previous year's starch is used for growing some of the current year's aboveground tissue, and that there is no metabolic cost to convert starch into tissue (Eq. (2)):

$$NPP = ANPP + BNPP - S_R \quad (2)$$

We compared the SJFM's NPP from 1999 to 2003 and 2005 to 2007 to NPP values in the Osiburck dataset (<http://www.esa-pubs.org/archive/ecol/E081/011/>) (Esser et al., 2000). This was done to determine if NPP at the SJFM was comparable to that reported for other marshes and ecosystems. The Osiburck dataset is a compilation of 700 estimates of NPP for natural ecosystems worldwide. Productivity in the Osiburck dataset is reported as grams of dry weight and was converted to carbon using a conversion factor of 0.45. We only used data from sites that reported species composition, ecosystem type, and author.

2.5. Constraining the NPP to GPP ratio

Ecosystem CUE can be calculated using several approaches. Our first estimate of CUE used linear regression to calculate NPP/GPP as the slope of the relationship between NPP and GPP. Regressions were forced through the origin whenever the intercept was not significant at the 95% confidence level. The 95% confidence interval for NPP/GPP was constructed with a Scheffe multiplier based on the F-distribution (Ramsey and Schafer, 2002). Least squares regressions were carried out with Sigmaplot 8.0 (SPSS, Chicago, IL). This approach is consistent with previous approaches used to calculate CUE (Waring et al.,

1998; Litton et al., 2007), but is limited because sampling uncertainty in NPP and GPP can markedly alter the slope.

Another approach for calculating ecosystem CUE is to integrate NPP and GPP over a long period and calculate the ratio between the two quantities. The limitation of this approach is that errors in the NPP/GPP are proportional to the measurement variability and uncertainty in NPP and GPP. Consequently, we used bootstrap analysis to calculate the uncertainty and 95% confidence interval for ecosystem CUE. The bootstrap technique includes a measure of the uncertainty in the ecosystem CUE by incorporating the variance associated with NPP and GPP, repeatedly sampling these estimates with substitution, and calculating a probability distribution for NPP/GPP. Ecosystem CUE was calculated by integrating our measures of NPP and GPP from 1999 to 2007 using the following equation:

$$\text{CUE} = \frac{\text{NPP}}{\text{GPP}} = \frac{\sum_{1999-2007} \text{NPP}}{\sum_{1999-2007} \text{GPP}} \quad (3)$$

The bootstrap analysis repeatedly sampled annual GPP and NPP 1000 times and calculated the CUE by integrating these estimates over the 9-year-time period and recalculating the CUE. One thousand of these estimates were then randomly chosen to represent the CUE probability distribution for the SJFM. This distribution represented the potential range of the CUE and allowed for the calculation of a 95% confidence interval for the mean (DiCiccio and Efron, 1996). Analyses were accomplished using the Bootstrap MATLAB Toolbox (http://www.csp.curtin.edu.au/downloads/bootstrap_toolbox.html) (Zoubir, 1993).

3. Results

3.1. Carbon allocation and biomass partitioning

Belowground harvests in 2006 and 2007 revealed that carbon was mostly allocated to aboveground biomass (Table 1). Most

Table 1 – Carbon partitioning to aboveground and belowground biomass components in 2006 and 2007

Component	2006 harvest (% of total)	2007 harvest (% of total)
Aboveground	72	54
Crown base	22	33
Roots	4	2
Rhizomes	3	11

of the carbon allocated belowground was used for the growth of crown bases, which represented 22–33% of total biomass. Rhizomes and roots represented a smaller fraction of total biomass (~7–13%). The average ratio of belowground to total biomass at the SJFM was consistent with that reported for other *Typha* dominated communities (reported range: 32–70%; Keefe, 1972; Gustafson, 1976; Bradbury and Grace, 1983). These results demonstrate that our annual collections of aboveground green biomass and crown bases captured 87–94% of the total biomass produced in a given year. This increases confidence in our measurement of NPP, and indicates that the uncertainty in NPP associated with our estimates of rhizome and root production is less than 10%.

3.2. ANPP, BNPP, and NPP

Cattail production exhibited marked interannual variability (Table 2, see also Rocha and Goulden, in press). Aboveground NPP comprised the majority of total NPP and varied from 419 gC m⁻² year⁻¹ to 1018 gC m⁻² year⁻¹. Belowground NPP was 32–59% of ANPP and varied from 194 gC m⁻² year⁻¹ to 420 gC m⁻² year⁻¹. Total NPP was positively related to both ANPP (r^2 : 0.98; $p < 0.01$) and BNPP (r^2 : 0.93; $p < 0.01$), and ranged from 458 gC m⁻² year⁻¹ to 1245 gC m⁻² year⁻¹. Cattail growth was negligible during 2004, as a result of a management decision to withhold water. Average total NPP during the other years was 867 gC m⁻² year⁻¹. The years when we made the supplemental belowground harvests (2006 and 2007) were representative of the range of NPPs observed. NPP in 2006 was the third highest recorded during the 1999–2003 & 2005–2008 period; NPP in 2007 was the second lowest recorded.

Table 2 – Aboveground NPP (ANPP), belowground NPP (BNPP), total net primary productivity (NPP), and gross primary productivity (GPP) at the SJFM from 1999 to 2007

Year	ANPP (gC m ⁻² year ⁻¹)	BNPP (gC m ⁻² year ⁻¹)	NPP (gC m ⁻² year ⁻¹)	GPP (gC m ⁻² year ⁻¹)
1999	580	297	722 ^a	1362
2000	938	386	1176	2000
2001	1018	420	1245	1363
2002	707	228	725	1424
2003	834	311	1031	1905
2004	0	0	0	0
2005	419	194	458 ^b	1196
2006	788	373	1064	1148
2007	436	258	507	1023
Average	715	308	867	1428

Average excludes the year of the dry down (2004).

^a Starch reserves (S_R) estimated from the average ratio of corrected to uncorrected NPP during the flooded years.

^b S_R estimated as 50% of BNPP in 2003.

Table 3 – Sensitivity of GPP to the model used to subtract out ecosystem respiration from daytime net ecosystem exchange of CO₂

Respiration model	Integration time	
	15 days	25 days
Simple (%)	–3	–1
Linear (%)	–3	0
Q ₁₀ (%)	2	0
Restricted Lloyd and Taylor (%)	2	5

Numbers represent percent deviations from the overall mean.

3.3. GPP

Annual GPP at the SJFM also exhibited marked interannual variability (Table 2, see also Rocha and Goulden, in press; Rocha et al., in press). GPP was negligible during 2004 as a result of the lack of water and canopy development. Average GPP during the other years was 1428 gC m⁻² year⁻¹, and ranged from 1023 gC m⁻² year⁻¹ to 2000 gC m⁻² year⁻¹. Inter-annual NPP variability, as measured by the coefficient of variation, was 12% larger than that observed for GPP. Interannual patterns of GPP differed from those observed for NPP. Years with high GPP did not always result in years with high NPP. For example, GPP was highest in 2000 and lowest in 2007, whereas NPP was highest in 2001 and lowest in 2005.

Annual estimates of GPP for the SJFM were minimally influenced by the models used to calculate respiration (Table 3). The simple respiration model produced the lowest estimates of GPP, while the restricted Lloyd and Taylor and Q₁₀ respiration models produced the highest. Changing the integration time also led to differences in annual GPP. The Lloyd and Taylor respiration model with long integration times tended to overestimate GPP because errors in the estimation of GPP increased with increasing temperature. The simple model with short integration times may have underestimated GPP because it incorporated a lower temperature sensitivity. Nonetheless, our results demonstrate that estimates of annual GPP are robust, and supports previous work that estimated a 10% uncertainty for eddy covariance based annual GPP (Hagen et al., 2006).

3.4. What is the relationship between NPP and GPP at the SJFM?

The amount of biomass produced in a given year was weakly related to the amount of gross carbon uptake in the same year ($r^2: 0.33; p: 0.14$) (Fig. 1A). The poor correlation between GPP and NPP may be attributed to the physiological characteristics of Cattail. Cattails are rhizomatous perennials that allocate a large proportion of their assimilated carbon to carbohydrate storage as starch (Kausch et al., 1981; Gustafson, 1976). Carbon assimilated in a prior year can be stored belowground and remobilized to supplement growth of new leaves in the current year (McNaughton, 1974; Gustafson, 1976; Dickson, 1991; Carbone and Trumbore, 2007). If NPP depends on a proportion of the prior year's GPP, then year-to-year differ-

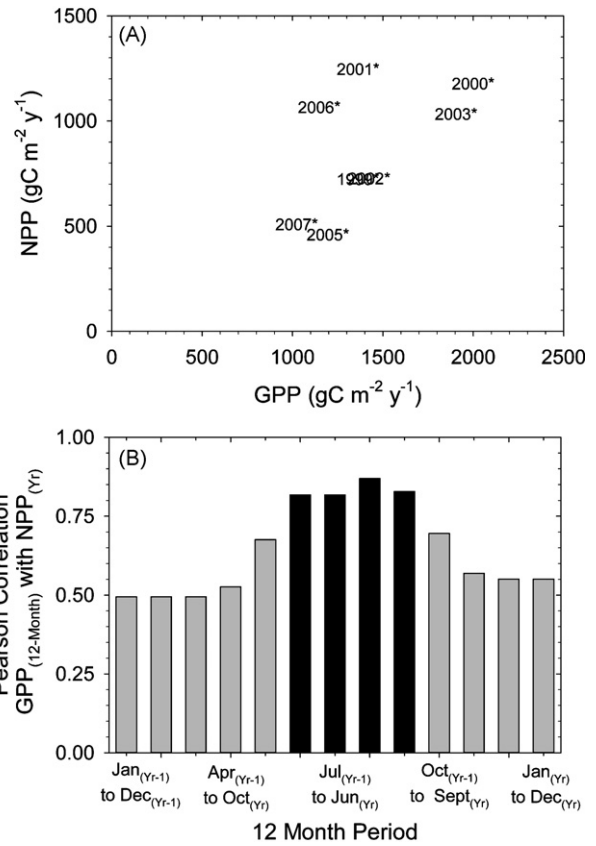


Fig. 1 – Relationship between annual GPP and NPP for the SJFM (A) ($r^2: 0.33; p: 0.14$). Pearson correlation coefficients for NPP and GPP calculated using a 12-month period lagged with a time step of a month (B). Black bars denote statistically significant relationships at the 95% confidence level.

ences in carbohydrate storage and translocation that result from interannual GPP variability could decouple the relationship between NPP and GPP in a given year. Consequently, we hypothesized that incorporating carbon uptake in the previous year would improve the correlation between NPP and GPP.

The incorporation of the previous year's carbon uptake markedly improved the correlation between NPP and GPP (Fig. 1B). Statistically significant relationships between NPP and GPP were observed by incorporating the previous year's late growing season gross carbon uptake. Defining GPP as the amount of carbon uptake from the previous August to the current July (GPP_{August-July}) resulted in the best relationship between annual GPP and NPP ($r^2: 0.76; p: 0.01$). Carbohydrates comprise 45% of belowground tissue and can supplement 15% of the carbon used for the current year's peak biomass (Gustafson, 1976; Kausch et al., 1981). The improved correlation between NPP and GPP from the previous year's August to the current year's July implies that carryover from carbohydrate reserves are important in driving year-to-year differences in NPP. Consequently, we used the slope from this relationship to derive NPP/GPP at the SJFM.

3.5. NPP to GPP ratio

The NPP to GPP ratio (the CUE) was robust and independent of the methodology used to derive it. The CUE derived from the slope between NPP and $GPP_{\text{August-July}}$ was 0.65 with a 95% confidence interval of 0.14 (Fig. 2A). The bootstrapping technique, which accounted for the variation in GPP and NPP, produced a statistically similar CUE (Fig. 2B). The CUE followed a normal probability distribution and ranged from 0.53 to 0.69. The average CUE from the bootstrapping approach was similar to that derived from the linear regression and was 0.61 with a 95% confidence interval of 0.05. We believe that the bootstrapped average NPP/GPP provided the best estimate of ecosystem CUE because it was less sensitive to uncertainty in NPP and GPP, and also included a degree of variability in annual measures of NPP and GPP. It should be noted that this CUE is much higher than the range reported by Waring et al. (1998) (0.47 ± 0.04) for forested ecosystems.

4. Discussion

4.1. Does the SJFM have a high NPP?

NPP varies both within and between terrestrial ecosystem types (Fig. 3). Tropical forests and freshwater marshes have the highest reported NPPs; deserts and tundra have the lowest NPPs. The average NPP was $992 \text{ gC m}^{-2} \text{ year}^{-1}$ for tropical forests and $1050 \text{ gC m}^{-2} \text{ year}^{-1}$ for freshwater marshes. Freshwater marshes exhibited large within ecosystem variability, ranging from $270 \text{ gC m}^{-2} \text{ year}^{-1}$ for an arrowhead (*Sagittaria lancifolia*) dominated ecosystem to $1602 \text{ gC m}^{-2} \text{ year}^{-1}$ for a Cattail (*Typha* spp.) dominated ecosystem. The 7-year mean (excluding 2004) NPP at the SJFM was $867 \text{ gC m}^{-2} \text{ year}^{-1}$, while the average NPP for freshwater marshes was $1050 \text{ gC m}^{-2} \text{ year}^{-1}$, indicating that the SJFM's productivity was typical for a productive freshwater marsh.

4.2. Is high SJFM NPP attributable to a high GPP?

We compared GPP data summarized in Falge et al. (2002) and elsewhere with the SJFM GPP from 1999 to 2007 to determine whether high NPP at the SJFM was associated with high annual GPP (Fig. 4). The GPPs for coniferous forests, grasslands, crops, deciduous forests and the SJFM were broadly comparable, while tropical rainforests had the highest GPPs ($3200 \text{ gC m}^{-2} \text{ year}^{-1}$). The comparison between tropical forest and SJFM production is particularly striking. The GPP of an Amazonian tropical forest was 130% greater than that at the SJFM, whereas the Total NPP at the tropical forest was 20% less than that at the SJFM (Figueira et al., in press). The annual rates of GPP observed at the SJFM were within the range of those reported for most other ecosystem types (Table 2; Fig. 4), including ones with comparatively low NPP. These results indicate that the GPP at the SJFM was similar to that reported for a variety of ecosystem types, and implies that high rates of marsh NPP are not a result of high GPP.

We also considered whether internal CO_2 recycling might increase GPP in a way that would not be detected by eddy covariance. Constable et al. (1992) found high concentrations of CO_2 in the aerenchyma of cattail and hypothesized that this

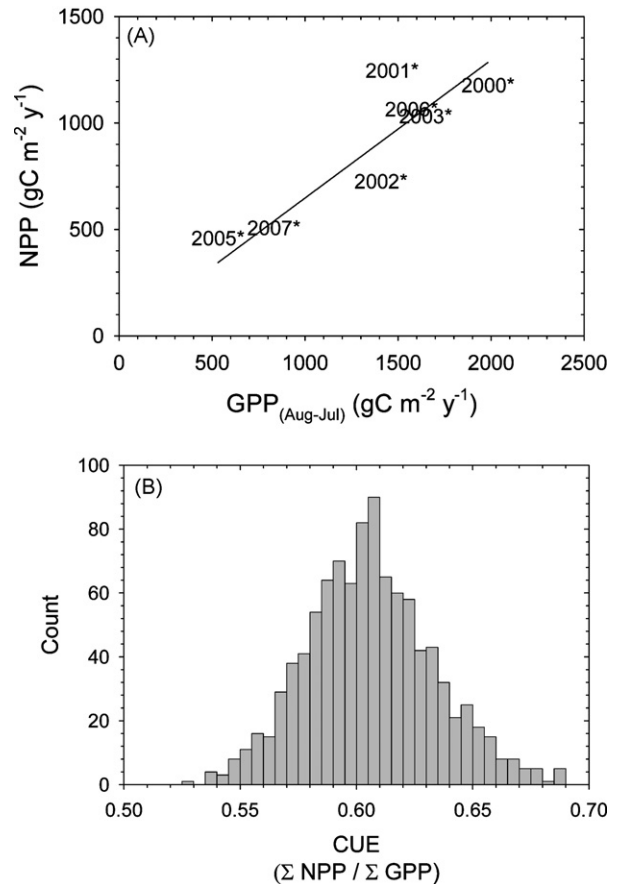


Fig. 2 – Relationship between NPP and GPP from the previous year's August to the current year's July ($\text{NPP} = 0.65\text{GPP}$; $r^2 = 0.76$; $p = 0.01$) at the SJFM (A). Histogram of the 1000 bootstrapped estimates of the SJFM's carbon use efficiency (NPP/GPP) (B).

CO_2 could be used as a supplementary source of carbon to accelerate photosynthesis and yield high NPP. However, studies using ^{14}C on *Typha* and other plants with aerenchyma (i.e. *Scirpus lacustris*, *Cyperus papyrus*, *Allium cepa*) have shown that little (i.e. 0.25–2.2%) of the CO_2 in the aerenchyma is recycled and used for photosynthesis (McNaughton and Fullen, 1970; Singer et al., 1994; Byrd et al., 1995). The isotopic signature of leaf $\delta^{13}\text{C}$ at the SJFM confirmed that CO_2 recycling does not play a major role in increasing GPP. Leaves that re-assimilate respired $\delta^{13}\text{C}$ should have an unusually negative leaf $\delta^{13}\text{C}$ (Vogel, 1978). However, the leaf $\delta^{13}\text{C}$ at the SJFM was typical of that reported for C3 plants (Goulden et al., 2007; Smith and Epstein, 1971), indicating that the eddy covariance measurements did not underestimate GPP due to internal CO_2 recycling. In summary, our analysis indicates that GPP cannot explain the high NPP at the SJFM.

4.3. Does the SJFM have a high CUE?

Comparing NPP/GPP between ecosystems indicates that the SJFM's CUE is high. The CUE we observed at the SJFM is much higher than has been reported for boreal (range: 0.23–0.45; mean: 0.31 ± 0.02), temperate (range: 0.07–0.68; mean:

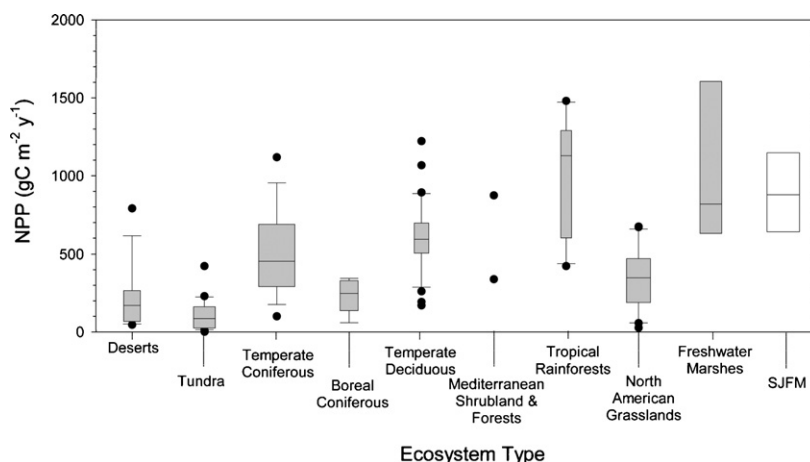


Fig. 3 – Net primary productivity (NPP: $\text{gC m}^{-2} \text{year}^{-1}$) at the SJFM (white box) compared to NPP observed in other ecosystem types (gray boxes). Boxes encompass the median and the 25th and 75th percentiles, while error bars encompass the 10th and 90th percentiles. Outliers are denoted as closed circles. The width of the bar is proportional to the sample size (n) with $n = 26$ for temperate coniferous forests and $n = 5$ for lowland tropical rainforests. Data from the Osneburck database (Esser et al., 2000).

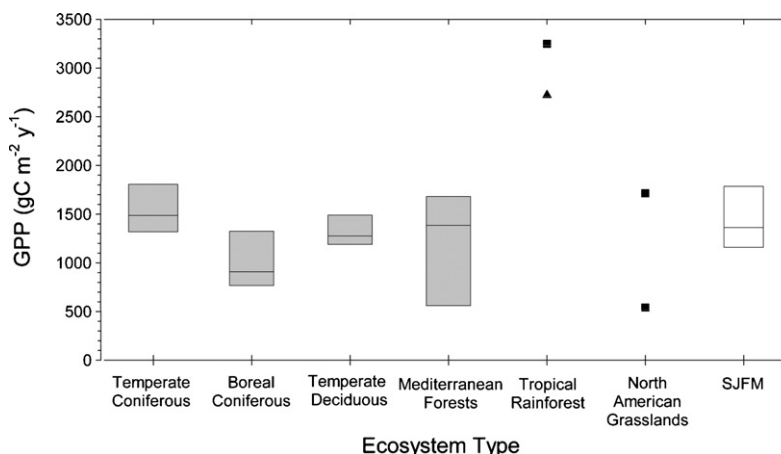


Fig. 4 – GPP ($\text{gC m}^{-2} \text{year}^{-1}$) at the SJFM (white box) compared to GPP observed in other ecosystem types (gray boxes). Boxes encompass the median and the 25th and 75th percentiles. Closed squares and triangle indicate single points. GPP data from the SJFM are the average annual sums of GPP calculated from the various respiration models (see Section 2). GPP data from other sites are from Falge et al. (2002) (boxes and closed squares) and Goulden et al. (2004) (closed triangle).

0.45 ± 0.03), and tropical ecosystems (range: 0.30–0.53; mean: 0.46 ± 0.05) (Amthor, 2000; DeLucia et al., 2007). There are few studies that report both NPP and GPP for marsh ecosystems with which to compare our estimates (Table 4). Gustafson

(1976) reported a CUE of 0.60 for a *Typha latifolia* dominated community in Wisconsin. Bonneville et al. (2007) reported a CUE of 0.65 for a *Typha* dominated community in Ontario, Canada based on peak aboveground biomass and crown base

Table 4 – Cattail carbon use efficiencies (CUE), as measured by the ratio of NPP to GPP (NPP/GPP), from the literature as compared with the SJFM

CUE (NPP/GPP)	How was NPP measured?	How was GPP measured?	Source/dominant spp.
0.60	Sequential aboveground and belowground harvests with carbohydrate storage correction.	Estimated from canopy photosynthesis model.	Gustafson (1976)/ <i>Typha latifolia</i>
0.65	Peak biomass. Did not include carbohydrate storage or rhizome or root productivity.	Eddy covariance with no energy budget correction.	Bonneville et al. (2007)/ <i>Typha latifolia</i>
0.61 ± 0.05	Peak biomass corrected for carbohydrate storage.	Eddy covariance with energy budget correction.	This study/ <i>Typha latifolia</i>

measurements. The CUE that we observed at the SJFM is comparable to CUE estimates from other freshwater marshes, and indicates that a high conversion efficiency of assimilated carbon to growth explains the high rates of NPP observed in freshwater marshes.

Our conclusion that the SJFM has a high CUE is conservative and includes several measures of uncertainty. Estimates of GPP were corrected for energy balance closure and were largely insensitive to gap-filling method. The use of peak biomass and the exclusion of leaf and root turnover may have underestimated both NPP and CUE by 12% (c.f. Dickerman et al., 1986). The similarity of CUE between the SJFM and other Cattail systems indicates that our results are consistent and representative. The greatest uncertainty in our conclusions results from the treatment of carbohydrate storage in calculating NPP. We may have overestimated carbohydrate storage because not all of the starch pool is available for growth (Gustafson, 1976; Kausch et al., 1981; Chapin et al., 1990). However, our conclusions remain conservative because overestimation of carbohydrate reserves decreases NPP and CUE, indicating that the CUE calculated from this approach is lower than the “true” CUE.

4.4. Summary: why are marshes so productive?

We found no evidence that the high rates of marsh NPP are a result of high gross photosynthetic rates. Rather, we attribute the previous reports of high marsh productivity to a high carbon use efficiency. Our conclusions are conservative and are not biased by the assumptions used in estimating GPP or the carbon use efficiency for the following reasons: (1) our estimate of GPP is constrained with the application of several gap filling techniques and all estimates are comparable with rates observed in other ecosystems with lower productivity, (2) carbon use efficiency was higher than observed for other ecosystems, despite the potential for underestimating CUE, and (3) a high carbon use efficiency is the only mechanism that can account for a high NPP and average GPP. NPP was poorly correlated with total photosynthesis in the same year, but incorporating a portion of the previous year's late growing season gross production into the calculation of GPP markedly improved the relationship between NPP and GPP. This improved relationship highlighted the importance of carbohydrate storage and translocation in determining NPP at the SJFM. This study underscores the importance of respiration and carbon allocation in determining marsh productivity and stresses the need to further understand the interaction between these two factors and NPP.

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REFERENCES

- Amthor, J.S., 1989. Respiration and Crop Productivity. Springer-Verlag, New York, pp. 215.
- Amthor, J.S., 2000. The McCree-de Wit-Penning de Vries-Thornley respiration paradigms: 30 years later. *Annals of Botany* 86, 1–20.
- Arneeth, A., Kelliher, F.M., McSeveny, T.M., Byers, J.N., 1998. Net ecosystem productivity, net primary productivity and ecosystem carbon sequestration in a *Pinus radiata* plantation subject to soil water deficit. *Tree Physiology* 18, 785–795.
- Bonneville, M.-C., Strachan, I.B., Humphreys, E.R., Roulet, N.T., 2007. Net ecosystem CO₂ exchange in a temperate cattail marsh in relation to biophysical properties. *Agricultural and Forest Meteorology* 148, 69–81.
- Bowden, W.B., 1987. The biogeochemistry of nitrogen in freshwater wetlands. *Biogeochemistry* 4, 313–348.
- Bradbury, I.K., Grace, J., 1983. Primary production in wetlands. In: Gore, A.J.P. (Ed.), *Mires: Swamp, Bog, Fen and Moor. Ecosystems of the world*, vol. 4A. Elsevier, Amsterdam, p. 440.
- Byrd, G.T., Loboda, T., Black, C.C., Brown, R.H., 1995. Leaf cavity CO₂ concentrations and CO₂ exchange in onion, *Allium cepa* L. *Photosynthesis Research* 44, 253–260.
- Carbone, M.S., Trumbore, S.E., 2007. Contribution of new photosynthetic assimilates to respiration by perennial grasses and shrubs: residence times and allocation patterns. *New Phytologist* 176, 124–135.
- Chapin, F.S., 1989. The cost of tundra plant structures: evaluation of concepts and currencies. *The American Naturalist* 133, 1–19.
- Chapin, F.S., Schulze, E.-D., Mooney, H.A., 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* 21, 423–447.
- Childers, D.L., 2006. A synthesis of long-term research by the Florida Coastal Everglades LTER Program. *Hydrobiologia* 569, 531–544.
- Constable, J.V.H., Grace, J.B., Longstreth, D.J., 1992. High carbon dioxide concentrations in aerenchyma of *Typha latifolia*. *American Journal of Botany* 79, 415–418.
- Curtis, P.S., Hanson, P.J., Bolstad, P., Barford, C., Randolph, J.C., Schmid, H.P., Wilson, K.B., 2002. Biometric and eddy-covariance based estimates of ecosystem carbon storage in five eastern North American deciduous forests. *Agricultural and Forest Meteorology* 113, 3–19.
- DeLucia, E.H., Drake, J.E., Thomas, R.B., Gonzalez-Meler, M., 2007. Forest carbon use efficiency: is respiration a constant fraction of gross primary production? *Global Change Biology* 13, 1157–1167.
- Dewar, R.C., Medlyn, B.E., McMurtie, R.E., 1998. A mechanistic analysis of light and carbon use efficiencies. *Plant, Cell, and Environment* 21, 573–588.
- DiCiccio, T.J., Efron, B., 1996. Bootstrap Confidence Intervals. *Statistical Science* 11, 189–212.
- Dickerman, J.A., Stewart, A.J., Wetzzel, R.G., 1986. Estimates of net annual aboveground production: sensitivity to sampling frequency. *Ecology* 67, 311–318.
- Dickson, R.E., 1991. Assimilate distribution and storage. In: Raghavendra, A.S. (Ed.), *Physiology of Trees*. John Wiley and Sons, Inc., New York, NY, USA, pp. 51–85.
- Dunham, R.M., Ray, A.M., Inouye, R.S., 2003. Growth, physiology, and chemistry of mycorrhizal and nonmycorrhizal *Typha latifolia* seedlings. *Wetlands* 23, 890–896.
- Esser, G., Lieth, H.F.H., Scurlock, J.M., Olson, R.J., 2000. Osnabrück net primary productivity data set. *Ecology* 81, 1177.

- Falge, E., Baldocchi, D.D., Tenhunen, J., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, C., Burba, G., Clement, R., Davis, K.J., Elbers, J.A., Goldstein, A.H., Grelle, A., Granier, A., Gudmundsson, J., Hollinger, D.Y., Kowalski, A.S., Katul, G., Law, B.E., Malhi, Y., Meyers, T., Monson, R.K., Munger, J.W., Oechel, W., Paw, U.K.T., Pilegaard, K., Rannik, U., Rebmann, C., Suyker, A., Valentini, R., Wilson, K., Wofsy, S., 2002. Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agricultural and Forest Meteorology* 113, 53–74.
- Figueira, A.M.S., Miller, S.D., de Sousa, A.D., Menton, M.C. Maia, A.R. da Rocha, H.R., Goulden, M.L., in press. Effects of selective logging on tropical forest tree growth, *Journal of Geophysical Research: Biogeosciences*.
- Gifford, R.M., 2003. Plant respiration in productivity models: conceptualization, representation and issues for global terrestrial carbon-cycle research. *Functional Plant Biology* 30, 171–186.
- Gough, C.M., Vogel, C.S., Schmid, H.P., Su, H.-B., Curtis, P.S., 2008. Multi-year convergence of biometric and meteorological estimates of forest carbon storage. *Agricultural and Forest Meteorology* 148, 158–170.
- Goulden, M.L., Daube, B.C., Fan, S.-M., Sutton, D.J., Bazzaz, A., Munger, J.W., Wofsy, S.C., 1997. Physiological responses of a Black Spruce forest to weather. *Journal of Geophysical Research* 102, 28,987–28,996.
- Goulden, M.L., Miller, S.D., da Rocha, H.R., Menton, M.C., Freitas, H.C., Figueira, A.M.S., de Sousa, C.A.D., 2004. Diel and seasonal patterns of tropical forest CO₂ exchange. *Ecological Applications* 14, S42–S54.
- Goulden, M.L., Litvak, M., Miller, S.D., 2007. Controls on *Typha* Marsh evapotranspiration. *Aquatic Botany* 58, 97–106.
- Gustafson, T.D., 1976. Production, Photosynthesis, and the Storage and Utilization of Reserves in a Natural Stand of *Typha latifolia* L. Ph.D. Thesis, University of Wisconsin, Madison. pp. 102.
- Hagen, S.C., Braswell, B.H., Linder, E., Frohling, S., Richardson, A.D., Hollinger, D.Y., 2006. Statistical uncertainty of eddy flux-based estimates of gross ecosystem carbon exchange at Howland Forest, Maine. *Journal of Geophysical Research* 111, 2005JD006154.
- Jervis, R.A., 1969. Primary production in the freshwater marsh ecosystem of Troy Meadows, New Jersey. *Bulletin of the Torrey Botanical Club* 96, 209–231.
- Kausch, A.P., Seago, J.L., Marsh, L.C., 1981. Changes in starch distribution in the overwintering organs of *Typha latifolia* (TYPHACEAE). *American Journal of Botany* 68, 877–880.
- Keddy, P.A., 2000. *Wetland Ecology: Principles and Conservation*. Cambridge University Press, pp. 614.
- Keefe, C.W., 1972. Marsh production: a summary of the literature. *Contributions in Marine Science* 16, 163–181.
- Litton, C.M., Raich, J.W., Ryan, M.G., 2007. Carbon allocation in forest ecosystems. *Global Change Biology* 13, 2089–2109.
- Longstreth, D.J., 1989. Photosynthesis and photorespiration in freshwater emergent and floating plants. *Aquatic Botany* 34, 287–299.
- Lorenzen, B., Brix, H., Mendelsson, I.A., McKee, K.L., Miao, S.L., 2001. Growth, biomass allocation and nutrient use efficiency in *Cladium jamaicense* and *Typha domingensis* as affected by phosphorus and oxygen availability. *Aquatic Botany* 70, 117–133.
- Mahrt, L., 1998. Flux sampling errors for aircraft and towers. *Journal of Atmospheric and Oceanic Technology* 15, 416–429.
- McNaughton, S.J., 1974. Developmental control of net productivity in *Typha latifolia* ecotypes. *Ecology* 55, 864–869.
- McNaughton, S.J., Fullem, L.W., 1970. Photosynthesis and photorespiration in *Typha latifolia*. *Plant Physiology* 45, 703–707.
- Medlyn, B.E., Dewar, R.C., 1999. Comment on the article by R.H. Waring, J.J. Landsberg, M. Williams relating net primary production to gross primary production. *Tree Physiology* 19, 137–138.
- Mitsch, W.J., Gosselink, J.G., 1993. *Wetlands*, 2nd ed. Van Nostrand Reinhold, New York, NY, USA, pp. 920.
- Morgan, J.M., 1984. Osmoregulation and water stress in higher plants. *Annual Review of Plant Physiology* 35, 299–319.
- Peat, H.J., Fitter, A.H., 1993. The distribution of arbuscular mycorrhizae in the British flora. *New Phytologist* 125, 845–854.
- Penning de Vries, F.W.T., Brunsting, A.H.M., van Laar, H.H., 1974. Products, requirements and efficiency of biosynthesis: a quantitative approach. *Journal of Theoretical Biology* 45, 339–377.
- Poorter, H., Villar, R., 1997. The fate of acquired carbon in plants: chemical composition and construction costs. In: Bazzaz, F.A., Grace, J. (Eds.), *Plant Resource Allocation*. Academic Press, San Diego, CA, USA, pp. 39–71, 303.
- Ramsey, F.L., Schafer, D.W., 2002. *The statistical sleuth: a course in methods of data analysis*, 2nd ed. Duxbury Press, Pacific Grove, CA.
- Richardson, A.D., Braswell, B.H., Hollinger, D.Y., Burman, P., Davidson, E.A., Evans, R.S., Flanagan, L.B., Munger, J.W., Savage, K., Urbanski, S.P., Wofsy, S.C., 2006. Comparing simple respiration models for eddy flux and dynamic chamber data. *Agricultural and Forest Meteorology* 141, 219–234.
- Rocha, A.V., 2008. The importance of intrinsic controls in driving interannual NEP variability. Ph.D. Dissertation, UC Irvine, Department of Earth Systems Science.
- Rocha, A.V., Goulden, M.L., in press. Large interannual CO₂ and energy exchange variability in a freshwater marsh under consistent environmental conditions, *JGR-Biogeosciences*.
- Rocha, A.V., Goulden, M.L., Dunn, A.L., Wofsy, S.C., 2006. On linking interannual tree ring variability with observations of whole-forest CO₂ flux. *Global Change Biology* 12, 1390–1399.
- Rocha, A.V., Potts D.L., Goulden M.L., in press. Standing litter as a driver of interannual CO₂ exchange variability in a freshwater marsh, *JGR-Biogeosciences*.
- Roxburgh, S.H., Berry, S.L., Buckley, T.N., Barnes, B., Roderick, M.L., 2005. What is NPP? Inconsistent accounting of respiratory fluxes in the definition of net primary production. *Functional Ecology* 19, 378–382.
- Sheehy, J.E., Cooper, J.P., 1973. Light interception, photosynthetic activity, and crop growth rate in canopies of six temperate forage grasses. *The Journal of Applied Ecology* 10, 239–250.
- Singer, A., Eshel, A., Agami, M., Beer, S., 1994. The contribution of aerenchymal CO₂ to the photosynthesis of emergent and submerged culms of *Scirpus lacustris* and *Cyperus papyrus*. *Aquatic Botany* 49, 107–116.
- Smith, B.N., Epstein, S., 1971. Two categories of ¹³C/¹²C ratios for higher plants. *Plant Physiology* 47, 380–384.
- Twine, T.E., Kustas, W.P., Norman, J.M., Cook, D.R., Houser, P.R., Meyers, T.P., Prueger, J.H., Starks, P.J., Wesely, M.L., 2000. Correcting eddy-covariance flux underestimates over a grassland. *Agricultural and Forest Meteorology* 103, 279–300.
- Valiela, I., 1995. *Marine Ecological Processes*. Springer-Verlag, New York, pp. 686.
- Van Iersel, M.W., 2003. Carbon use efficiency depends on growth respiration, maintenance respiration, and relative growth rate. A case study with lettuce. *Plant, Cell, & Environment* 26, 1441–1449.
- Vogel, J.C., 1978. Recycling of carbon in a forest environment. *Oecologia Plantarum* 13, 89–94.

- Waring, R.H., Landsberg, J.J., Williams, M., 1998. Net primary production of forests: a constant fraction of gross primary production? *Tree Physiology* 18, 129–134.
- Westlake, D.F., 1963. Comparisons of plant productivity. *Biological Reviews* 38, 385–425.
- Whittaker, R.H., 1975. *Communities and Ecosystems*. MacMillan, New York, NY, pp. 385.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavenger-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. *Nature* 428, 821–827.
- Zoubir, A.M., 1993. Bootstrap: theory and applications. In: Luk, F.T. (Ed.), *Proceedings of SPIE on Advanced Signal Processing Algorithms, Architectures and Implementations*, vol. 2027, San Diego, USA, July, pp. 216–235.