Only macroalgal detritus can remain viable for months

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1 SPECIAL ISSUE: PLANT SENESCENCE

2 RESEARCH IN CONTEXT

3 **Only macroalgal detritus can remain viable for months**

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8

9 **Running title**

10 Only macroalgal detritus can remain viable for months

11

12 **Abstract**

13 **Background and Aims** Seaweed detritus, particularly that of kelps, can maintain photosynthesis

14 over several months following detachment. By delaying and even counteracting decomposition,

15 detrital photosynthesis may have a substantial effect on detrital dynamics and thus carbon

16 cycling. Viability of detritus could be explained by limited tissue differentiation, as is common in

17 non-vascular plants. However, it remains unclear if detrital photosynthesis is restricted to this

18 group.

19 **Methods** I excised leaves of the seagrasses *Amphibolis antarctica* and *Halophila ovalis* by

20 cutting the petiole, mimicking detachment caused by hydrodynamics or herbivory which

21 prematurely induces senescence. Leaves were weighed down on sediment in mesh bags, supplied

22 with fresh flowing seawater and light, and periodically destructively sampled to measure light-

23 saturated net photosynthesis in closed oxygen incubations. To view my research in context, I

1 performed a meta-analysis of detrital photosynthesis and chlorophyll against time post-excision

2 across >10^4 observations from 127 independent studies on 92 species from 37 families and 23

3 orders of terrestrial and aquatic plants.

4 **Key Results** Here I show that detrital photosynthesis *per se* is not restricted to non-vascular

5 plants. Seagrasses exhibit detrital photosynthesis, but only up to a month post-excision. This is

6 substantially longer than for terrestrial and freshwater plants (one week) but also much shorter

7 than for seaweeds (several months, possibly up to a year).

8 **Conclusions** Detrital photosynthesis is clearly a phenomenon beyond the realm of seaweeds.

9 The intermediate longevity of seagrass detritus is likely due to convergent evolution with

10 seaweeds. However, months-long detrital photosynthesis is unique to macroalgae. So physiology

11 probably only substantially influences detrital recalcitrance in this plant group. My findings call

12 into question our grasp of the key predictors of seaweed decomposition and thereby of blue

13 carbon in general.

14

15 **Keywords**

16 Laminariales, Alismatales, Hydrocharitaceae, Cymodoceaceae, paddle weed, wire weed, leaf

17 litter, drift, dislodgement, abscission, degradation, decay.

18

19 **Introduction**

20

21 *...tossed and swept like dead leaves from one spot to another, never resting, never giving back*

22 *their goodness to the earth, never fully dead but in some vast limbo between life and extinction,*

23 *tossing and tumbling without end…* – Philip Pullman (1994) *The Tin Princess*

2

1

2 Seaweed detrital dynamics are strongly influenced by physiology. Kelp detritus can remain

3 physiologically viable for months (de Bettignies *et al.*, 2020; Frontier *et al.*, 2021; Wright and

4 Foggo, 2021; Wright *et al.*, 2022; Wright and Kregting, 2023; Wright *et al.*, 2024). Floating kelp

5 detritus sinks before it stops photosynthesising (Graiff *et al.*, 2013, 2016; Tala *et al.*, 2019). And

6 if the fragment happens to be reproductive tissue, detritus can even be a vector for dispersal

7 (Macaya *et al.*, 2005; Fraser *et al.*, 2018; Tala *et al.*, 2019; de Bettignies *et al.*, 2020). This stands

8 in stark contrast to the traditional ecological definition of detritus as "dead organic matter"

9 (Moore *et al.*, 2004, cf. Wright and Kregting, 2023). Detrital photosynthesis provides the

10 strongest evidence in support of the viability of detritus. But the fundamental impact on detrital

11 dynamics only becomes apparent when comparing decomposition rates between live and dead or

12 senescent detritus. In the absence of physiology, seaweed detritus decomposes at least twice as

13 fast (Birch *et al.*, 1983; Brouwer, 1996; de Bettignies *et al.*, 2020; Smith and Foreman, 1984 vs.

14 Albright *et al.*, 1982, Bedford and Moore, 1984). This is likely due to maintenance of growth and

15 chemical defence (Tala *et al.*, 2019; de Bettignies *et al.*, 2020; Frontier *et al.*, 2021; Wright *et al.*,

16 2022), probably making physiology an important source of detrital recalcitrance (Wright *et al.*,

17 2022, 2024).

18

19 There is currently no baseline for detrital photosynthesis. The term was first introduced quite

20 recently in the context of kelp decomposition (Frontier *et al.*, 2021; Wright *et al.*, 2022) although

21 there was clearly awareness of the phenomenon in much earlier phycology research which

22 deemed it necessary to pre-kill detritus (Birch *et al.*, 1983; Smith and Foreman, 1984; Brouwer,

23 1996). Other fields of botany do not use the term but there certainly has been abundant research

1   into physiology of excised leaves of terrestrial and freshwater plants (e.g. Lovell *et al.*, 1972;

2   Thimann and Satler, 1979; Jana and Choudhuri, 1980; Kar and Choudhuri, 1986). The literature

3   also includes some discussion on the meaning of chlorophyll persistence in senescing seagrass

4   (Knauer and Ayers, 1977; Pellikaan, 1982; Strother and Vatta, 1986). Yet no attempt has been

5   made to align these seemingly incongruous research trajectories in a formal comparison. We

6   consequently don't know if detrital photosynthesis is as unique as it seems. Instead, it may be

7   quite prevalent among plants. A reviewer once wrote to me that detrital photosynthesis in kelps

8   "is really not surprising, since macroalgae are much less differentiated than higher plants and,

9   thus, there is no reason why the single cell shouldn't be able to continue its activity for a while".

10   To satisfy their mentality I added a statement to the effect that detrital photosynthesis is "readily

11   explained" by the ability of all macroalgal tissues to independently photosynthesise to some

12   extent (Wright and Kregting, 2023). In truth, nothing is "readily explained" due to our lack of

13   reference points. The mechanism underlying the ability of seaweeds to maintain photosynthesis

14   in the detrital phase remains unclear. It could be their aquatic nature which removes reliance on

15   roots for water, nutrient provisioning from the surrounding water, non-vascularity, minimal

16   tissue differentiation and/or something altogether different. To understand the prerequisite for

17   detrital photosynthesis and thus predict prevalence among plants, model systems beyond

18   seaweeds are needed.

19

20   Seagrasses are suitable candidates for further investigation of detrital photosynthesis. While also

21   marine macrophytes, they are fundamentally different from seaweeds. Seagrasses are vascular

22   plants which, due to their terrestrial ancestry (Olsen *et al.*, 2016), are differentiated into roots,

23   rhizomes or stems, and leaves. However, convergent evolution with seaweeds (Olsen *et al.*,

4

1 2016) has reduced their reliance on roots for nutrient uptake. Seagrass leaves tend to outperform

2 their roots in suppling nutrients to the plant (Pedersen and Borum, 1992; Stapel *et al.*, 1996;

3 Pedersen *et al.*, 1997; Gras *et al.*, 2003; Viana *et al.*, 2019). This suggests that seagrass leaves

4 can independently photosynthesise, seemingly reducing the primary function of the roots to

5 anchorage, analogous to the holdfast of seaweeds. However, given the usually greater

6 ammonium concentration in sediment pore water, roots can supply more nitrogen despite the

7 leaves' greater uptake affinity (Short and McRoy, 1984; Lee and Dunton, 1999, but see Pedersen

8 and Borum, 1992) and nutrients are translocated to leaves (Short and McRoy, 1984; Viana *et al.*,

9 2019), even those tens of centimetres from the source (Marbà *et al.*, 2002). Roots can also tap

10 into nutrient pools that are unavailable to leaves, such as particulate (Evrard *et al.*, 2005) and

11 microbial (Patriquin and Knowles, 1972; Mohr *et al.*, 2021) nitrogen. Clearly the photosynthetic

12 emancipation of seagrass leaves is at a halfway point between terrestrial plants and macroalgae,

13 so seagrasses probably display detrital photosynthesis to some extent. Relatively slow and light-

14 dependent chlorophyll degradation in seagrass detritus (Knauer and Ayers, 1977; Pellikaan,

15 1982; Strother and Vatta, 1986) provides some support for this, but there are currently no data on

16 seagrass detrital photosynthesis. Freshwater and terrestrial plants are expected to exhibit detrital

17 photosynthesis to a similar and lesser extent respectively compared to seagrasses.

18

19 Here I aim to verify the existence of detrital photosynthesis in seagrasses and test its extent in

20 plants more broadly to determine potential influences on plant detrital dynamics. I conducted a

21 brief *ex situ* decomposition experiment with the two diverse seagrasses *Halophila ovalis*

22 (Hydrocharitaceae) and *Amphibolis antarctica* (Cymodoceaceae). Apart from their phylogenetic

23 (diverged 105 Ma ago, Waycott *et al.*, 2018) and obvious morphological (de los Santos *et al.*,

5

1   2012, 2016) differences, I chose these genera because they give some indication of the

2   possibility of detached photosynthesis (Kenworthy *et al.*, 1989; Pedersen *et al.*, 1997). I excised

3   fresh leaves and left them to decompose on sediment, measuring net photosynthesis of

4   destructively sampled leaves at regular intervals. Excision was intended to mimic detachment of

5   non-senescent leaves rather than abscission. I then compared my evidence with published data on

6   seaweeds as well as terrestrial and freshwater plants by pulling together various lines of research

7   in a single meta-analysis.

8

9   **Materials and methods**

10   *Experiment (the research)*

11   *Halophila ovalis* ramets with several leaf pairs and intact roots were collected from Pelican Point

12   in the brackish Swan Estuary (31.98715°S, 115.82101°E) alongside sediment from adjacent

13   Matilda Bay (31.97572°S, 115.82324°E) on 15th September 2022. I filled the bottom of a 220-L

14   glass flow-through seawater tank with the sediment and planted the ramets to briefly acclimatise

15   them to ambient seawater temperature and salinity and a 12-12-h light-dark cycle (11 ± 1.6 µmol

16   photons m^{-2} s^{-1}, mean ± s.d.). *Amphibolis antarctica* stems with several leaf clusters were

17   collected from fully marine Marmion Lagoon (31.85303°S, 115.75092°E) on 13th October 2022.

18

19   The *ex situ* decomposition experiment was commenced on the respective day of collection by

20   excising individual leaves (*H. ovalis*) or leaf clusters (*A. antarctica*), hereinafter leaves, and

21   immediately measuring photosynthesis (see next paragraph) of six (*H. ovalis*) or nine (*A.*

22   *antarctica*) samples. The remaining leaves were enclosed in mesh (3-mm ∅). Mesh bags were

23   weighed down with inert aquarium pebbles and placed on the sediment in the 220-L tank. At

1   each of five (*A. antarctica*) to six (*H. ovalis*) timepoints over 34 d following excision, six

2   destructive samples were taken from the mesh bags to measure photosynthesis.

3

4   Light-saturated net photosynthesis (P_{max}) of leaves was measured using closed oxygen (O_2)

5   incubations (c.f. Wright *et al.*, 2024). *A. antarctica* leaf clusters weigh roughly ten times as much

6   as *H. ovalis* leaves (in light of my data the mass ratio seems to be closer to 14:1). Since I wanted

7   to measure both seagrasses in the same volume for the same duration, I incubated ten *H. ovalis*

8   leaves or single *A. antarctica* leaf clusters alongside seawater blanks in sealed glass jars filled

9   with water collected from the flow-through system. Each jar was equipped with a magnetic stir

10   bar and a self-adhesive planar O_2 sensor spot (SP-PSt3-SA-NAU-D5-YOP, PreSens Precision

11   Sensing GmbH, Regensburg, Germany) and placed on a magnetic stirrer under a saturating

12   (Masini and Manning, 1997; Jamaludin *et al.*, 2006; Said *et al.*, 2021) irradiance of 420 ± 19

13   μmol photons m^{-2} s^{-1} (Zeus, Ledzeal, Shenzhen Topline Lighting Technology Co. Ltd.,

14   Shenzhen, China) in a 20ºC room. Care was taken to exclude air from jars. Dissolved O_2 (μM)

15   was measured fibre-optically through the glass every 10 s over at least 35 min with a four-

16   channel O_2 meter (OXY-4 SMA G2, PreSens Precision Sensing GmbH, Regensburg, Germany).

17   The O_2 meter was calibrated using anoxic (1% w/v Na_2SO_3) and air-saturated (bubbled with air)

18   ultrapure water. All measurements were corrected for incubation temperature (18 ± 0.73 ºC),

19   pressure (1020 ± 6 hPa) and salinity (35 ± 0.48 ‰) using a single temperature dipping probe

20   connected to the first channel of the O_2 meter's built-in temperature sensor and placed in a fifth

21   jar filled with seawater, the O_2 meter's built-in pressure sensor and a handheld refractometer

22   respectively. I blotted and weighed (0.01-g accuracy, 440-33N, Kern & Sohn GmbH, Balingen,

7

1   Germany) leaves and gravimetrically determined jar volume with ultrapure water to standardise

2    $P_{\max}$ as shown in the Equation 1.

3

4   Data analysis and visualisation were performed in R v4.2.3 (R Core Team, 2025) with the

5   tidyverse package family v2.0.0 (Wickham *et al.*, 2019) within the integrated development

6   environment RStudio v2023.06.0+421 (RStudio Team, 2025). Hamiltonian Monte Carlo models

7   were written in Stan (Carpenter *et al.*, 2017) and run with the R interface cmdstanr v0.5.3 (Gabry

8   *et al.*, 2024) via CmdStan v2.30.1 (Lee *et al.*, 2017). All models were run with 8 Markov chains

9   spread across all cores with 10^4 warmup and sampling iterations each. Convergence and smooth

10   sampling were optimised by assessing effective sample sizes and $\hat{R}$ scores and visually

11   scrutinising trace rank and pair plots with bayesplot v1.11.1 (Gabry *et al.*, 2019). All reported

12   results are posterior probabilities and derived central tendencies and intervals calculated with

13   tidybayes v3.0.7 (Kay, 2024). The R script can be consulted for detailed information on data

14   analysis (github.com/lukaseamus/seagrass-detrital-photosynthesis). Vector illustrations were

15   made in Affinity Designer v1.10.6 (Serif Ltd., Nottingham, UK).

16

17   In the first instance, simple linear models with centred incubation time ($t - \bar{t}$, min) as the

18   predictor and dissolved O_2 (μM) as the response variable were fit to measurements from each

19   sample and blank incubation. This yielded posterior probability distributions for slopes (β, μM

20   min^{-1}) which were converted to mass-based $P_{\max}$ (μmol g^{-1} h^{-1}) as

21

22   $$P_{\max} = \frac{(\beta_s - \beta_b) \times V \times \Delta t}{m} \qquad\qquad (1)$$

23

1   where subscript s and b denote sample and blank incubations from the same measurement group,

2   V is the incubation volume (175 ± 0.17 mL) in litres, m is the sample blotted mass (0.52 ± 0.23

3   g) in grams and Δt is the desired period (60 min h^{-1}) in minutes.

4

5   To predict P_{max} with detrital age (A, d), I chose a logistic regression of the form

6

7   $P_{max} \sim N(\, P_\mu \, , P_\sigma \,)$ (2)

8   $P_\mu = \dfrac{\alpha + \tau}{1 + e^{k \times (A - \mu)}} - \tau$

9

10   where α is baseline photosynthesis (μmol g^{-1} h^{-1}), τ is the community oxygen consumption of

11   dead detritus (μmol g^{-1} h^{-1}), k is the logistic rate of decay (d^{-1}) and μ is the midpoint of

12   photosynthetic death (d). The naming of parameters is inspired by the Hebrew word אמת

13   (graecised τμα) which means truth and is composed of the first, middle and last letters of the

14   Hebrew alphabet, symbolising life (א), transition (מ) and death (ת). Inscribed on the golem's

15   brow this word lends life, but removing א changes the meaning from truth to death (מת) and the

16   golem dies. As in the story of the golem, the logistic function is optimal for modelling a shift

17   between two alternate states and is thus the logical choice here. I previously modelled detrital

18   photosynthesis with linear regressions instead, because data either did not span enough

19   timepoints to inform a more complex model (Wright *et al.*, 2022) or macroalgal tissue

20   disintegration coinciding with photosynthetic death prevented estimation of μ and τ (Wright *et*

21   *al.*, 2024). However, in the present case these limitations do not apply, since I collected data at

22   six to seven timepoints and seagrass leaves do not disintegrate at or shortly after photosynthetic

23   death, allowing me to choose the optimal model. The downside of using more complex models is

1   that multiple regression to account for technical confounders (Wright *et al.*, 2024) is not

2   straightforward. So I opted for a separate multiple linear regression of P_{max} against the

3   standardised potential confounders initial incubation O_2 (µM), mean incubation temperature

4   (°C), mean incubation pressure (hPA), incubation salinity (‰) and leaf blotted mass (g) (Figure

5   S1).

6

7   Prior probability distributions for parameters were chosen based on published estimates and

8   logic. For the linear regressions of O_2 against incubation time, I gave the intercept a normal prior

9   centred on regional average seawater O_2 and the slope a normal prior with a mean of zero. For *a*

10   (Equation 2), I chose a gamma prior informed by various published P_{max} estimates for *H. ovalis*

11   (40 ± 57 µmol g^{-1} h^{-1}, 1.8 ± 2.5 µmol $leaf^{-1}$ h^{-1}, n = 32, Björk *et al.*, 1997; Jamaludin *et al.*,

12   2006; Borum *et al.*, 2016; Lamit and Tanaka, 2021; Said *et al.*, 2021, 2024) and *A. antarctica* (14

13   ± 9 µmol g^{-1} h^{-1}, 8.8 ± 5.5 µmol $leaf^{-1}$ h^{-1}, n = 8, Masini and Manning, 1997; Borum *et al.*,

14   2016; Said *et al.*, 2024). Units were converted where necessary by multiplying by mean dry-

15   fresh mass ratios for *H. ovalis* (0.21 g dry mass g^{-1} fresh mass) and *A. antarctica* (0.29 g dry

16   mass g^{-1} fresh mass) (de los Santos *et al.*, 2012; Borum *et al.*, 2016) and my own leaf fresh

17   masses for *H. ovalis* (0.04 ± 0.01 g $leaf^{-1}$) and *A. antarctica* (0.61 ± 0.27 g $leaf^{-1}$). For τ

18   (Equation 2), I chose a gamma prior to logically rule out net photosynthesis of dead detritus and

19   centred it around published estimates of O_2 consumption by litter of *Zostera marina* (17 ± 5.6

20   µmol g^{-1} h^{-1}, n = 16, Blum and Mills, 1991) and *Posidonia oceanica* (1.3 ± 1.3 µmol g^{-1} h^{-1}, n =

21   46, Mateo and Romero, 1996, 1997). Units were again converted by multiplying by mean dry-

22   fresh mass ratios for *Z. marina* (0.23 g dry mass g^{-1} fresh mass, Evans *et al.*, 1986) and *P.*

23   *oceanica* (0.24 g dry mass g^{-1} fresh mass, Apostolaki *et al.*, 2024). I decided *k* (Equation 2)

1   would best be restricted to positive values to ensure photosynthetic decay and would likely be

2   higher than for seaweeds, so chose a gamma prior with a mean of 0.2 d^{-1}, the maximum for

3   *Ecklonia radiata* (Wright *et al.*, 2024). For μ (Equation 2), since detrital age is inherently

4   positive, I settled on a gamma prior with a mean of 17 d, half the experimental duration. I chose

5   a reasonable s.d. for each prior distribution based on published estimates and prior simulation.

6   Importantly, to enforce an x-intercept close to 1, I put an additional joint prior on k and μ which

7   favoured a logistic intercept ($k \times \mu$, log odds at $A = 0$) close to 4 ± 1, or about 0.97 ± 0.024 on the

8   probability scale. This was coded as `target += gamma_lpdf( k .* mu | 4^2 /`

9   `1^2 , 4 / 1^2 )` in Stan (Carpenter *et al.*, 2017). Priors are visualised alongside posteriors

10   for scrutiny.

11

12   Finally, the treatment of uncertainty deserves brief mention. Firstly, I propagated measurement

13   error. Specifically, β and V (Equation 1) as well as initial incubation O_2 and incubation

14   temperature are measured with error, which I incorporated into the downstream models as s.d. of

15   posterior distributions. Wherever a variable is measured with error, I visualised each observation

16   as a distribution rather than a point. Secondly, I applied partial pooling to the species variable to

17   estimate uncertainty within and across species and make predictions for new seagrasses.

18

19   ***Meta-analysis (the context)***

20   I searched the literature using keyword strings such as "(photosynthesis OR chlorophyll) AND

21   ('induced senescence' OR detrit* OR detach* OR excis* OR cut) AND (week* OR day* OR

22   hour* OR minute* OR time OR age)" in Web of Science (webofscience.com/wos) and Google

23   Scholar (scholar.google.com). Once I had a selection of suitable papers, I used Crossref

1   Metadata Search (search.crossref.org) to find similar papers. I accepted various photosynthesis

2   response variables, including O_2 and CO_2 gas exchange, carbon assimilation (^{14}C concentration),

3   chlorophyll fluorescence (F_v/F_m), photosystem I and II electron transport rates (Mehler and Hill

4   reactions), RuBisCo activity or concentration, carbonic anhydrase activity and photorespiration

5   (glycolate concentration), as well as total chlorophyll (Chl), Chl *a* or a chlorophyll indicator.

6   This resulted in 127 suitable independent studies between 1957 and the present study (see

7   supplementary references), from which I extracted data by copying tables or digitising plots

8   using WebPlotDigitizer v5.2 (Rohatgi, 2025). In two cases I contacted authors for their raw data

9   and in five cases the data were my own. It is noteworthy that apart from these seven cases, raw

10   data were not available.

11

12   Data were collated into variables Reference, DOI, Group, Phylum, Order, Family, Species,

13   Light, Water, Series, Day, Mean, SEM, N, Response, Method, Unit and Source. Some of these

14   are self-explanatory, but most are not. Group classes observations into four non-taxonomic

15   groups of interest: terrestrial plants (66 species), freshwater plants (6 species), seagrasses (5

16   species) and seaweeds (15 species). It is noteworthy that all freshwater plants belonged to the

17   order Alismatales, like seagrasses, and all seaweeds belonged to the green and brown algae

18   (Table S1). My distinction between freshwater and terrestrial plants is based on whether or not

19   the leaves are submerged. There were no studies on freshwater macroalgae, so seaweeds are

20   presumed to be representative. Phylum, Order, Family and Species represent the currently

21   accepted taxonomy according to Plants of the World Online (POWO, 2025) and AlgaeBase

22   (Guiry and Guiry, 2025). Light and Water are binary classifiers of whether or not the

23   experimental plant tissue had access to light or water. Series numbers the measurement

1   timeseries within a given study since most studies reported several experiments, response

2   variables, species or individuals. Only measurement series with at least three timepoints were

3   accepted. Day is the time post-excision given in d ($\frac{wk}{7}$, h × 24, min × 1440). Mean is either an

4   observation or the mean of several observations at a given timepoint. When the case is the latter,

5   SEM and N are the standard error of the mean (s.e.m.) and its sample size (n). Uncertainty was

6   mostly given as s.e.m., but when s.d. was provided instead, this was converted as s.e.m. $= \frac{s.d.}{\sqrt{n}}$. In

7   a few cases uncertainty was given as a 95% confidence interval (CI) or interquartile range (IQR).

8   In the former case, I converted as s.e.m. $= \frac{0.5 \times CI_{0.95}}{\Phi^{-1}(0.975)}$, in the latter I assumed mean = median and

9   conservatively converted the larger of the two quartile ranges ($Q_3 - Q_2$ or $Q_2 - Q_1$) as s.e.m. =

10   $\frac{QR}{\Phi^{-1}(0.75) \times \sqrt{n}}$. Response dichotomises data into photosynthesis and chlorophyll measurements

11   since these measures are decoupled and probably senesce on different timescales. Method details

12   how the response variable was measured, Unit provides the original response unit, and Source

13   directs the reader to the data source in the paper. Please refer to the data publication (Wright,

14   2025) and github.com/lukaseamus/detrital-photosynthesis for further details.

15

16   The resulting 535 measurement series contained a mixture of observations and means. To jointly

17   analyse data with such different levels of uncertainty one must either condense observations to

18   means and s.e.m. or s.d. and build a measurement error model or expand means to observations. I

19   opted for the latter and obtained 10566 observations by simulating draws from the normal

20   distribution using `rnorm( N , Mean , SEM * sqrt(N) )` in R (R Core Team, 2025),

21   or mathematically $X_{1:N} \sim N($ Mean, $(SEM \times \sqrt{N})^2)$. Prior to analysis, I normalised observations

22   to proportions by dividing by the initial observation or mean of initial observations in the

1   timeseries. This was the favourable choice as opposed to min-max normalisation, since many

2   detrital photosynthesis data already come expressed as % or proportion of initial. The drawback

3   is that data aren't fully brought onto the same scale because some variables allow negative

4   proportions (e.g. net gas exchange) while most don't (e.g. Chl, F_v/F_m etc.). I assume that the

5   effect of this on the outcome of the analysis is minimal due to the relative scarcity of net gas

6   exchange data and enforcing $\tau = 0$ (Equation 2).

7

8   Analysis was carried out as described above to model detrital viability over time, using a

9   simplified Equation 2 with $a = 1$ and $\tau = 0$. Additive categorical predictors caused convergence

10   issues, so I created a composite grouping variable from Group, Light and Response. Water is

11   only relevant to a relatively small subset of terrestrial plant data and was therefore excluded as a

12   predictor. No partial pooling was applied here because I did not want to make predictions for

13   plants at large and introducing hyperparameters led to convergence issues. The gamma prior for

14   k was centred on 0.22 d^{-1}, the mean across seagrasses which emerged from the experimental

15   component of this study (Table 1) and is assumed to be intermediate between seaweeds and

16   terrestrial plants. Experimental durations varied substantially across studies (Table S1), so half of

17   the mean experimental duration was picked as the prior mean for μ. I again chose a reasonable

18   s.d. based on prior simulation and put an additional joint prior on k and μ. Several terrestrial

19   plant studies reported photosynthetic decay over periods of only minutes post-excision (Table

20   S1). These data pull the intercept down when given a weak joint prior, necessitating a much

21   tighter prior. The logistic intercept was therefore constrained to 4 ± 0.1, equivalent to $0.98 \pm$

22   0.0018 on the probability scale: `target += gamma_lpdf( k .* mu | 4^2 / 0.1^2`

23   `, 4 / 0.1^2 ).`

1

2   **Results**

3   *Experiment (the research)*

4   *Halophila ovalis* photosynthesised for longer post-excision than *Amphibolis antarctica*. After 34

5   d, the duration of the experiment, all *H. ovalis* leaves were still obviously net autotrophic while

6   all *A. antarctica* leaves were apparently dead. Comparing logistic decay rates (k) and times of

7   death (μ) of light-saturated net photosynthesis (P_{max}) clarifies this difference. On a mass basis, *A.*

8   *antarctica* started with a similar P_{max} to *H. ovalis*, but its P_{max} decayed 1.5 times faster and

9   expired 20 ± 2.4 d (mean ± s.d.) earlier (Figure 1a, Table 1). On a leaf basis, *A. antarctica* P_{max}

10   only decayed 40% faster and expired 15 ± 3 d earlier than that of *H. ovalis* (Figure 1b, Table 1).

11   This difference between mass- and leaf-based estimates was primarily due to varying trends for

12   *H. ovalis* (Figure 1a vs. b). While *A. antarctica* displayed comparable k ($\Delta = 0.038 \pm 0.059$ d^{-1}, P

13   $= 0.75$) and μ ($\Delta = 1.2 \pm 2$ d, P $= 0.73$), leaf-based *H. ovalis* P_{max} declined 53% (P $= 0.92$) faster

14   and expired 6.5 ± 3.3 d (P $= 0.98$) earlier.

15

16   When accounting for leaf mass, *H. ovalis* thus seems to be able to photosynthesise longer post-

17   excision. The immediate reason for this was the linear decline of leaf mass in *H. ovalis* ($\alpha =$

18   0.052 ± 0.005 g leaf^{-1}, $\beta = -0.58 \pm 0.26$ mg leaf^{-1} d^{-1} or -1.1 ± 0.43 % d^{-1}, P$_{\beta < 0} = 0.99$) while

19   *A. antarctica* leaf mass remained almost unchanged ($\alpha = 0.64 \pm 0.053$ g leaf^{-1}, $\beta = -2 \pm 2.7$ mg

20   leaf^{-1} d^{-1} or -0.3 ± 0.41 % d^{-1}, P$_{\beta < 0} = 0.78$). But it remains unclear why *H. ovalis* leaves of

21   reduced mass photosynthesised disproportionally. The most likely reason is that filamentous

22   green algae, which I observed colonising *H. ovalis* but not *A. antarctica*, contributed much to

23   photosynthesis but very little to leaf mass. This renders the leaf-based *H. ovalis* estimates more

15

1 trustworthy and may have exacerbated the reported differences between the two seagrasses but is

2 unlikely to have confounded the general trend.

3

4 Despite their phylogenetic and morphological diversity, both seagrasses displayed quite

5 consistent tendencies, allowing relatively precise prediction for seagrasses in general (Figure 1,

6 Table 1). The discussed discrepancy between mass- and leaf-based P_{max} of *H. ovalis* only

7 marginally affected estimates on this higher level. Overall, seagrasses had similar k ($\Delta = 0.0055$

8 ± 0.075 d^{-1}, P = 0.54) and μ ($\Delta = 1.4 \pm 4.8$ d, P = 0.62) across mass- and leaf-based models

9 (Table 1). It therefore seems that seagrass P_{max} generally decays at a rate of 0.22 d^{-1} and persists

10 for around 17 d.

11

12 ***Meta-analysis (the context)***

13 Comparison across plants revealed that only seaweeds can maintain detrital photosynthesis for

14 several months. Seagrasses are limited to less than a month and freshwater and terrestrial plants

15 to about a week (Figure 2, Table 2). Under light, k of seaweeds is 96% ($\Delta = 0.51 \pm 0.052$ d^{-1}, P =

16 1) smaller than that of terrestrial plants. Seagrass photosynthesis decays 7.5 times ($\Delta = 0.15 \pm$

17 0.025 d^{-1}, P = 1) faster than that of seaweeds and 68% ($\Delta = 0.36 \pm 0.058$ d^{-1}, P = 1) slower than

18 that of terrestrial plants. Correspondingly, μ of seaweeds occurs 210 ± 102 d (P = 1) later than in

19 terrestrial plants. Seagrass detritus again takes an intermediate position, losing the ability to

20 photosynthesise 190 ± 102 d (P = 1) earlier than seaweed detritus and 18 ± 3.6 d (P = 1) later

21 than terrestrial plant detritus.

22

1   Photosynthesis and chlorophyll (Chl) followed fairly consistent trends for seagrasses and

2   terrestrial and freshwater plants (Figure 2, Table 2). This indicates that for these plants detrital

3   Chl is a reasonable predictor of detrital photosynthesis. Seaweeds again form an exception and

4   had 69% smaller k and 3 times larger μ for Chl than photosynthesis (Table 2), meaning that Chl

5   tends to overestimate longevity of detrital photosynthesis fourfold for this group (Figure 2).

6   Nonetheless, since there are no data on photosynthetic senescence under light for freshwater

7   plants, Chl enables a mostly representative comparison of all plant groups. Surprisingly,

8   freshwater plant detritus lost Chl at similar rates to terrestrial plant detritus ($\Delta = 0.023 \pm 0.087$

9   d^{-1}, P = 0.6), and consequently 1.4 times ($\Delta = 0.36 \pm 0.094$ d^{-1}, P = 1) and 102 times ($\Delta = 0.61 \pm$

10   0.066 d^{-1}, P = 1) faster than seagrass and seaweed detritus respectively. Accordingly,

11   photosynthetic death of freshwater plants occurs at the same time ($\Delta = 0.21 \pm 0.91$ d, P = 0.6) as

12   terrestrial plants, and therefore 10 ± 4.4 d (P = 1) and 850 ± 577 d (P = 1) earlier than that of

13   seagrasses and seaweeds respectively.

14

15   Light ameliorated photosynthetic decay in all except freshwater plants (Figure 2, Table 2).

16   However, it only substantially extended detrital longevity in seaweeds. Whereas the effect is

17   negligible for freshwater plants and only on the order of a couple days to a week for terrestrial

18   plants and seagrasses, seaweed photosynthesis decays 25 times faster and terminates 96% earlier

19   in darkness (Table 2). Consequently, under darkness seaweed detritus only remains viable for

20   comparable durations to terrestrial ($\Delta = 4.2 \pm 7.3$ d, P = 0.89) and freshwater ($\Delta = 4.4 \pm 7.3$ d, P

21   = 0.9) plants. This suggests that the extreme detrital longevity observed in seaweeds is highly

22   light-dependent.

23

1   **Discussion**

2   Despite the existence of various relevant literature, the phenomenon of detrital photosynthesis

3   had not been explored beyond kelps. In part, this is probably due to diverse research objectives

4   which obscure the connection between quantitatively comparable data. There was also data

5   scarcity in some important plant groups, especially the seagrasses. Here I filled this knowledge

6   gap by presenting the first data on photosynthesis in seagrass detritus and subsequently the first

7   meta-analysis of detrital photosynthesis across all plants.

8

9   Detrital photosynthesis *per se* is not restricted to non-vascular plants. Seagrass detritus can also

10   photosynthesise for at least a couple weeks. The physiology of diverse seagrasses responds

11   similarly to detrital age and observed differences may simply be attributable to varying

12   colonisation by biofilm algae. Alternatively, *Amphibolis antarctica* leaves may be more reliant

13   on their roots for nutrient provisioning. But there is no other evidence to suggest this (Pedersen

14   *et al.*, 1997) and the 15–20 d earlier photosynthetic death of isolated *A. antarctica* leaves

15   compared to *Halophila ovalis* is surprising given their 1.7 times ($\Delta = 47$ d) longer attached

16   lifespan (Hemminga *et al.*, 1999). Seagrass detrital photosynthesis, despite persisting for weeks,

17   may not necessarily counteract decomposition, a process which can a year for these plants

18   (Harrison, 1989; Cebrián *et al.*, 1997; Trevathan-Tackett *et al.*, 2020). While live *Halophila*

19   *decipiens* ramets do indeed decompose slower than buried ones (Kenworthy *et al.*, 1989),

20   decomposition rates are similar between live and senescent or buried *Thalassia testudinum*

21   leaves (Rublee and Roman, 1982; Fourqurean and Schrlau, 2003; Rosch and Koch, 2009) and

22   meta-analysis suggests that live seagrass leaves actually tend to decompose faster than senescent

23   or dead ones (Harrison, 1989; Trevathan-Tackett *et al.*, 2020).

1

2   Macroalgae uniquely exhibit long-term detrital photosynthesis. In fact, there is nothing to

3   suggest that detritus produced by these plants cannot remain viable for up to a year. As expected,

4   seagrasses exhibit intermediate detrital longevity between seaweeds and terrestrial plants, which

5   photosynthesise for at most one week post-excision. The extreme contrast to terrestrial plants has

6   been demonstrated but is in fact somewhat dampened in my formal analysis. When given light

7   but no water, which is the normal fate of terrestrial plant detritus, detached leaves of various

8   trees tend to lose the ability to photosynthesise in just a few minutes (e.g. (Gauthier and Jacobs,

9   2018; Kar *et al.*, 2021). This is due to breakdown of stomatal conductance following a loss in

10 water pressure (Powles *et al.*, 2006; Gauthier and Jacobs, 2018). What surprised me is that

11 detrital viability of freshwater plants is like that of terrestrial plants and not seagrasses. One

12 explanation is excess production of hydrogen peroxide during photosynthesis in the detached leaf

13 which leads to chlorophyll degradation, as demonstrated for *Hydrilla verticillata* (Kar and

14 Choudhuri, 1986, 1987) and is likely also the case for other freshwater angiosperms (Jana and

15 Choudhuri, 1982). In contrast, there is no evidence for increased chlorophyll breakdown in

16 isolated seagrass leaves exposed to light (Strother and Vatta, 1986) and photodegradation is only

17 apparent in dead leaves (Vähätalo *et al.*, 1998). Emancipation of leaf photosynthesis from the

18 rest of the plant is apparently not favoured by an aquatic but rather by a marine nature in vascular

19 plants. What exactly happened to allow this during the transition of angiosperms from lakes and

20 rivers to the sea remains unclear. Perhaps the answer lies in convergent evolution with seaweeds,

21 in particular alterations to the light harvesting complexes and cell wall features that enhance gas

22 exchange (Olsen *et al.*, 2016)?

23

19

1   Senescence mechanisms determine the impact physiology can have on detrital dynamics.

2   Seagrass detritus often incudes green leaves (Knauer and Ayers, 1977; Ochieng and Erftemeijer,

3   1999; Jiménez-Ramos *et al.*, 2023). This may be in part because nutrient resorption prior to

4   abscission is low relative to terrestrial plants (Harrison, 1989; Pedersen and Borum, 1992;

5   Pedersen *et al.*, 1997; Hemminga *et al.*, 1999; Rosch and Koch, 2009). But the most likely

6   mechanism is premature detachment caused by external factors such as hydrodynamics and

7   herbivory (Cebrián *et al.*, 1997) paired with seasonal weakening of the ligule (Jiménez-Ramos *et*

8   *al.*, 2023). Viable seagrass detritus is clearly produced under natural conditions, but due to the

9   mentioned mismatch between rapid photosynthetic decay and slow decomposition this is

10   expected to have little influence on detrital dynamics. Seaweeds tell a different story. Their

11   detritus can photosynthesise for many months, matching their decomposition timescale, if we

12   assume that excision mirrors detrital export in nature. Distally eroded and abscised tissue almost

13   certainly exhibits reduced detrital photosynthesis due to fragmentation and attached senescence,

14   which can greatly accelerate decomposition (de Bettignies *et al.*, 2020). But up to half of kelp

15   detritus is released by dislodgement of whole plants or large fragments (de Bettignies *et al.*,

16   2013; Pessarrodona *et al.*, 2018; Pedersen *et al.*, 2020). The visible detrital pool therefore

17   consists mostly of tissue that displays limited senescence and probably can remain

18   photosynthetic for many months.

19

20   I have previously suggested that detrital photosynthesis influences kelp blue carbon by providing

21   an additional dimension to detrital recalcitrance (Wright *et al.*, 2022, 2024). Its uniqueness

22   among plants, as evidenced here, suggests that it may play a disproportionate role in determining

23   the fate of macroalgal carbon. Most of our understanding of seaweed decomposition is based on

1   freshly excised blades (Albright *et al.*, 1982; Bedford and Moore, 1984; Frontier *et al.*, 2021;

2   Filbee-Dexter *et al.*, 2022; Wright *et al.*, 2022) as opposed to senescent (de Bettignies *et al.*,

3   2020) or dead (Birch *et al.*, 1983; Smith and Foreman, 1984; Brouwer, 1996) fragments. But as

4   mentioned, less than half of seaweed detritus can be considered fully viable when exported.

5   Additionally, decomposition experiments are usually carried out in the shallow subtidal with

6   access to light, but proponents of seaweed carbon sinks invariably place them in the darkness of

7   the deep sea (Krause-Jensen and Duarte, 2016; Filbee-Dexter *et al.*, 2024). My meta-analysis

8   suggests that darkness has a stronger detrimental effect on detrital photosynthesis in seaweeds

9   than any other plant. If detrital photosynthesis is granted the ecological significance I attribute to

10   it, these contradictions must make one wonder. Perhaps it is time to question existing

11   preconceptions in seaweed blue carbon?

12

13   To conclude, I show that vascular plants also photosynthesise after detachment, but this varies

14   greatly from a few minutes in tree leaves without access to water, over several days on average

15   in terrestrial and freshwater plants to a couple weeks in seagrasses. Macroalgae alone can

16   photosynthesise for months post-excision. The powerful effect of detrital photosynthesis on

17   decomposition and thereby blue carbon has already been evidenced to some extent (Birch *et al.*,

18   1983; Brouwer, 1996; de Bettignies *et al.*, 2020). What now remains to be investigated is (1)

19   decomposition trajectories of macroalgal detritus with and without physiology and how these

20   compare with seagrasses as the most functionally similar plants, (2) the prevalence of

21   photosynthesis in eroding, abscised and other senescing tissues, and (3) the proportion of the

22   detrital pool that photosynthesises *in situ*.

23

21

Supplementary data

Supplementary data are available at *Annals of Botany* online and consist of the following.

Figure S1: Effect of confounding variables associated with incubation on light-saturated net seagrass photosynthesis. Table S1: Species included in meta-analysis. References: Studies included in the meta-analysis in addition to the present study.

Data availability

Experimental data and annotated code are available at github.com/lukaseamus/seagrass-detrital-photosynthesis. The dataset used for meta-analysis is published (Wright, 2025) and can also be accessed at github.com/lukaseamus/detrital-photosynthesis. I place no restrictions on data and code availability within the constraints of the specified copyleft licence: GNU General Public License.

1

2   **Figure legends**

3

4   **Figure 1**. Seagrass detrital photosynthesis. Light-saturated net photosynthesis (P_{max}) per gram of

5   blotted mass (**A**) and per leaf (*H. ovalis*) or leaf cluster (*A. antarctica*) (**B**) as a function of time

6   post-excision. Distributions are kernel density estimates of priors and posteriors for parameters

7   (Equation 2) with vertical lines demarking the central 50, 80 and 90% of probability density. In

8   **B**, distributions for α and τ are not shown because they were modelled on the sample mass scale

9   with an appropriate prior that cannot be converted to the leaf mass scale (see Table 1 for

10   numerical estimates of α and τ). Violins are kernel density estimates of posterior probability

11   distributions for observations (Equation 1), showing the measurement error which is associated

12   with my method and was incorporated into the model. Lines and intervals are medians and the

13   central 50, 80 and 90% of posterior probability for P_μ, the mean prediction of P_{max} (Equation 2).

14   Light grey lines encompass the central 90% of prior probability.

15

16   **Figure 2**. Detrital photosynthesis meta-analysis. Photosynthesis (*P*) and chlorophyll (*Chl*)

17   variables as a function of time post-excision across four major plant groups: terrestrial plants

18   (Streptophyta excluding aquatic plants), freshwater plants (Alismatales excluding seagrasses),

19   seagrasses, and seaweeds (Chlorophyta and Heterokontophyta excluding freshwater macroalgae).

20   Distributions are kernel density estimates of priors and posteriors for parameters with vertical

21   lines demarking the central 50, 80 and 90% of probability density. Points are observations and

22   lines and intervals are medians and the central 50, 80 and 90% of posterior probability for the

23   mean prediction. Light grey lines encompass the central 90% of prior probability. Note that

1   several observations outside prior probability space were excluded from the plot for clarity but

2   not from the analysis.

3

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Table 1. General and specific seagrass parameter estimates (mean ± s.d., Equation 2) based on 8^4 posterior samples. Leaf-based α and τ were not estimated across seagrasses since generalisation on that scale is not insightful and models were run on a sample mass basis. Δ is the absolute difference between estimates for *Halophila ovalis* and *Amphibolis antarctica*. P is the probability that estimates for *Halophila ovalis* and *Amphibolis antarctica* are different, given the priors and data. P = 0.5 is equivalent to a coin toss. P > 0.9 is highlighted in bold.

	Seagrasses	*Halophila ovalis*	*Amphibolis antarctica*	Δ	P
Mass-based					
α (μmol g^{-1} h^{-1})	32 ± 1.7	32 ± 1.6	33 ± 1.8	1.1 ± 1.8	0.74
τ (μmol g^{-1} h^{-1})	1.4 ± 0.93	1.2 ± 1.2	1.3 ± 1.1	0.052 ± 1.1	0.54
k (d^{-1})	0.22 ± 0.055	0.11 ± 0.023	0.27 ± 0.043	0.16 ± 0.047	**1**
μ (d)	18 ± 3.6	32 ± 2.3	12 ± 1	20 ± 2.4	**1**
Leaf-based					
α (μmol leaf^{-1} h^{-1})		1.5 ± 0.11	22 ± 2	20 ± 2	**1**
τ (μmol leaf^{-1} h^{-1})		0.079 ± 0.063	0.91 ± 0.67	0.83 ± 0.67	**0.97**
k (d^{-1})	0.22 ± 0.051	0.16 ± 0.034	0.23 ± 0.041	0.066 ± 0.054	**0.91**
μ (d)	16 ± 3.1	26 ± 2.3	11 ± 1.7	15 ± 3	**1**

Table 2. Plant group parameter estimates (mean ± s.d., Equation 2) based on 8^4 posterior samples. Only k and μ are shown since response units were normalised and α and τ were therefore set to 1 and 0 respectively. Δ is the absolute difference between light and dark estimates within photosynthesis or chlorophyll. Δ with subscript is the absolute difference between photosynthesis and chlorophyll within light (Δ_L) or dark (Δ_D). P as in Table 1, i.e. the probability mass of $\Delta > 0$. P = 0.5 is equivalent to a coin toss. P > 0.9 is highlighted in bold. Selected pairwise differences between plant groups are provided in text.

|	Photosynthesis				Chlorophyll							
	Light	Dark	Δ	P	Light	Dark	Δ	P	Δ_L	P_L	Δ_D	P_D
Terrestrial plants												
k (d^{-1})	0.53 ± 0.052	0.75 ± 0.06	0.22 ± 0.079	**1**	0.59 ± 0.055	0.95 ± 0.053	0.36 ± 0.077	**1**	0.069 ± 0.076	0.82	0.21 ± 0.08	**1**
μ (d)	6.7 ± 0.64	5.2 ± 0.39	1.5 ± 0.75	**0.98**	6.7 ± 0.61	4 ± 0.19	2.6 ± 0.64	**1**	0.011 ± 0.88	0.51	1.2 ± 0.44	**1**
Freshwater plants												
k (d^{-1})		0.81 ± 0.11			0.62 ± 0.066	0.62 ± 0.077	0.0045 ± 0.1	0.51			0.19 ± 0.13	**0.94**
μ (d)		5 ± 0.61			6.5 ± 0.67	6.5 ± 0.79	0.032 ± 1	0.51			1.5 ± 1	**0.94**
Seagrasses												
k (d^{-1})	0.17 ± 0.025				0.26 ± 0.066	0.51 ± 0.12	0.25 ± 0.13	**0.98**	0.093 ± 0.071	**0.92**		
μ (d)	25 ± 3.6				17 ± 4.4	8.2 ± 1.9	8.3 ± 4.7	**0.98**	8.1 ± 5.6	**0.93**		
Seaweeds												
k (d^{-1})	0.02 ± 0.0047	0.51 ± 0.24	0.49 ± 0.24	**1**	0.006 ± 0.0025				0.014 ± 0.0053	**0.99**		
μ (d)	218 ± 102	9.4 ± 7.3	208 ± 102	**1**	861 ± 577				640 ± 586	**0.99**		
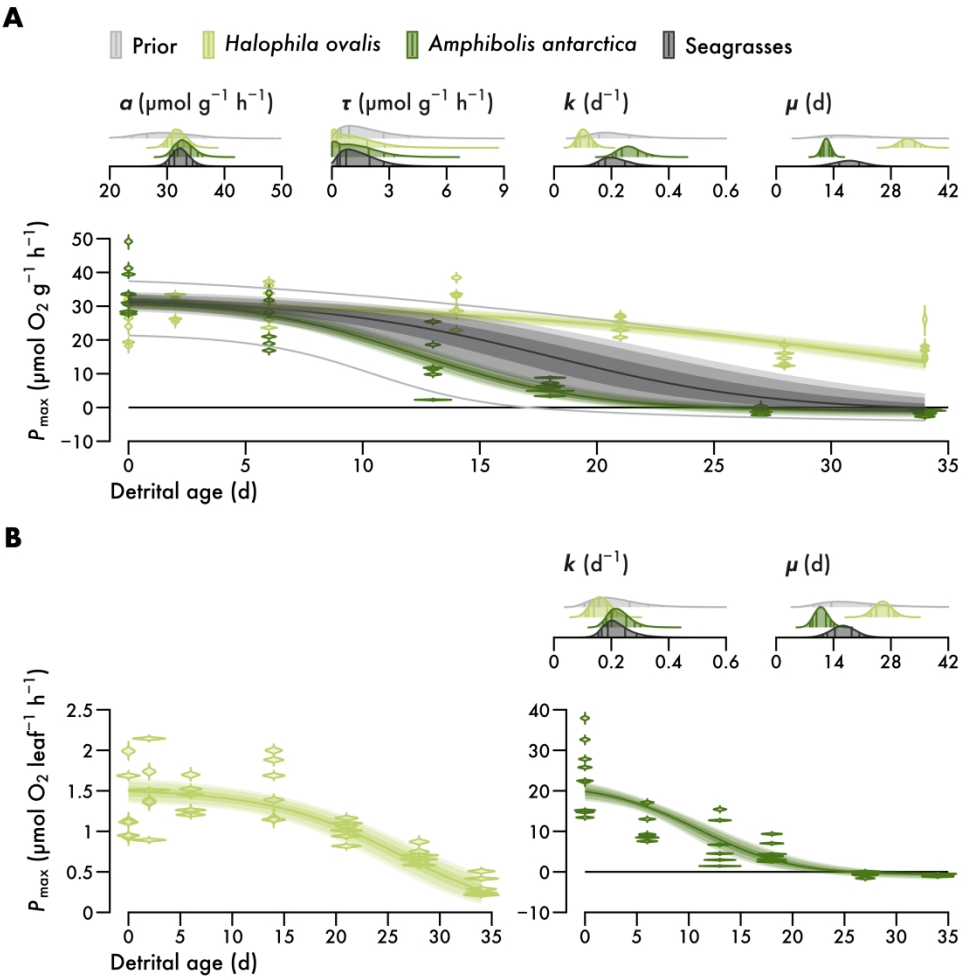
Figure 1. Seagrass detrital photosynthesis. Light-saturated net photosynthesis (Pmax) per gram of blotted mass (A) and per leaf (H. ovalis) or leaf cluster (A. antarctica) (B) as a function of time post-excision. Distributions are kernel density estimates of priors and posteriors for parameters (Equation 2) with vertical lines demarking the central 50, 80 and 90% of probability density. In B, distributions for α and τ are not shown because they were modelled on the sample mass scale with an appropriate prior that cannot be converted to the leaf mass scale (see Table 1 for numerical estimates of α and τ). Violins are kernel density estimates of posterior probability distributions for observations (Equation 1), showing the measurement error which is associated with my method and was incorporated into the model. Lines and intervals are medians and the central 50, 80 and 90% of posterior probability for Pμ, the mean prediction of Pmax (Equation 2). Light grey lines encompass the central 90% of prior probability.
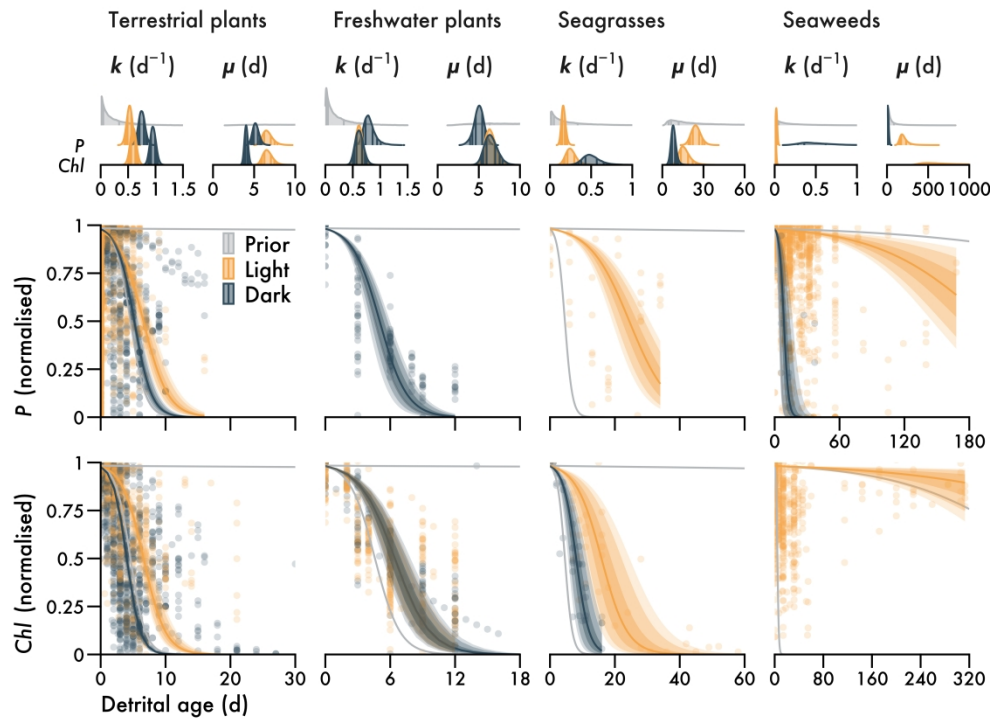
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Figure 2. Detrital photosynthesis meta-analysis. Photosynthesis (P) and chlorophyll (Chl) variables as a function of time post-excision across four major plant groups: terrestrial plants (Streptophyta excluding aquatic plants), freshwater plants (Alismatales excluding seagrasses), seagrasses, and seaweeds (Chlorophyta and Heterokontophyta excluding freshwater macroalgae). Distributions are kernel density estimates of priors and posteriors for parameters with vertical lines demarking the central 50, 80 and 90% of probability density. Points are observations and lines and intervals are medians and the central 50, 80 and 90% of posterior probability for the mean prediction. Light grey lines encompass the central 90% of prior probability. Note that several observations outside prior probability space were excluded from the plot for clarity but not from the analysis.
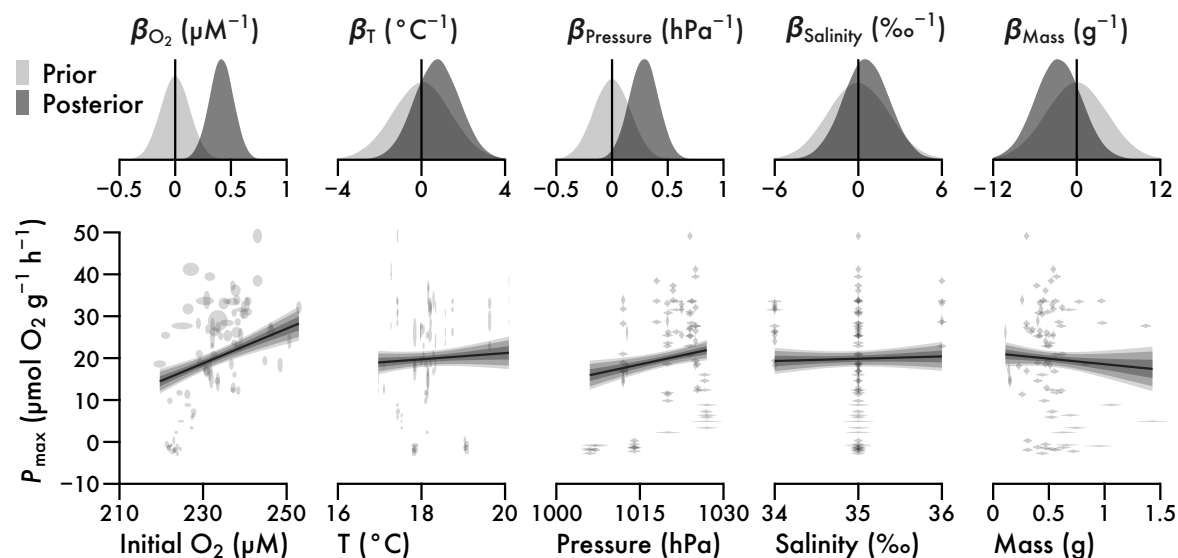
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Only macroalgal detritus remains viable for months

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Figure 1. Effect of confounding variables associated with incubation on light-saturated net seagrass photosynthesis (P_{max}) per gram of blotted mass. Distributions are kernel density estimates of priors and posteriors for slopes of the multiple linear regression. P_{max}, initial oxygen (O_2) and temperature (T) are measured with error. Ellipses and violins are bi- and univariate posterior probability distributions for observations. Lines and intervals are means and the central 50, 80 and 90% of posterior probability for the mean prediction of P_{max}.

Table S1. Species included in the meta-analysis. Phyla are given in bold and orders are underlined. Seaweeds are comprised of Chlorophyta and Heterokontophyta. Seagrasses are marked with an asterisk. All remaining Alismatales are freshwater plants and the rest of Streptophyta is terrestrial. The longest experimental durations and largest numbers of studies and observations in each non-taxonomic group are highlighted in bold.

	Species	Days	Studies	Observations
Chlorophyta				
<u>Ulvales</u>				
Ulvaceae	*Ulva clathrata*	30	1	6
	Ulva intestinalis	30	1	6
	Ulva reticulata	30	1	6
Heterokontophyta				
<u>Desmarestiales</u>				
Desmarestiaceae	*Desmarestia anceps*	**313**	1	65
<u>Fucales</u>				
Durvillaeaceae	*Durvillaea antarctica*	14	2	448
Sargassaceae	*Sargassum fallax*	14	1	84
	Sargassum spinuligerum	14	1	159
Seirococcaceae	*Scytothalia dorycarpa*	14	1	48
<u>Laminariales</u>				

Laminariaceae	*Laminaria digitata*	46	3	162
	Laminaria hyperborea	168	**6**	**533**
	Laminaria ochroleuca	56	4	416
	Macrocystis pyrifera	55	3	363
	Saccharina latissima	39	1	42
Lessoniaceae	*Ecklonia radiata*	119	2	117
<u>Tilopteridales</u>				
Phyllariaceae	*Saccorhiza polyschides*	39	1	38
Streptophyta				
<u>Alismatales</u>				
Cymodoceaceae	*Amphibolis antarctica**	34	**1**	39
Hydrocharitaceae	*Elodea densa*	16	2	43
	*Halophila ovalis**	34	**1**	42
	Hydrilla verticillata	12	**7**	**506**
	*Thalassia testudinum**	52	**1**	14
	Vallisneria americana	**104**	1	5
	Vallisneria spiralis	9	6	59
Potamogetonaceae	*Potamogeton sp.*	**104**	1	5
	Stuckenia pectinata	9	5	55
Zosteraceae	*Zostera marina**	**85**	**1**	10
	*Zostera muelleri**	16	**1**	**58**
<u>Apiales</u>				
Apiaceae	*Coriandrum sativum*	9	1	24
	Petroselinum crispum	7	1	7
<u>Asterales</u>				
Asteraceae	*Chrysanthemum × morifolium*	12	1	30
	Helianthus annuus	0.024	1	36
	Helianthus tuberosus	0.026	1	36
	Inula racemosa	0.025	1	36
	Smallanthus connatus	0.026	1	36
<u>Brassicales</u>				
Brassicaceae	*Arabidopsis thaliana*	6	2	60
	Brassica napus	1.7	1	125
	Brassica oleracea	10	1	22
	Nasturtium officinale	5	2	39
	Raphanus raphanistrum	6	1	20
	Sinapis alba	6	1	20
Tropaeolaceae	*Tropaeolum majus*	8	2	27
<u>Caryophyllales</u>				
Amaranthaceae	*Amaranthus cruentus*	0.026	1	36
	Celosia argentea	0.024	1	36
	Chenopodium berlandieri	0.27	1	26
	Gomphrena serrata	0.024	1	36
	Spinacia oleracea	10	3	85
Polygonaceae	*Koenigia weyrichii*	0.028	1	36
<u>Cucurbitales</u>				
Cucurbitaceae	*Cucumis sativus*	13	2	13
	Sicyos edulis	10	1	48
<u>Ericales</u>				
Theaceae	*Camellia sinensis*	4	1	11
<u>Fabales</u>				
Fabaceae	*Cercis canadensis*	0.0052	1	576

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Order	Family	Species			
		Lathyrus oleraceus	17	2	42
		Phaseolus vulgaris	2.1	1	10
		Trifolium subterraneum	7	2	25
		Vigna unguiculata	4	1	170
Fagales					
	Betulaceae	*Betula pendula*	0.029	1	36
	Fagaceae	*Quercus alba*	0.01	1	24
		Quercus muehlenbergii	0.0052	1	192
		Quercus robur	0.024	2	228
		Quercus rubra	0.01	1	24
	Juglandaceae	*Juglans nigra*	0.01	1	24
Lamiales					
	Lamiaceae	*Salvia officinalis*	11	1	8
Laurales					
	Lauraceae	*Cinnamomum tamala*	21	1	36
Pinales					
	Pinaceae	*Larix sibirica*	0.025	1	36
		Pinus sibirica	0.023	1	33
		Pinus sylvestris	0.022	1	33
Poales					
	Cyperaceae	*Bolboschoenus fluviatilis*	**104**	1	5
	Poaceae	*Avena sativa*	8	8	161
		Hordeum vulgare	11	**13**	466
		Lolium multiflorum	5	1	44
		Lolium pratense	7	5	112
		Oryza sativa	27	11	327
		Panicum miliaceum	5	2	69
		Secale cereale	5	2	102
		Triticum aestivum	10	**13**	646
		Triticum turgidum	6	1	7
		Triticum vulgare	6	1	48
		Zea mays	6	3	58
	Typhaceae	*Typha angustifolia*	**104**	1	5
Polypodiales					
	Nephrolepidaceae	*Nephrolepis exaltata*	10	1	24
Rosales					
	Rosaceae	*Fragaria × ananassa*	0.0056	1	663
		Malus domestica	21	3	150
		Malus hupehensis	15	1	18
Sapindales					
	Rutaceae	*Citrus × aurantium*	10	1	5
	Sapindaceae	*Acer saccharinum*	0.25	1	36
		Acer truncatum	0.0052	1	192
Solanales					
	Convolvulaceae	*Ipomoea batatas*	3	1	24
	Solanaceae	*Nicotiana rustica*	10	1	180
		Nicotiana tabacum	9	1	24
		Solanum lycopersicum	5	1	192
		Solanum melongena	16	1	24
		Solanum tuberosum	0.026	1	36
Vitales					
	Vitaceae	*Vitis vinifera*	0.0052	1	**1280**

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