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RESEARCH IN CONTEXT

**Plants in limbo — only macroalgal detritus can remain viable for months**

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**Running title**

Only macroalgal detritus can remain viable for months

**Abstract**

**Background and Aims** Seaweed detritus, particularly that of kelps, can maintain photosynthesis over several months following detachment. By delaying and even counteracting decomposition, detrital photosynthesis may have a substantial effect on detrital dynamics and thus carbon cycling. Viability of detritus could be explained by limited tissue differentiation, as is common in non-vascular plants. However, it remains unclear if detrital photosynthesis is restricted to this group. Here I look for detrital photosynthesis in seagrasses for which there is data scarcity and then compare them to seaweeds and other plants *sensu lato* to determine the relative influence of plant physiology on decomposition.

**Methods** I excised leaves of the seagrasses *Amphibolis antarctica* and *Halophila ovalis* by cutting the petiole, mimicking detachment caused by hydrodynamics or herbivory which prematurely induces senescence. Leaves were weighed down on sediment in mesh bags, supplied with fresh flowing seawater and light, and periodically destructively sampled to measure light-saturated net photosynthesis in closed oxygen incubations. To view my research in context, I performed a meta-analysis of detrital photosynthesis and chlorophyll against time post-excision across >104 observations from 127 independent studies on 92 species from 37 families and 23 orders of terrestrial and aquatic plants.

**Key Results** Here I show that detrital photosynthesis *per se* is not restricted to non-vascular plants. Seagrasses exhibit detrital photosynthesis, but only up to a month post-excision. This is substantially longer than for terrestrial and freshwater plants (one week) but also much shorter than for seaweeds (several months, possibly up to a year).

**Conclusions** Detrital photosynthesis is clearly a phenomenon beyond the realm of seaweeds. The intermediate longevity of seagrass detritus is likely due to convergent evolution with seaweeds. However, months-long detrital photosynthesis is unique to macroalgae. So physiology probably only substantially influences detrital recalcitrance in this plant group. My findings call into question our grasp of the key predictors of seaweed decomposition and thereby of blue carbon in general.

**Keywords**

Laminariales, Alismatales, Hydrocharitaceae, Cymodoceaceae, paddle weed, wire weed, leaf litter, drift, dislodgement, abscission, degradation, decay.

**Introduction**

*…tossed and swept like dead leaves from one spot to another, never resting, never giving back their goodness to the earth, never fully dead but in some vast limbo between life and extinction, tossing and tumbling without end*… — Philip Pullman (1994) *The Tin Princess*

Seaweed detrital dynamics are strongly influenced by physiology. Except for wrack, kelp detritus—*sensu lato* tissue that becomes detached—can remain physiologically viable for months (de Bettignies *et al.*, 2020; Frontier *et al.*, 2021; Wright and Foggo, 2021; Wright *et al.*, 2022; Wright and Kregting, 2023; Wright *et al.*, 2024), often resulting in atypical decomposition trajectories (Kennedy and Blain, 2025). Floating kelp detritus sinks before it stops photosynthesising (Graiff *et al.*, 2013, 2016; Tala *et al.*, 2019). And if the fragment happens to be reproductive tissue, detritus can even be a vector for dispersal (Macaya *et al.*, 2005; Fraser *et al.*, 2018; Tala *et al.*, 2019; de Bettignies *et al.*, 2020). This stands in stark contrast to the traditional ecological definition of detritus as “dead organic matter” (Moore *et al.*, 2004, cf. Wright and Kregting, 2023). There is no word for plant material that is detached but living and since detached seaweed—except for holopelagic species—has been referred to as detritus or less commonly as drift or litter all along, I propose to continue using detritus for any detached tissue and detritus *sensu stricto* for detached and dead tissue. Detrital photosynthesis provides the strongest evidence in support of the viability of detritus. But the fundamental impact on detrital dynamics only becomes apparent when comparing decomposition rates between live and dead or senescent detritus. When it is dead, seaweed detritus decomposes at least twice as fast (Birch *et al.*, 1983; Brouwer, 1996; de Bettignies *et al.*, 2020; Smith and Foreman, 1984 vs. Albright *et al.*, 1982, Bedford and Moore, 1984). This is likely due to maintenance of growth and chemical defence (Tala *et al.*, 2019; de Bettignies *et al.*, 2020; Frontier *et al.*, 2021; Wright *et al.*, 2022), probably making physiology an important source of detrital recalcitrance (Wright *et al.*, 2022, 2024).

There is currently no baseline for detrital photosynthesis—the persistence of photosynthesis in the detrital phase. The term was first introduced quite recently in the context of kelp decomposition (Frontier *et al.*, 2021; Wright *et al.*, 2022) although there was clearly awareness of the phenomenon in much earlier phycology research which deemed it necessary to pre-kill detritus (Birch *et al.*, 1983; Smith and Foreman, 1984; Brouwer, 1996). Other fields of botany do not use the term but there certainly has been abundant research into physiology of excised leaves of terrestrial and freshwater plants (e.g. Lovell *et al.*, 1972; Thimann and Satler, 1979; Jana and Choudhuri, 1980; Kar and Choudhuri, 1986). The literature also includes some discussion on the absence of chlorophyll degradation in senescing seagrass (Knauer and Ayers, 1977; Pellikaan, 1982; Strother and Vatta, 1986). Yet no attempt has been made to align these seemingly incongruous research trajectories in a formal comparison. We consequently don’t know if detrital photosynthesis is as unique as it seems. Instead, it may be quite prevalent among plants. A reviewer once wrote to me that detrital photosynthesis in kelps “is really not surprising, since macroalgae are much less differentiated than higher plants and, thus, there is no reason why the single cell shouldn’t be able to continue its activity for a while”. To satisfy their mentality I added a statement to the effect that detrital photosynthesis is “readily explained” by the ability of all macroalgal tissues to independently photosynthesise to some extent (Wright and Kregting, 2023). In truth, nothing is “readily explained” due to our lack of reference points. The mechanism underlying the ability of seaweeds to maintain photosynthesis in the detrital phase remains unclear. It could be their aquatic nature which removes reliance on roots for water, nutrient provisioning from the surrounding water, non-vascularity, minimal tissue differentiation and/or something altogether different. To understand the prerequisite for detrital photosynthesis and thus predict prevalence among plants, model systems beyond seaweeds are needed.

Seagrasses are suitable candidates for further investigation of detrital photosynthesis. While also marine macrophytes, they are fundamentally different from seaweeds. Seagrasses are vascular plants which, due to their terrestrial ancestry (Olsen *et al.*, 2016), are differentiated into roots, rhizomes or stems, and leaves. However, convergent evolution with seaweeds (Olsen *et al.*, 2016) has reduced their reliance on roots for nutrient uptake. Seagrass leaves tend to outperform their roots in suppling nutrients to the plant (Pedersen and Borum, 1992; Stapel *et al.*, 1996; Pedersen *et al.*, 1997; Gras *et al.*, 2003; Viana *et al.*, 2019). This suggests that seagrass leaves can independently photosynthesise, seemingly reducing the primary function of the roots to anchorage, analogous to the holdfast of seaweeds. However, given the usually greater ammonium concentration in sediment pore water, roots can supply more nitrogen despite the leaves’ greater uptake affinity (Short and McRoy, 1984; Lee and Dunton, 1999, but see Pedersen and Borum, 1992) and nutrients are translocated to leaves (Short and McRoy, 1984; Viana *et al.*, 2019), even those tens of centimetres from the source (Marbà *et al.*, 2002). Roots can also tap into nutrient pools that are unavailable to leaves, such as particulate (Evrard *et al.*, 2005) and microbial (Patriquin and Knowles, 1972; Mohr *et al.*, 2021) nitrogen. Clearly the photosynthetic emancipation of seagrass leaves is at a halfway point between terrestrial plants and macroalgae, so seagrasses probably display detrital photosynthesis to some extent. Relatively slow and light-dependent chlorophyll degradation in seagrass detritus (Knauer and Ayers, 1977; Pellikaan, 1982; Strother and Vatta, 1986) provides some support for this, but there are currently no data on seagrass detrital photosynthesis. Freshwater and terrestrial plants are expected to exhibit detrital photosynthesis to a similar and lesser extent respectively compared to seagrasses.

Here I aim to quantify detrital photosynthesis in seagrasses and plants more broadly to predict the extent to which it may influence plant detrital dynamics. I hope this information will allow us to re-evaluate seaweed and seagrass decomposition in the context of plants at large. To address these aims I conducted a brief *ex situ* decomposition experiment with the two diverse seagrasses *Halophila ovalis* (Hydrocharitaceae) and *Amphibolis antarctica* (Cymodoceaceae). Apart from their phylogenetic (diverged 105 Ma ago, Waycott *et al.*, 2018) and obvious morphological (de los Santos *et al.*, 2012, 2016) differences, I chose these genera because they give some indication of the possibility of detached photosynthesis (Kenworthy *et al.*, 1989; Pedersen *et al.*, 1997). I excised fresh leaves and left them to decompose on sediment, measuring net photosynthesis of destructively sampled leaves at regular intervals. Excision was intended to mimic detachment of non-senescent leaves rather than abscission. I then compared my evidence with published data on seaweeds as well as terrestrial and freshwater plants by pulling together various lines of research in a single meta-analysis.

**Materials and methods**

***Experiment (the research)***

*Halophila ovalis* ramets with several leaf pairs and intact roots were collected from Pelican Point in the brackish Swan Estuary (31.98715°S, 115.82101°E) alongside sediment from adjacent Matilda Bay (31.97572°S, 115.82324°E) on 15th September 2022. I filled the bottom of a 220-L glass flow-through seawater tank with the sediment and planted the ramets to acclimatise them to ambient seawater temperature and salinity and a 12-12-h light-dark cycle (11 ± 1.6 µmol photons m–2 s–1, mean ± s.d., cf. Masini and Manning, 1997) for about two hours. *Amphibolis antarctica* stems with several leaf clusters were collected from fully marine Marmion Lagoon (31.85303°S, 115.75092°E) on 13th October 2022 and immediately used in the experiment. Sediment and seagrasses were collected from less than one metre depth.

The *ex situ* decomposition experiment was commenced on the respective day of collection by excising individual leaves (*H. ovalis*) or leaf clusters (*A. antarctica*), hereinafter leaves, and immediately measuring photosynthesis (see next paragraph) of six (*H. ovalis*) or nine (*A. antarctica*) samples. The remaining leaves were enclosed in mesh (3-mm ⌀). Mesh bags were weighed down with inert aquarium pebbles and placed on the sediment in the same 220-L tank under identical photon fluence rate of 11 ± 1.6 µmol photons m–2 s–1, which is more than sufficient for detrital photosynthesis to play a role (Wright *et al.*, 2024) and is representative of the light environment experienced by detritus in the understorey of kelp forests and seagrass meadows or on deeper sediment flats. To measure photosynthesis at each of five (*A. antarctica*) to six (*H. ovalis*) timepoints over 34 d following excision, six destructive samples were taken from the mesh bags which were kept submerged for the entire duration of the experiment.

Light-saturated net photosynthesis (*P*max) of leaves was measured using closed oxygen (O2) incubations (cf. Wright *et al.*, 2024). *A. antarctica* leaf clusters weigh roughly ten times as much as *H. ovalis* leaves (in light of my data the mass ratio seems to be closer to 14:1). Since I wanted to measure both seagrasses at a comparable leaf mass per volume for the same duration, I incubated ten *H. ovalis* leaves or single *A. antarctica* leaf clusters alongside seawater blanks in sealed glass jars filled with water collected from the flow-through system. Each jar was equipped with a magnetic stir bar and a self-adhesive planar O2 sensor spot (SP-PSt3-SA-NAU-D5-YOP, PreSens Precision Sensing GmbH, Regensburg, Germany) and placed on a magnetic stirrer under a saturating (Masini and Manning, 1997; Jamaludin *et al.*, 2006; Said *et al.*, 2021) irradiance of 420 ± 19 µmol photons m–2 s–1 (Zeus, Ledzeal, Shenzhen Topline Lighting Technology Co. Ltd., Shenzhen, China) in a 20ºC room. Care was taken to exclude air from jars. Dissolved O2 (µM) was measured fibre-optically through the glass every 10 s over at least 35 min with a four-channel O2 meter (OXY-4 SMA G2, PreSens Precision Sensing GmbH, Regensburg, Germany). The O2 meter was calibrated using anoxic (1% w/v Na2SO3) and air-saturated (bubbled with air) ultrapure water. All measurements were corrected for incubation temperature (18 ± 0.73 ºC), pressure (1020 ± 6 hPa) and salinity (35 ± 0.48 ‰) using a single temperature dipping probe connected to the first channel of the O2 meter’s built-in temperature sensor and placed in a fifth jar filled with seawater, the O2 meter’s built-in pressure sensor and a handheld refractometer respectively. I blotted and weighed (0.01-g accuracy, 440-33N, Kern & Sohn GmbH, Balingen, Germany) leaves and gravimetrically determined jar volume with ultrapure water to standardise *P*max as shown in the Equation 1.

Data analysis and visualisation were performed in R v4.2.3 (R Core Team, 2025) with the tidyverse package family v2.0.0 (Wickham *et al.*, 2019) within the integrated development environment RStudio v2023.06.0+421 (RStudio Team, 2025). Hamiltonian Monte Carlo models were written in Stan (Carpenter *et al.*, 2017) and run with the R interface cmdstanr v0.5.3 (Gabry *et al.*, 2024) via CmdStan v2.30.1 (Lee *et al.*, 2017). All models were run with 8 Markov chains spread across all cores with 104 warmup and sampling iterations each. Convergence and smooth sampling were optimised by assessing effective sample sizes and scores and visually scrutinising trace rank and pair plots with bayesplot v1.11.1 (Gabry *et al.*, 2019). All reported results are posterior probabilities and derived central tendencies and intervals calculated with tidybayes v3.0.7 (Kay, 2024). The R script can be consulted for detailed information on data analysis (github.com/lukaseamus/plant-limbo). Vector illustrations were made in Affinity Designer v1.10.6 (Serif Ltd., Nottingham, UK).

In the first instance, simple linear models with centred incubation time (*t* − , min) as the predictor and dissolved O2 (µM) as the response variable were fit to measurements from each sample and blank incubation. This yielded posterior probability distributions for slopes (*β*, µM min−1) which were converted to mass-based *P*max (µmol g−1 h−1) as

(1)

where subscriptsandb denote sample and blank incubations from the same measurement group, *V* is the incubation volume (175 ± 0.17 mL) in litres, *m* is the sample blotted mass (0.52 ± 0.23 g) in grams and Δ*t* is the desired period (60 min h−1) in minutes.

To predict *P*max with detrital age (*A*, d), I chose a logistic regression of the form

(2)

where *α* is baseline photosynthesis (µmol g−1 h−1), *τ* is the oxygen consumption of dead detritus (µmol g−1 h−1), *k* is the logistic rate of decay (d−1) and *µ* is the midpoint of photosynthetic death, i.e. half-life of photosynthesis (d). The naming of parameters is inspired by the Hebrew word אמת (graecised τμα) which means truth and is composed of the first, middle and last letters of the Hebrew alphabet, symbolising life (א), transition (מ) and death (ת). Inscribed on the golem’s brow this word lends life, but removing א changes the meaning from truth to death (מת) and the golem dies. As in the story of the golem, the logistic function is optimal for modelling a shift between two alternate states and is thus the logical choice here. I previously modelled detrital photosynthesis with linear regressions instead, because data either did not span enough timepoints to inform a more complex model (Wright *et al.*, 2022) or macroalgal tissue disintegration coinciding with photosynthetic death prevented estimation of *µ* and *τ* (Wright *et al.*, 2024). However, in the present case these limitations do not apply, since I collected data at six to seven timepoints and seagrass leaves do not disintegrate at or shortly after photosynthetic death, allowing me to choose the optimal model. The downside of using more complex models is that multiple regression to account for technical confounders (Wright *et al.*, 2024) is not straightforward. So I opted for a separate multiple linear regression of *P*max against the standardised potential confounders initial incubation O2 (µM), mean incubation temperature (°C), mean incubation pressure (hPA), incubation salinity (‰) and leaf blotted mass (g) (Figure S1).

Prior probability distributions for parameters were chosen based on published estimates and logic. For the linear regressions of O2 against incubation time, I gave the intercept a normal prior centred on regional average seawater O2 and the slope a normal prior with a mean of zero. For *ɑ* (Equation 2), I chose a gamma prior informed by various published *P*max estimates for *H. ovalis* (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.*, 2006; Borum *et al.*, 2016; Lamit and Tanaka, 2021; Said *et al.*, 2021, 2024) and *A. antarctica* (14 ± 9 µmol g−1 h−1, 8.8 ± 5.5 µmol leaf−1 h−1, n = 8, Masini and Manning, 1997; Borum *et al.*, 2016; Said *et al.*, 2024). Units were converted where necessary by multiplying by mean dry-fresh mass ratios for *H. ovalis* (0.21 g dry mass g−1 fresh mass) and *A. antarctica* (0.29 g dry mass g−1 fresh mass) (de los Santos *et al.*, 2012; Borum *et al.*, 2016) and my own leaf fresh masses for *H. ovalis* (0.04 ± 0.01 g leaf−1) and *A. antarctica* (0.61 ± 0.27 g leaf−1). For *τ* (Equation 2), I chose a gamma prior to logically rule out net photosynthesis of dead detritus and centred it around published estimates of O2 consumption by litter of *Zostera marina* (17 ± 5.6 µmol g−1 h−1, n = 16, Blum and Mills, 1991) and *Posidonia oceanica* (1.3 ± 1.3 µmol g−1 h−1, n = 46, Mateo and Romero, 1996, 1997). Units were again converted by multiplying by mean dry-fresh mass ratios for *Z. marina* (0.23 g dry mass g−1 fresh mass, Evans *et al.*, 1986) and *P. oceanica* (0.24 g dry mass g−1 fresh mass, Apostolaki *et al.*, 2024). I decided *k* (Equation 2) would best be restricted to positive values to ensure photosynthetic decay and would likely be higher than for seaweeds, so chose a gamma prior with a mean of 0.2 d−1, the maximum for *Ecklonia radiata* (Wright *et al.*, 2024). For *µ* (Equation 2), since detrital age is inherently positive, I settled on a gamma prior with a mean of 17 d, half the experimental duration. I chose a reasonable s.d. for each prior distribution based on published estimates and prior simulation. Importantly, to enforce an x-intercept close to 1, I put an additional joint prior on *k* and *µ* which favoured a logistic intercept (*k* × *µ*, log odds at *A* = 0) close to 4 ± 1, or about 0.97 ± 0.024 on the probability scale. This was coded as target += gamma\_lpdf( k .\* mu | 4^2 / 1^2 , 4 / 1^2 ) in Stan (Carpenter *et al.*, 2017). Priors are visualised alongside posteriors for scrutiny.

Finally, the treatment of uncertainty deserves brief mention. Firstly, I propagated measurement error. Specifically, *β* and *V* (Equation 1) as well as initial incubation O2 and incubation temperature are measured with error, which I incorporated into the downstream models as s.d. of posterior distributions. Wherever a variable is measured with error, I visualised each observation as a distribution rather than a point. Secondly, I applied partial pooling to the species variable to estimate uncertainty within and across species and make predictions for new seagrasses.

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

I searched the literature using keyword strings such as “(photosynthesis OR chlorophyll) AND (‘induced senescence’ OR detrit\* OR detach\* OR excis\* OR cut OR isolate\*) AND (week\* OR day\* OR hour\* OR minute\* OR time OR age)” in Web of Science ([webofscience.com/wos](https://www.webofscience.com/wos)) and Google Scholar ([scholar.google.com](https://scholar.google.com/)). Once I had a selection of suitable papers, I used Crossref Metadata Search ([search.crossref.org](https://search.crossref.org/)) to find similar papers. I accepted papers on all plants *sensu lato* (Bolton, 2016) that induced senescence by excision or detachment at an exact timepoint and repeatedly measured photosynthesis to assess viability of the excised or detached tissue over any interval. Studies on holopelagic plants, such as *Sargassum fluitans* and *S. natans*, and abscission were not considered since the predictor variable detrital age cannot be exactly determined, either because the plant is detached to begin with or senescence started at an unknown time prior to detachment. I accepted various photosynthesis response variables, including O2 and CO2 gas exchange, carbon assimilation (14C concentration), chlorophyll fluorescence (Fv/Fm), photosystem I and II electron transport rates (Mehler and Hill reactions), RuBisCo activity or concentration, carbonic anhydrase activity and photorespiration (glycolate concentration), as well as total chlorophyll (Chl), Chl *a* or a chlorophyll indicator. Microbial photosynthesis was generally assumed to be negligible since most of the mentioned response variables would likely not detect it. Regardless, they should be considered measures of holobiont photophysiology. This resulted in 127 suitable independent studies between 1957 and the present study (see supplementary references), from which I extracted data by copying tables or digitising plots using WebPlotDigitizer v5.2 (Rohatgi, 2025). In two cases I contacted authors for their raw data and in five cases the data were my own. It is noteworthy that apart from these seven cases, raw data were not available.

Data were collated into variables Reference, DOI, Group, Phylum, Order, Family, Species, Light, Water, Series, Day, Mean, SEM, N, Response, Method, Unit and Source. Some of these are self-explanatory, but most are not. Group classes observations into four non-taxonomic groups of interest: terrestrial plants (66 species), freshwater plants (6 species), seagrasses (5 species) and seaweeds (15 species). It is noteworthy that all freshwater plants belonged to the order Alismatales, like seagrasses, and all seaweeds belonged to the green and brown algae (Table S1). My distinction between freshwater and terrestrial plants is based on whether or not the leaves are submerged. There were no studies on freshwater macroalgae, so seaweeds are presumed to be representative. Phylum, Order, Family and Species represent the currently accepted taxonomy according to Plants of the World Online (POWO, 2025) and AlgaeBase (Guiry and Guiry, 2025). Light and Water are binary classifiers of whether or not the experimental plant tissue had access to light or water. Series numbers the measurement timeseries within a given study since most studies reported several experiments, response variables, species or individuals. Only measurement series with at least three timepoints were accepted. Day is the time post-excision given in d (, , ). Mean is either an observation or the mean of several observations at a given timepoint. When the case is the latter, SEM and N are the standard error of the mean (s.e.m.) and its sample size (n). Uncertainty was mostly given as s.e.m., but when s.d. was provided instead, this was converted as . In a few cases uncertainty was given as a 95% confidence interval (CI) or interquartile range (IQR). In the former case, I converted as , in the latter I assumed mean = median and conservatively converted the larger of the two quartile ranges (Q3 − Q2 or Q2 − Q1) as . Response dichotomises data into photosynthesis and chlorophyll measurements since these measures are decoupled and probably senesce on different timescales. Method details how the response variable was measured, Unit provides the original response unit, and Source directs the reader to the data source in the paper. Please refer to the data publication (Wright, 2025) and github.com/lukaseamus/detrital-photosynthesis for further details.

The resulting 535 measurement series contained a mixture of observations and means. To jointly analyse data with such different levels of uncertainty one must either condense observations to means and s.e.m. or s.d. and build a measurement error model or expand means to observations. I opted for the latter and obtained 10566 observations by simulating draws from the normal distribution using rnorm( N , Mean , SEM \* sqrt(N) ) in R (R Core Team, 2025), or mathematically . Prior to analysis, I normalised observations to proportions by dividing by the initial observation or mean of initial observations in the timeseries. This was the favourable choice as opposed to min-max normalisation, since many detrital photosynthesis data already come expressed as % or proportion of initial. The drawback is that data aren’t fully brought onto the same scale because some variables allow negative proportions (e.g. net gas exchange) while most don’t (e.g. Chl, Fv/Fm etc.). I assume that the effect of this on the outcome of the analysis is minimal due to the relative scarcity of net gas exchange data and enforcing *τ* = 0 (Equation 2).

Analysis was carried out as described above to model detrital viability over time, using a simplified Equation 2 with *ɑ* = 1 and *τ* = 0. Additive categorical predictors caused convergence issues, so I created a composite grouping variable from Group, Light and Response. Water is only relevant to a relatively small subset of terrestrial plant data and was therefore excluded as a predictor. No partial pooling was applied here because I did not want to make predictions for plants at large and introducing hyperparameters led to convergence issues. The gamma prior for *k* was centred on 0.22 d−1, the mean across seagrasses which emerged from the experimental component of this study (Table 1) and is assumed to be intermediate between seaweeds and terrestrial plants. Experimental durations varied substantially across studies (Table S1), so half of the mean experimental duration was picked as the prior mean for *µ*. I again chose a reasonable s.d. based on prior simulation and put an additional joint prior on *k* and *µ*. Several terrestrial plant studies reported photosynthetic decay over periods of only minutes post-excision (Table S1). These data pull the intercept down when given a weak joint prior, necessitating a much tighter prior. The logistic intercept was therefore constrained to 4 ± 0.1, equivalent to 0.98 ± 0.0018 on the probability scale: target += gamma\_lpdf( k .\* mu | 4^2 / 0.1^2 , 4 / 0.1^2 ).

**Results**

***Experiment (the research)***

*Halophila ovalis* photosynthesised for longer post-excision than *Amphibolis antarctica*. After 34 d, the duration of the experiment, all *H. ovalis* leaves were still obviously net autotrophic while all *A. antarctica* leaves were apparently dead. Comparing logistic decay rates (*k*) and times of death (*µ*) of light-saturated net photosynthesis (*P*max) clarifies this difference. On a mass basis, *A. antarctica* started with a similar *P*max to *H. ovalis*, but its *P*max decayed 1.5 times faster and expired 20 ± 2.4 d (mean ± s.d.) earlier (Figure 1a, Table 1). On a leaf basis, *A. antarctica* *P*max only decayed 40% faster and expired 15 ± 3 d earlier than that of *H. ovalis* (Figure 1b, Table 1). This difference between mass- and leaf-based estimates was primarily due to varying trends for *H. ovalis* (Figure 1a vs. b). While *A. antarctica* displayed comparable *k* (Δ = 0.038 ± 0.059 d−1, P = 0.75) and *µ* (Δ = 1.2 ± 2 d, P = 0.73), leaf-based *H. ovalis* *P*max declined 53% (P = 0.92) faster and expired 6.5 ± 3.3 d (P = 0.98) earlier.

When accounting for leaf mass, *H. ovalis* thus seems to be able to photosynthesise longer post-excision. The immediate reason for this was the linear decline of leaf mass in *H. ovalis* (*α* = 0.052 ± 0.005 g leaf−1, *β* = −0.58 ± 0.26 mg leaf−1 d−1 or −1.1 ± 0.43 % d−1, P*β* < 0 = 0.99) while *A. antarctica* leaf mass remained almost unchanged (*α* = 0.64 ± 0.053 g leaf−1, *β* = −2 ± 2.7 mg leaf−1 d−1 or −0.3 ± 0.41 % d−1, P*β* < 0 = 0.78). But it remains unclear why *H. ovalis* leaves of reduced mass photosynthesised disproportionally. The most likely reason is that periphyton, which I observed colonising *H. ovalis* but not *A. antarctica*, contributed much to photosynthesis but very little to leaf mass. This renders the leaf-based *H. ovalis* estimates more trustworthy and may have exacerbated the reported differences between the two seagrasses but is unlikely to have confounded the general trend.

Despite their phylogenetic and morphological diversity, both seagrasses displayed quite consistent tendencies, allowing relatively precise prediction for seagrasses in general (Figure 1, Table 1). The discussed discrepancy between mass- and leaf-based *P*max of *H. ovalis* only marginally affected estimates on this higher level. Overall, seagrasses had similar *k* (Δ = 0.0055 ± 0.075 d−1, P = 0.54) and *µ* (Δ = 1.4 ± 4.8 d, P = 0.62) across mass- and leaf-based models (Table 1). It therefore seems that seagrass *P*max generally decays at a rate of 0.22 d−1 and persists for around 17 d.

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

Comparison across plants revealed that only seaweeds can maintain detrital photosynthesis for several months. Seagrasses are limited to less than a month and freshwater and terrestrial plants to about a week (Figure 2, Table 2). Under light, *k* of seaweeds is 96% (Δ = 0.51 ± 0.052 d−1, P = 1) smaller than that of terrestrial plants. Seagrass photosynthesis decays 7.5 times (Δ = 0.15 ± 0.025 d−1, P = 1) faster than that of seaweeds and 68% (Δ = 0.36 ± 0.058 d−1, P = 1) slower than that of terrestrial plants. Correspondingly, *µ* of seaweeds occurs 210 ± 102 d (P = 1) later than in terrestrial plants. Seagrass detritus again takes an intermediate position, losing the ability to photosynthesise 190 ± 102 d (P = 1) earlier than seaweed detritus and 18 ± 3.6 d (P = 1) later than terrestrial plant detritus.

Photosynthesis and chlorophyll (Chl) followed fairly consistent trends for seagrasses and terrestrial and freshwater plants (Figure 2, Table 2). This indicates that for these plants detrital Chl is a reasonable predictor of detrital photosynthesis. Seaweeds again form an exception and had 69% smaller *k* and 3 times larger *µ* for Chl than photosynthesis (Table 2), meaning that Chl tends to overestimate longevity of detrital photosynthesis fourfold for this group (Figure 2). Nonetheless, since there are no data on photosynthetic senescence under light for freshwater plants, Chl enables a mostly representative comparison of all plant groups. Surprisingly, freshwater plant detritus lost Chl at similar rates to terrestrial plant detritus (Δ = 0.023 ± 0.087 d−1, P = 0.6), and consequently 1.4 times (Δ = 0.36 ± 0.094 d−1, P = 1) and 102 times (Δ = 0.61 ± 0.066 d−1, P = 1) faster than seagrass and seaweed detritus respectively. Accordingly, photosynthetic death of freshwater plants occurs at the same time (Δ = 0.21 ± 0.91 d, P = 0.6) as terrestrial plants, and therefore 10 ± 4.4 d (P = 1) and 850 ± 577 d (P = 1) earlier than that of seagrasses and seaweeds respectively.

Light ameliorated photosynthetic decay in all except freshwater plants (Figure 2, Table 2). However, it only substantially extended detrital longevity in seaweeds. Whereas the effect is negligible for freshwater plants and only on the order of a couple days to a week for terrestrial plants and seagrasses, seaweed photosynthesis decays 25 times faster and terminates 96% earlier in darkness (Table 2). Consequently, under darkness seaweed detritus only remains viable for comparable durations to terrestrial (Δ = 4.2 ± 7.3 d, P = 0.89) and freshwater (Δ = 4.4 ± 7.3 d, P = 0.9) plants. This suggests that the extreme detrital longevity observed in seaweeds is highly light-dependent.

**Discussion**

Despite the existence of various relevant literature, the phenomenon of detrital photosynthesis had not been explored beyond kelps. In part, this is probably due to diverse research objectives which obscure the connection between quantitatively comparable data. There was also data scarcity in some important plant groups, especially the seagrasses. Here I filled this knowledge gap by presenting the first data on photosynthesis in seagrass detritus and subsequently the first meta-analysis of detrital photosynthesis across all plants.

Detrital photosynthesis *per se* is not restricted to non-vascular plants. Seagrass detritus can also photosynthesise for at least a couple weeks. The physiology of diverse seagrasses responds similarly to detrital age and observed differences may simply be attributable to varying colonisation by periphyton which, given a leaf mass per area of 2.7 and 6.8 mg cm−2 for *Halophila ovalis* and *Amphibolis antarctica* respectively (de los Santos *et al.*, 2012, 2016), could contribute 12–172% of initial seagrass photosynthesis (Neely and Wetzel, 1997). Alternatively, *A*. *antarctica* leaves may be more reliant on their roots for nutrient provisioning. But there is no other evidence to suggest this (Pedersen *et al.*, 1997) and the 15–20 d earlier photosynthetic death of isolated *A. antarctica* leaves compared to *H*. *ovalis* is surprising given their 1.7 times (Δ = 47 d) longer attached lifespan (Hemminga *et al.*, 1999). Seagrass detrital photosynthesis, despite persisting for weeks, may not necessarily counteract decomposition, a process which can a year for these plants (Harrison, 1989; Cebrián *et al.*, 1997; Trevathan-Tackett *et al.*, 2020). While live *Halophila decipiens* ramets do indeed decompose slower than buried ones (Kenworthy *et al.*, 1989), decomposition rates are similar between live and senescent or buried *Thalassia testudinum* leaves (Rublee and Roman, 1982; Fourqurean and Schrlau, 2003; Rosch and Koch, 2009) and meta-analysis suggests that live seagrass leaves actually tend to decompose faster than senescent or dead ones (Harrison, 1989; Trevathan-Tackett *et al.*, 2020).

Macroalgae uniquely exhibit long-term detrital photosynthesis. In fact, there is nothing to suggest that detritus produced by these plants cannot remain viable for up to a year. As expected, seagrasses exhibit intermediate detrital longevity between seaweeds and terrestrial plants, which photosynthesise for at most one week post-excision. The extreme contrast to terrestrial plants has been demonstrated but is in fact somewhat dampened in my formal analysis. When given light but no water, which is the normal fate of terrestrial plant detritus, detached leaves of various trees tend to lose the ability to photosynthesise in just a few minutes (e.g. Gauthier and Jacobs, 2018; Kar *et al.*, 2021). This is due to breakdown of stomatal conductance following a loss in water pressure (Powles *et al.*, 2006; Gauthier and Jacobs, 2018). What surprised me is that detrital viability of freshwater plants is like that of terrestrial plants and not seagrasses. One explanation is excess production of hydrogen peroxide during photosynthesis in the detached leaf which leads to chlorophyll degradation, as demonstrated for *Hydrilla verticillata* (Kar and Choudhuri, 1986, 1987) and is likely also the case for other freshwater angiosperms (Jana and Choudhuri, 1982). In contrast, there is no evidence for increased chlorophyll breakdown in isolated seagrass leaves exposed to light (Strother and Vatta, 1986) and photodegradation is only apparent in dead leaves (Vähätalo *et al.*, 1998). Emancipation of leaf photosynthesis from the rest of the plant is apparently not favoured by an aquatic but rather by a marine nature in vascular plants. What exactly happened to allow this during the transition of angiosperms from lakes and rivers to the sea remains unclear. Perhaps the answer lies in convergent evolution with seaweeds, in particular alterations to the light harvesting complexes and cell wall features that enhance gas exchange (Olsen *et al.*, 2016)?

Senescence mechanisms determine the impact physiology can have on detrital dynamics. Seagrass detritus often incudes green leaves (Knauer and Ayers, 1977; Ochieng and Erftemeijer, 1999; Jiménez-Ramos *et al.*, 2023). This may be in part because nutrient resorption prior to abscission is low relative to terrestrial plants (Harrison, 1989; Pedersen and Borum, 1992; Pedersen *et al.*, 1997; Hemminga *et al.*, 1999; Rosch and Koch, 2009). But the most likely mechanism is premature detachment caused by external factors such as hydrodynamics and herbivory (Cebrián *et al.*, 1997) paired with seasonal weakening of the ligule (Jiménez-Ramos *et al.*, 2023). Viable seagrass detritus is clearly produced under natural conditions, but due to the mentioned mismatch between rapid photosynthetic decay and slow decomposition this is expected to have little influence on detrital dynamics. Seaweeds tell a different story. Their detritus can photosynthesise for many months, matching their decomposition timescale, if we assume that excision mirrors detrital export in nature. Distally eroded and abscised tissue almost certainly exhibits reduced detrital photosynthesis due to fragmentation and attached senescence, which can greatly accelerate decomposition (de Bettignies *et al.*, 2020). But up to half of kelp detritus is released by dislodgement of whole plants or large fragments (de Bettignies *et al.*, 2013; Pessarrodona *et al.*, 2018; Pedersen *et al.*, 2020). The visible detrital pool therefore consists mostly of tissue that displays limited senescence and probably can remain photosynthetic for many months.

I have previously suggested that detrital photosynthesis influences kelp blue carbon by providing an additional dimension to detrital recalcitrance (Wright *et al.*, 2022, 2024). Its uniqueness among plants, as evidenced here, suggests that it may play a disproportionate role in determining the fate of macroalgal carbon. They key implication is that seaweed decomposition rates are not directly comparable to those of other plants. It is even hard to make comparisons within seaweeds when not explicitly modelling detrital photosynthesis (Kennedy and Blain, 2025). Most of our understanding of seaweed decomposition is based on freshly excised blades (Albright *et al.*, 1982; Bedford and Moore, 1984; Frontier *et al.*, 2021; Filbee-Dexter *et al.*, 2022; Wright *et al.*, 2022) as opposed to senescent (de Bettignies *et al.*, 2020) or dead (Birch *et al.*, 1983; Smith and Foreman, 1984; Brouwer, 1996) fragments. But as mentioned, less than half of seaweed detritus can be considered fully viable when exported. Additionally, decomposition experiments are usually carried out in the shallow subtidal with access to light, but proponents of seaweed carbon sinks invariably place them in the darkness of the deep sea (Krause-Jensen and Duarte, 2016; Filbee-Dexter *et al.*, 2024). My meta-analysis suggests that darkness has a stronger detrimental effect on detrital photosynthesis in seaweeds than any other plant. If detrital photosynthesis is granted the ecological significance I attribute to it, these contradictions must make one wonder. Perhaps it is time to question existing preconceptions in seaweed blue carbon?

To conclude, I show that vascular plants also photosynthesise after detachment, but this varies greatly from a few minutes in tree leaves without access to water, over several days on average in terrestrial and freshwater plants to a couple of weeks in seagrasses. Macroalgae alone can photosynthesise for months post-excision. The powerful effect of detrital photosynthesis on decomposition and thereby blue carbon has already been evidenced to some extent (Birch *et al.*, 1983; Brouwer, 1996; de Bettignies *et al.*, 2020). What now remains to be investigated is (1) decomposition trajectories of macroalgal detritus with and without physiology and how these compare with seagrasses as the most functionally similar plants, (2) an improved decomposition model for macroalgae that explicitly accounts for detrital photosynthesis, (3) the prevalence of photosynthesis in eroding, abscised and other senescing tissues, and (4) the proportion of the detrital pool that photosynthesises *in situ*.

**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.

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**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.

**Figure legends**

**Figure 1**. Seagrass detrital photosynthesis. Light-saturated net photosynthesis (*P*max) 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 *P*µ, the mean prediction of *P*max (Equation 2). Light grey lines encompass the central 90% of prior probability.

**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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