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Diversity in xanthophyll cycle pigments content and related non- photochemical quenching (NPQ) among microalgae: implications for growth strategy and ecology

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Abstract :

Xanthophyll cycle-related non-photochemical quenching, which is present in most photoautotrophs, allows dissipating excess light energy. Xanthophyll cycle-related NPQ depends principally on xanthophyll cycle pigments composition and their effective involvement in non-photochemical quenching. Xanthophyll cycle-related NPQ is tightly controlled by environmental conditions in a species/strain specific manner. These features are especially relevant in microalgae living in a complex and highly variable environment. The goal of this study was to perform a comparative assessment of non-photochemical quenching ecophysiologies across microalgal taxa in order to underline specific involvement of non-photochemical quenching in growth adaptations and strategies. We used both published results and data acquired in our laboratory to understand the relationships between growth conditions (irradiance, temperature and nutrient availability), xanthophyll cycle composition and xanthophyll cycle pigments quenching efficiency in microalgae from various taxa. We found that in diadinoxanthin-containing species, the xanthophyll cycle pigment pool is controlled by energy pressure in all species. At any given energy pressure, however, the diatoxanthin content is higher in diatoms than in other diadinoxanthin-containing species. XC pigments quenching efficiency is species-specific and decreases with acclimation to higher irradiances. We found a clear link between the natural light environment of species/ecotypes and quenching efficiency amplitude. The presence of diatoxanthin or zeaxanthin at steady state in all species examined at moderate and high irradiances suggests that cells maintain a light-harvesting capacity in excess to cope with potential decrease in light intensity.

Keywords : Xanthophyll cycle pigments microalgae, photoacclimation, non-photochemical quenching, NPQ, diversity, diatoxanthin, zeaxanthin

List of abbreviations: XC, xanthophyll cycle; NPQ, non-photochemical quenching; Dt, diatoxanthin; Dd, diadinoxanthin; Z, zeaxanthin; V, violaxanthin; A, antheraxanthin; LHC, light-harvesting antenna complexes; QE, quenching efficiency; K_E, Light saturation parameter for growth; E, Growth irradiance; μ, growth rate; DES, xanthophyll de-epoxidation state**,** Y_0, Y-intercept.

INTRODUCTION

What is the xanthophyll cycle (XC)-related non-photochemical quenching (NPQ)?

XC is one of the most important photoprotection mechanisms in photosynthetic organisms (Demmig-Adams 1990, Masojídek et al. 2004, Brunet and Lavaud 2010, Goss and Jakob 2010). XC protects plastids from over-excitation of the photosynthetic pigments and over-reduction of the electron transport chain that may led to the generation of reactive oxygen species (ROS). It thereby prevents potential damages that mainly result from the ROS-generated oxidative stress, the primary target of photodamage being the PsbA (D1) protein of photosystem II (PSII). XC allows the safe dissipation of excess excitation energy as heat in the light-harvesting antenna complexes (LHC) of PSII. Because this process is mirrored by chlorophyll *a* (Chl *a*) fluorescence changes, it is commonly evaluated via the so-called non-photochemical quenching of chlorophyll *a* fluorescence (NPQ; Demmig-Adams et al. 2014). The main part of NPQ that is related to the XC process is called qE, the 'energy dependent quenching' and is the main NPQ component among most eukaryotic photoautotrophic taxa (see Niyogi and Truong 2013, Derks et al. 2015, Goss and Lepetit 2015 for further details). Note that although widely distributed, the XC-mediated NPQ is not present in all photosynthetic lineages, and several groups and species have been reported to show no XC-NPQ and/or alternative XC regulation (see for instance the recent reports by Kaňa et al. 2012, Cheregi et al. 2015, Quaas et al. 2015, Christa et al. 2017, Berne et al. 2018, well illustrating the amazingly complex functional biodiversity of the XC-NPQ process Goss and Lepetit 2015).

There are two main XC (note that there is also a lutein cycle in plants, see Esteban and García-Plazaola [2014]): i) the violaxanthin (V) cycle, found in higher plants, in the green (Chlorophyta) and brown algae (Phaeophyceae) and in the Chromeraceae *Chromera velia* (member of the Alveolate clade), and ii) the diadinoxanthin (Dd) cycle, found in the main algal classes Bacillariophyceae (denoted as 'diatoms' elsewhere in the text), Xanthophyceae, Haptophyceae, and Dinophyceae (Goss and Jakob 2010, Goss and Lepetit 2015). In Dd-containing algae, the V cycle can also be observed depending on species and light conditions (Lohr and Wilhelm 1999, Blommaert et al. 2017). The V cycle consists of two de-epoxidation steps in which V is sequentially converted into anteraxanthin (A)

and zeaxanthin (Z). The Dd cycle consists of one de-epoxidation step that converts Dd into diatoxanthin (Dt). Z (and A) and Dt interact with antenna complexes to convert the PSII LHC antenna into a heat-dissipating state. The regulation of the XC and mediated NPQ at the molecular level has been the object of intense research in various photosynthetic organisms (see the recent syntheses by Niyogi and Truong 2013, Demmig-Adams et al. 2014, Goss and Lepetit 2015, Magdaong and Blankenship 2018, Pinnola and Bassi 2018). In microalgae, its peculiarities have been extensively studied in green representatives (Finazzi and Minagawa 2014, Erickson et al. 2015), in the Heterokont diatoms (Lepetit et al. 2012, Büchel 2014, Lavaud and Goss 2014) and Eustigmatophyceae *Nannochloropsis* sp. (Cao et al. 2013, Bína et al. 2017, Park et al. 2019), and in *Chromera velia* (Kotabová et al. 2011, Quigg et al. 2012, Kuthanová Trsková et al. 2018).

The importance of the environment in triggering the XC and related NPQ: stress vs. acclimation.
The accumulation of xanthophyll pigments in response to excessive light intensity was first described in higher plants more than 55 years ago (Yamamoto et al. 1962). XC-related energy dissipation is now generally thought to be the result of an imbalance between the energy availability (source) and the demand for photosynthates (sink; Adams et al. 2014). Exposure to more light than can be utilized by the photosynthetic process leads to a relative compensatory increase in XC-mediated NPQ that decreases PSII quantum yield efficiency and thus the amount of energy directed to photochemistry. Accumulation of Z (and A) or Dt and the concomitant increase in XC-mediated NPQ was described in response to high irradiance in higher plants (Demmig et al. 1987), green algae (Niyogi et al. 1997, Finazzi and Minagawa 2014), diatoms (Olaizola et al. 1994, Lavaud and Goss 2014) and brown algae (Harker et al. 1999, Lavaud and Goss 2014). It has been also reported in response to other abiotic factors affecting photosynthetic performance and growth such as for instance, low temperature and nutrient availability in higher plants (Huner et al. 1998, Morales et al. 2014) and microalgae (Wykoff et al. 1998, Mock and Hoch 2005, Allen et al. 2008, Petrou et al. 2012), drought stress in higher plants (Morales et al. 2014), desiccation in mosses and lichens (Bilger 2014), as well as in response to a combination of several environmental stresses (i.e., light, temperature and salinity; see for instance in a variety of taxa; Petrou et al. 2011, García-Plazaola et al. 2012, Verhoeven 2014, Laviale et al.

2015). Removal of photosynthetic electron sinks (e.g., young, developing leaves and/or fruits) can also lead to XC-mediated NPQ in plants (Adams et al. 2014).

Light history is also important in determining the level of photoprotective capacity in plants and algae (Raven and Geider 2003, Demmig-Adams and Adams 2006). In that framework, XC-mediated NPQ is a key mechanism in cell response to natural diel light cycle. Several studies have examined how diel changes in XC pigment content and related NPQ allow to optimize photosynthesis under changing natural illumination in land plants (Demmig-Adams et al. 1996), seagrasses (Ralph et al. 2002), macroalgae (Schofield et al. 1998, Gévaert et al. 2003) and microalgae (Masojídek et al. 2004, van Leeuwe et al. 2008, Dimier et al. 2009a, Quigg et al. 2012, Schuback et al. 2016). Under relatively steady light exposure, high light acclimated cells/organisms have much larger xanthophyll pools (Dd+Dt or Z+A+V), often leading to a greater capacity for XC-mediated NPQ in both plants (Demmig-Adams et al. 2012) and algae (Goss and Jakob 2010, Brunet et al. 2011, Lavaud and Goss 2014). XC pigments and related NPQ induction and relaxation kinetics are also modified by environmental growth conditions related to habitat characteristics. For example, plant leaves acclimated to shade and sunflecks show a minor pre-existing Z pool and a fast onset and relaxation kinetics of XC-mediated NPQ (Demmig-Adams et al. 2012, Demmig-Adams et al. 2014). On the contrary, plants and trees acclimated to sun and intermittent cold temperatures, or long-term frozen soils, show full Z retention and thus sustained NPQ (sometimes named qZ, see García-Plazaola et al. 2012, Demmig-Adams et al. 2014, Verhoeven 2014, Míguez et al. 2015). Similar retention of Z or Dt and related NPQ under different conditions of light and temperature has been reported in several groups of microalgae (Perkins et al. 2011, Berne et al. 2018). For instance, polar diatoms grown at 0°C and high irradiance show a strong retention of Dt and related sustained NPQ (Lacour et al. 2018).

In macroalgae, a strong relationship between incident irradiance and XC and related NPQ ability relates to depth: it can be observed among species that colonize different levels of the intertidal/tidal shore continuum (Harker et al. 1999, Rodrigues et al. 2002, Nitschke et al. 2012), and in surface vs. deep blades of the same giant kelp individual, *Macrocystis pyrifera* (García-Mendoza and Colombo-Pallotta 2007). In microalgae, light fluctuations inherent to the water column optical features and hydrodynamics influence XC and related NPQ kinetics over time scales from seconds to seasons (Brunet and Lavaud 2010, Brunet et al. 2011, Giovagnetti et al. 2014). The ability to rapidly

modulate the XC and related NPQ kinetics and extent as a function of unpredictable light intensity fluctuations is believed to be a key feature of the physiological and metabolic flexibility in microalgae (Wilhelm et al. 2014).

Differences between taxa: ecological implications.

The involvement of XC-NPQ in the ecology of photosynthetic organisms has shown growing interest, especially for marine phytoplankton (Lavaud and Goss 2014, Petrou et al. 2016). Comparative ecophysiology including evolutionary biology (Niyogi and Truong 2013, Quaas et al. 2015, Christa et al. 2017, Magdaong and Blankenship 2018) has strongly helped to better understand the physiological fundamentals of XC and related NPQ, particularly in plants and trees (Adams and Demmig-Adams, 2014). Photoautotrophs show great interspecific differences in XC pigment pool, de-epoxidation state (DES = Dt/[Dt+Dd] or [Z+A]/[Z+A+V]) and related NPQ, partially because they experience different *in situ* growth environments (e.g., typically sun *vs.* shade acclimation in plants; Demmig-Adams et al. 2012). Species and ecotypes grown under similar conditions retain differences in XC pool size, DES, and effective and potential related NPQ as reported in plants (Demmig-Adams and Adams 2006, García-Plazaola et al. 2012, Míguez et al. 2017), macroalgae (Christa et al. 2017), and microalgae (Lavaud et al. 2007, Bailleul et al. 2010, Giovagnetti et al. 2012, Stamenković et al. 2014, Quaas et al. 2015). For example, plant annual species show lower XC-mediated NPQ than evergreens and different kinetics of XC-mediated NPQ induction and relaxation (Adams and Demmig-Adams 2014, Míguez et al. 2017). In microalgae, it was proposed that the XC-characteristics are influenced by ecological niche adaptation (see the many examples in Lavaud and Goss 2014, Petrou et al. 2016) and growth forms (Cartaxana et al. 2011, Shi et al. 2016, Blommaert et al. 2017) with no obvious phylogenetic connection (Barnett et al. 2015, Quaas et al. 2015). Furthermore, the XC and related NPQ characteristics were proposed as an adaptive trait that could explain the geographical/spatial species distribution in land plants adapted to natural sun and shade environments (i.e., desert vs. forest canopy; Demmig-Adams et al. 2008, 2014), overwintering evergreen trees (i.e. as a function of height distribution; (Demmig-Adams et al. 2008, 2014)), and in macroalgae (as a function of depth distribution; Rodrigues et al. 2002, Nitschke et al. 2012). In microalgae XC and mediated NPQ features were positively related to i) latitude (Bailleul et al. 2010, Stamenković et al. 2014, Laviale et

al. 2015), ii) different marine (lagoon vs. coast vs. open ocean; Dimier et al. 2007, 2009b, Lavaud et al. 2007, Six et al. 2008) and freshwater (river vs. lake vs. pool; Stamenković et al. 2014, Quaas et al. 2015, Shi et al. 2016) ecosystems, iii) different habitats of the same ecosystem, i.e. spring to summer shift from ice-covered to ice-free water column in polar systems (Petrou et al. 2016) or different sediment types in estuarine intertidal flats (Cartaxana et al. 2011, Barnett et al. 2015), iv) as well as the temporal/seasonal succession of phytoplankton (Meyer et al. 2000, Dimier et al. 2007, Petrou and Ralph 2011, Polimene et al. 2014).

What can control differences in NPQ beyond the XC pigment content? Quenching efficiency (QE). Beyond the apparently direct NPQ regulation by the XC pigment content (i.e., the more XC pigments, the higher NPQ), the quenching efficiency (QE) of xanthophyll pigments is an important factor for the ability to dissipate excess energy. It can be easily illustrated as the slope of the NPQ vs. Dt or Z+A linear relationship. In plants as well as in algae, different species and clones can show similar XC pool size and DES with a drastically different XC-mediated NPQ (and vice versa; i.e., similar NPQ extent with different XC pigment content), implying strong differences in QE of, presumably, functionally different pools of Dt or Z+A molecules (Lavaud and Lepetit 2013, Quaas et al. 2015). Indeed, XC pigments are not totally and exclusively involved in the NPQ process, which contributes to their apparent global QE, because they have additional photoprotective functions such as, in particular, antioxidants (Esteban and García-Plazaola 2014, Havaux and García-Plazaola 2014). An apparently loser link between XC content, DES and related NPQ depends on many intracellular variables including the synthesis and function of NPQ regulatory partners other than the XC pigments, and firstly a large diversity of proteins of the light-harvesting system-LHC (Büchel 2014, Wobbe et al. 2016). Specific LHC proteins have been demonstrated to play a crucial role in modulating xanthophylls QE, especially LHCSR in green microalgae (Peers et al. 2009, Erickson et al. 2015), and LHCX in diatoms (Bailleul et al. 2010, Lepetit et al. 2017, Taddei et al. 2018). Nevertheless, QE has been considered as a good indicator of the adaptation of a species/strain to a light environment (Lavaud et al. 2007, Goss and Jakob 2010).

Objectives of the study.

Although the diversity of molecular mechanisms involved in XC and related NPQ induction and relaxation has been described before for a variety of taxa (Goss and Lepetit 2015), the diversity of XC pigments and related NPQ responses to environmental conditions (physiodiversity sensu Wilhelm and Wirth 2015) has not been studied quantitatively. This is especially relevant in microalgae as regards the broad spanning of evolutionary trajectories and ecological niches they have colonized that have generated a highly diversified molecular composition, organization and regulation of LHC antennas dynamics (Büchel 2015, Giovagnetti and Ruban 2018).

The goal of our study was to better understand the diversity of the XC-related NPQ across microalgal taxa and its variability among growth conditions, including light, temperature and nutrient availability. We used published results to decipher the relationship between growth conditions, XC pigment content and QE in microalgae. The discussion also considers some of the ecophysiological implications of our findings and it endeavors to answer the following questions: i) How does the growth environment control the XC pigment content? ii) Does the XC pigment content change across taxa under similar growth conditions or similar physiological status? iii) Does Quenching efficiency-QE change among taxa, and does it vary with growth conditions? iv) Does it reveal taxa adaptation to their ecological niche environmental features?

MATERIALS AND METHODS

XC and related NPQ data available in the literature.

Light, temperature and nutrient data.

Additional data were retrieved from previous studies (i.e., works on unialgal cultures) that included measurements of XC pigments at various irradiances and temperatures under nutrient replete lab-controlled conditions. We only selected the studies that included the measurement of growth rate (μ) under several irradiances, allowing the computation of the light saturation parameter for growth (K_E, see computation below). It considerably limited the number of qualifying works as most of them measured μ under one or two (typically 'low light' and 'high light') irradiances which is insufficient for a reliable determination of K_E. Table S1 in the Supporting Information synthesizes the studies under consideration, the species that were investigated, the growth temperature and the number of

incident growth irradiance steps at which μ was measured. In all cases, physiological parameters were determined after some period of acclimation to the growth conditions, i.e. cells were in a fully (photo)acclimated state under balanced growth conditions (i.e., in contrast to a sudden change from their steady-state growth conditions).

K_E was determined using the following Poisson function with two parameters, μ_m and K_E, as proposed by MacIntyre et al. (2002): $\mu = \mu_m (1-\exp[-E/K_E])$ where μ is the specific growth rate (d^{-1}), μ_m is the maximum growth rate, E is the growth irradiance (μmol photons · m^{-2} · s^{-1}) and K_E is the light saturation parameter for growth (μmol photons · m^{-2} · s^{-1}). The relationship was fitted to the data by non-linear least-squares.

The data supporting the relationship between nutrient-limited growth and the amount of XC pigments are scarce; they were extracted from two studies: Goericke and Montoya (1998) and Stolte et al. (2000). Datasets documenting the effect of different growth temperatures are also scarce, and were limited to our own data (Lacour et al. 2018; T. Lacour, unpub. data; see Table S1)

Quenching efficiency-QE (NPQ *vs.* de-epoxidized xanthophyll content relationship).

Our analysis was based on data from previous studies that include simultaneous measurement of NPQ and the de-epoxidized forms of xanthophyll pigments: Dt or Z and A (normalized to the total pool of Chl *a*); note that only the two main XC were considered. The relationship between NPQ and Dt or Z(+A) is generally linear, at least over a certain range (see for instance, and for a variety of organisms: Brugnoli et al. (1998), Lavaud et al. (2004), Dimier et al. (2009a), Masojídek et al. (2004), Stamenković et al. (2014), and Barnett et al. (2015). We computed the slopes and the y-intercepts (Y_0) of NPQ vs. Dt or Z(+A) content by fitting the data by linear least-squares. In few cases, when NPQ saturated for high Dt or Z(+A) content (see for instance Lavaud et al. 2002), the slope and Y_0 were computed on the initial linear part of the relationship (see an example in Fig. S1 in the Supporting Information). Tables S2 and S3 in the Supporting Information synthesize the studies under consideration, the species that were investigated, the values of the slopes and of Y_0, the evidence for possible NPQ saturation (only observed in some diatoms, see Table S2), and the number of data points.

RESULTS AND DISCUSSION

Pigments of the diadinoxanthin (Dd) cycle: effect of growth irradiance (E), temperature and nutrient availability

Irradiance.

We normalized XC pigments (Dd + Dt) to Chl *a* as it has been done routinely in previous studies. It allows scaling XC pigments to the amount of Chl *a*, the most abundant photosynthetic pigment, common to all photosynthetic eukaryotes, which is found in LHCs (together with Chl *b* and *c*) and in PSI and PSII (constant across eukaryotes). XC cycle pigments normalized by Chl *a* is therefore a good estimator for the number of XC pigments per photosynthetic electron transport chain. We pooled existing data (see Table S1). (Dd + Dt)/Chl *a* increased with growth irradiance in all taxa (Fig. 1, A and B). Such an increase has been already discussed before (see MacIntyre et al. 2002) and is in agreement with the concept of an increase in the potential for photoprotection, and for XC-mediated NPQ in particular, as acclimation to growth irradiance (E) increases. The relationship between Dd+Dt and E was generally linear although both the slope and y intercept (Y_0) were highly variable, especially in taxa other than diatoms (Fig. 1, A and B). Noticeably, Y_0, which represents the basal amount of XC pigments, was remarkably conserved (8 ± 2 mol Dd+Dt · [100 mol Chl *a*]$^{-1}$) among diatoms. Dt/Chl *a* also increased with growth irradiance in all taxa and the slope was highly variable (Fig. 2, A and B). Y_0 was generally ≤ 0, as at low irradiance, most of the Dd+Dt pool remains in the form of Dd until reaching an irradiance threshold beyond which Dd starts being de-epoxidized in Dt (see Lavaud et al. 2012).

As previously proposed by Geider et al. (1998), photoacclimation of pigments is accomplished through mechanisms that 'integrate' the mean E, species sensitivity for light and other environmental conditions (as, for instance, temperature and nutrients, see below). It is accomplished through the combined effects of reactions down-stream PSII and relative to the photon flux, and therefore the excitation pressure. Microalgae appear to well adapt to the light conditions of their specific habitat, which is reflected in their growth *vs.* E relationship (Edwards et al. 2015). For example, open-ocean isolates tend to have a lower light saturation parameter for growth (K_E), implying adaptation to lower average irradiance, than coastal isolates (Edwards et al. 2015, Lacour et al. 2017). This adaptation was

shown to relate, in part, to the ability for XC-mediated NPQ (Strzepek and Harrison 2004, Lavaud et al. 2007). In general, at a given E, the need for photoprotection can be expected to be higher in low-light adapted species/strains than in high-light adapted ones (Raven and Geider 2003). However, scaling photoacclimatory biological variables (such as pigments) to E alone is insufficient in comparative studies because of the species-specific variation in K_E (MacIntyre et al. 2002). Therefore, it was proposed and successfully used (Geider et al. 1996, 1997, MacIntyre et al. 2002, Lacour et al. 2017, 2018), to normalize the growth irradiance E to K_E to provide a relative scaling of the energy pressure on the photosynthetic apparatus. When analyzed against E/K_E, the amount of XC pigments was better conserved among temperate and polar microalgal species (see Table S1) and conditions (FigS. 1, D-F, 2, C and D; Fig. S2 in the Supporting Information). This was particularly true for Dt/Chl *a* vs. E/K_E relationships within both diatoms and non-diatoms species (Fig. 2, C and D, S2). It shows that for all the microalgal species examined here, energy pressure governs photoprotective capacity in a manner which is independent of taxa. From an evolutionary standpoint, such uniform response among Dd-containing microalgal groups and species suggests no distinct general taxonomy-based difference in the capacity to synthesize XC pigments. Instead, it appears that species/strain-specific sensitivity to irradiance, which is an adaptive trait that is influenced by ecological niche adaptation (Edwards et al. 2015), is one of the main drivers which determines the XC response to the environment. Recently, Lepetit et al. (2013) highlighted the importance of the redox state of the PQ pool in light acclimation in a diatom. Specifically, they suggested that the level of excitation energy pressure in the plastid and its balance within the photosynthetic electron transport chain governs the XC pigments response to irradiance changes. It is possible that this feature could be extended to all diatoms and even to the Dd-containing algae with secondary plastids. Furthermore, while the relationship between (Dd+Dt)/Chl *a* vs. E/K_E was not significantly different between diatoms (Fig. 1C) and other species (Fig. 1F) (ANCOVA, $F_{1,130}= 3.86$, $P>0.05$), the slope of the Dt/Chl *a vs.* E/K_E linear regression was 3x higher in diatoms (1.45 vs. 0.47; Fig. 2, C and D). It indicates that for a given level of excitation energy pressure, diatoms synthesize the same amount of Dd+Dt and from this pool they produce, in general, 3 times more Dt than other Dd-containing algae. It suggests that for a given level of energy pressure, all Dd-containing species have a similar potential for XC-mediated NPQ

(similar Dd+Dt/Chl *a*, and aside from other regulatory partners), but diatoms show, in general, higher NPQ at steady state growth irradiance E.

Temperature.

Low temperatures deeply modify the photoacclimation status of cells by affecting differentially the photosynthetic dark and light reactions which generally leads to a decrease in μ_m and K_E (Yoder 1979, Verity 1982), and thus an increase of the excitation pressure on the photosynthetic electron transport chain. The best illustration of this statement in our dataset (see Table S1; Figs. 3, S3 in the Supporting Information) comes from the response of two diatom polar strains that have contrasted light sensitivity and related niche: *Thalassiosira gravida* (K_E ~12 µmol photons · m^{-2} · s^{-1}) is generally found in low light environments, often underneath the sea-ice floe at the beginning of the Arctic spring bloom, while *Chaeotoceros neogracile* ((K_E = ~35 µmol photons · m^{-2} · s^{-1}) can bloom later in summer and generally at the surface of open waters (i.e., free of sea-ice; Lacour et al. 2017). As expected, at a given irradiance, *T. gravida* synthesized higher amounts of Dt+Dd/Chl *a* and Dt/Chl *a* vs. E. The corresponding slopes were 1.7x and 2x higher at 0°C than at 5°C, respectively (Fig. 3, A and C; see also Lacour et al. 2018). Remarkably, when normalized to E/K_E, the amounts of XC pigments were very similar in both species independent of the temperature (Figs. 3, B and D, S3).

Nutrients.

Beyond irradiance and temperature, numerous studies have reported that nutrient 'stress' leads to an accumulation of XC pigments (Geider et al. 1993). Nutrient stress is a term often used for both limitation and starvation (sensu MacIntyre and Cullen 2005) while they lead to very distinct physiological responses (Parkhill et al. 2001). For example, Lacour et al. (2012) showed that nutrient starvation enhances triacylglycerol accumulation while nutrient limitation generates the opposite effect. Also, starvation experiments are difficult to compare between each other because they use microalgal cultures that are in unbalanced growth. Hence, in order to examine the XC pigment response to nutrient stress in microalgae, we selected studies that specifically used chemostats to maintain cultures under true nutrient limitation (i.e., balanced growth). For this reason, the only data we could find are from Stolte et al. (2000) and Goericke and Montoya (1998) which deal with Dd-

containing microalgae exposed to nitrogen (N) or phosphate (P) limitation (Fig. 4). The species examined, including diatoms and others, show a similar behaviour: (Dt+Dd)/Chl *a* remained almost unchanged over a large range of nutrient limitation values and increased only when limitation generated a strong decrease (-70-80%) in growth rate (i.e., $\mu/\mu_m < 0.2$-0.3). This was true for N and for P limitation (but we could find only one species under P limitation).

Under nutrient limitation, cells generally decrease their light harvesting capacity as growth decreases (and as limitation increases), adjusting their ability to capture light to the growth conditions, and thus, preventing an imbalance between excitation energy and the ability to use it via photochemistry and carbon fixation (source vs. sink; Halsey et al. 2010). Figure 4 shows that under moderate nutrient limitation, most of the species examined (with the exception of *Isochrysis galbana*) seem to regulate their Chl *a* content to prevent excitation energy imbalance rather than increasing the size of their XC pigments pool to potentially enhance their capacity for dissipating excessive energy. It suggests that, when growth is not drastically limited by nutrients, light and temperature appear to be the main environmental drivers of the XC pigment pool size (see Laviale et al. 2015 and references therein).

The only Dt/Chl *a* data we found were measured in *Emiliania huxleyi* under N or P limitation by Stolte et al. (2000). They observed constant Dt/Chl *a* over a large range of N limitation and a significant increase in Dt/Chl *a* with increasing P limitation. Although the results from one study cannot be generalized, in *E. huxleyi*, while the Dd+Dt pool size appears independent from the type of nutrient stress (at least for N and P; Fig. 4), the synthesis of Dt seems to be influenced by the type of limiting nutrient.

Pigments of the violaxanthin (V) cycle: effect of growth irradiance

XC pigments content of the V cycle vs. E data are scarce in plants (4 species, Fig. S4, Table S4 in the Supporting Information), and we could not find any from mosses, lichens, green and brown macroalgae. Therefore, we included in our dataset green microalgae (Chlorophyceae and Prasinophyceae) only (Table S1). Also, we could not find exploitable data in conditions of different temperatures or nutrient limitation, and as growth rates were not measured, K_E values were not computable. (V+A+Z)/Chl *a*, (Z+A)/Chl *a* and Z/Chl *a* increased with growth irradiance (Fig. S5 in

the Supporting Information) with variable slopes from a species to another (see also in plants in Fig. S4). The Y_0 of the (V+A+Z)/Chl *a* vs. E linear regression was similar in the species examined (i.e., = 3.6 ± 0.83 mol V+A+Z (100 mol Chl *a*)$^{-1}$; Fig. S5); a similar value was also found in plants (see Fig. S4). This is ~2x lower than the Y_0 of the (Dd+Dd)/Chl *a* vs. E relationship. It suggests that i) in V-containing microalgae, de-epoxidized xanthophylls do not play such an important role in global photoprotection as in Dd-containing species; and/or ii) they have a lower potential for XC-related NPQ than Dd-containing species, at least when E is low; and/or iii) Z quenching efficiency is higher than the one of Dt (see also below 'Quenching efficiency'). Lower Y_0 may also reveal differences in fast photoprotection strategy. State transitions play an important role in lowering excitation pressure on PSII in green microalgae (Finazzi and Minagawa 2014), which is contrary to, for instance, diatoms. In addition, alternative electron flows appear to be of significant importance in re-routing excess energy in both Chlorophyceae (*Chlamydomonas reinhardtii*) and Prasinophyceae (*Ostreococcus* sp.; Cardol et al. 2008, Finazzi and Minagawa 2014, Saroussi et al. 2019). Physiological and metabolic distinctions between 'brown' and 'green' counterparts have been listed and discussed before (Wilhelm et al. 2006) and also tested experimentally in the context of changing light climate (Wagner et al. 2006). Although this later work was based on one green microalga (*Chlorella vulgaris*) and one diatom (*P. tricornutum*) species, it clearly showed that, in contrast to constant light, under fluctuating light, the diatom performed better with a much higher conversion efficiency of photosynthetic energy into biomass, in part based on a stronger and more flexible XC-related NPQ capacity (Wagner et al. 2006, Lepetit et al. 2017). Obviously, more studies of this kind are needed that include the diversity of microalgal groups and species-specific response (see for instance Su et al. 2012, Halsey et al. 2013).

Similar to Dd-containing species, in V-containing species, the Y_0 of the linear relationships between Z/Chl *a* and Z+A/Chl *a* vs. E were close to 0, illustrating the absence of these quenchers when E was close to 0 µmol photons · m^{-2} · s^{-1} in the species examined here.

Quenching efficiency-QE: diversity, influence of irradiance and ecophysiological implications

Although the XC pigment content is informative of light (and/or other growth conditions) acclimation, it is not necessarily a proxy for NPQ-related capacity because de-epoxidized

xanthophylls Dt, Z and A can play other photoprotective roles than triggering NPQ (see for instance Havaux and García-Plazaola 2014, Smerilli et al. 2019). XC-mediated NPQ is also determined by the QE of the de-epoxidized xanthophylls. As described above, a linear relationship between the content of de-epoxidized xanthophylls and the concomitant induction of NPQ is generally observed, and the slope of the regression represents the QE of xanthophyll quenchers Dt, or Z and A (Goss and Jakob 2010), i.e., a slope value of 0.5 means that 1 mol of xanthophyll quencher (here normalized to 100 mol Chl *a*) is needed to trigger 0.5 units of NPQ (see an example in Fig. S1). We thus compiled NPQ vs. Dt and Z (or Z+A) relationship for a number of microalgal species and clones grown under different light conditions (see Tables S2 and S3 and Fig. S6 in the Supporting Information).

Dd-containing species.

QE values were highly variable across planktonic and benthic strains, and even between clones of the diatom *Phaeodactylum tricornutum* (*P. t.2* and *P. t.4* strains, see De Martino et al. 2007) ranging from 0.05 (in a dinoflagellate) to 2.03 (in a diatom-dominated sea-ice community), and with a mean value of 0.54 ± 0.08 mol Chl *a* · (0.01 mol Dt)$^{-1}$ (SE, n=32; Table S2). The higher QEs were found in species inhabiting extreme ecosystems: i) intertidal bare mudflats for *Opephora sp.* and *Fragilaria cf. subsalina* (slope of 1.13 and 1.28, respectively, Table S2) which are benthic non-motile epipsammon species (i.e., that generally live attached to the particles of intertidal sandy sediments; i.e. exposed to potentially high irradiance and high light fluctuations; Cartaxana et al. 2011, Barnett et al. 2015, Blommaert et al. 2017), and ii) sea-ice for a microalgal community dominated by diatoms (*Detonula confervacea*, slope of 2.03; Katayama and Taguchi 2013) which are exposed to sub-zero temperatures, very high salinity and potentially moderate irradiances when the snow cover starts to melt in spring. High QEs of ca. 1 (Table S2) were found in diatom strains that are exposed to high light and/or high light fluctuations in their natural habitat, i.e. for instance *Phaeodactylum tricornutum* (P. t.2 strain, tychoplanktonic, i.e., both planktonic and benthic growth forms, isolated from a supralittoral rock pool, brackish waters), *Cylindrotheca fusiformis* (tychoplanktonic and coastal species), *Ditylum brightwellii* (neritic). A similar QE value (ca. 0.90) was reported for species other than diatoms (i.e., Prymnesiophyceae, Bolidophyceae and Dictyochophyceae; see Dimier et al. 2009b for further details). Lower QEs (below 0.5; Table S2), were found in strains adapted to a lower

average irradiance and/or to lower light fluctuations such as *Skeletonema costatum* (planktonic, semi-enclosed Mediterranean bay), *Pelagomonas calceolata* (picoplanktonic, Red Sea deep-chlorophyll maximum), and tychoplanktonic species inhabiting estuarine intertidal mudflats (i.e., *Brockmanniella brockmanii*, *Plagiogrammopsis vanheurckii*) which are often suspended in turbid waters with high tide or buried in sediments with low tide (see Barnett et al. 2015). Low QEs were also found in benthic motile epipelon (i.e., that generally inhabits intertidal fine muddy sediments) for which photoprotection via XC-NPQ is counterbalanced by behavioural phototactic motility (Cartaxana et al. 2011, Barnett et al. 2015, Blommaert et al. 2017).

Within the same genus (*Thalassiosira* sp.) and for the same growth form (i.e., planktonic and marine), QE varied from close to 1 (*T. weissflogii* and *T. rotula*) down to 0.19 (*T. pseudonana*; Table S2). While *T. weissflogii* and *T. rotula* originate from coastal estuary and offshore habitats, respectively, characterized by high light fluctuations, *T. pseudonana* originates from a coastal enclosed bay. Unfortunately, we do not have data for the oceanic species *T. oceanica* which NPQ is very low (Strzepek and Harrison 2004, Lavaud et al. 2007), i.e., lower than for instance *S. costatum* (QE of 0.5) and in the same range than benthic epipelon diatoms (mean QE of 0.39; Table S2). Different QEs could also be found in clones/ecotypes of the same species (*P. tricornutum*) with the example of the tychoplanktonic *P. t.2* and *P. t.4* strains. Both strains were respectively isolated from estuarine coastal waters (England Channel coast), and at higher latitudes (Finland Baltic sea coast; De Martino et al. 2007), *P. t.4* being thus adapted to lower average irradiances (Bailleul et al. 2010). As a result, QE in *P. t.4* was 3x lower than the one in *P. t.2* when grown under the same low light intensity (0.32 ± 0.08 and 0.96 ± 0.10, respectively; Table S2). At the molecular level, this large difference is due to a lower synthesis of the LHCx1 protein which is involved in XC-mediated NPQ induction (Bailleul et al. 2010, Lepetit et al. 2017) and which is believed to bind Dd-Dt pigments (Lavaud and Goss 2014, Goss and Lepetit 2015). Hence, for the same Dt synthesis in both strains, XC-mediated NPQ, and as a consequence QE, are lower in P.t.4.

The link between the natural light climate of species/ecotypes and QE amplitude was generally supported by our analysis. It strengthens the view (see otherwise discussions by Dimier et al. 2009b, Petrou et al. 2011, Lavaud and Lepetit 2013, Barnett et al. 2015) that Dd-containing growth forms, species and ecotypes adapt their fast light-response to the light climate of their natural habitat, in

terms of average irradiance and light fluctuations, through the molecular control of NPQ by Dt synthesis (Lepetit et al. 2017, Taddei et al. 2018). Dimier et al. (2007, 2009b) even proposed a classification of Dd-containing microalgae (distributed among pico-, nano- and micro-phytoplankton) in three distinct ecological groups based on their XC properties vs. irradiance and light fluctuations. Nevertheless, and to be complete, one should note exceptions to this general view with, for instance in the highly diverse and complex consortium of intertidal flat benthic diatoms, low QE values in non-motile epipsammon species such as *Plagiogramma staurophorum* (0.26) and relatively high QE values in the tychoplanktonic (*Cylindrotheca closterium*; 0.59), motile epipsammic (*Nitzschia cf. frustulum*; 0.80), and epipelic (*Seminavis robusta*; 0.64) species (Barnett et al. 2015). Possibly this is explained by the E growth used in this study and which was on the upper or lower limit of light phenotypic plasticity range for these strains (see for instance the higher range of Es for a lowering of QE in *P. tricornutum* vs. *C. meneghiniana*; Table S2).

Also, it was early reported (Demers et al. 1991) that QE can be modulated as a function of acclimation to E (and likely the light dose), i.e. the same cells acclimated to low or high Es showed different QE values with a ca. 2-5x lower QE for high light acclimated cells of *P. tricornutum*, *S. costatum* and *C. meneghiniana* (Table S2, Fig. 5). This QE difference between low vs. high E is due to a change in the size of the different Dd pools with a larger pool, and consequently a higher Dt proportion, that does not contribute to NPQ under higher E (Schumann et al. 2007, Lavaud and Lepetit 2013). Also, the 'saturation' of NPQ *vs*. Dt relationships was reported in several species (Table S2), i.e., while being high for a range of NPQ and Dt amount, QE suddenly decreases with prolonged exposure to over-saturating irradiances (from ca. 15 to 45 min on, depending on the species; see Blommaert et al. 2017 for the most recent example). This feature, as well as the lower QE under high light acclimation, have been attributed to the synthesis of additional Dt molecules that do not bind to the LHC system, and therefore do not participate to NPQ (Schumann et al. 2007, Lavaud and Lepetit 2013, Lavaud and Goss 2014). It is believed that these additional Dt molecules could participate to the direct scavenging of free radicals and the prevention of lipid peroxidation in thylakoid membranes (Lepetit et al. 2010).

Finally, but noteworthy, is the fact that in most species examined Y_0 was close to 0 with no positive intercepts (Table S2). It confirms that in the Dd-containing species, Dt synthesis is mandatory for

NPQ induction (see Lavaud et al. 2012). In three cases, Y_0 was negative meaning that when the photosynthetic system is reoxidized (i.e., after a period of darkness or low light), some Dt molecules remained. It was observed under extreme conditions (Table S2): i) in *P. tricornutum* grown under over-saturating irradiance (1000 µmol photons · m^{-2} · s^{-1}), and ii) in sea-ice community exposed to extreme environmental stress.

V-containing species.

The relationship between Z (or Z+A) and NPQ was generally linear with a QE for Z and A+Z of 0.32 ± 0.05 mol Chl *a* · (0.01 mol Z)$^{-1}$ (SE, n=15) and 0.19 ± 0.03 mol Chl *a* · (0.01 mol Z+A)$^{-1}$ (SE, n=15), respectively (Table S3). In general, and although there is only half the data, mean QE in V-containing microalgae was ca. half the one of Dd-containing microalgae (Fig. S6B), and with a much lower maximum value (0.64 in *Chlorella vulgaris*; Table S2). It confirms the generally stronger involvement of de-epoxidized xanthophylls in NPQ in Dd-containing algae, and especially in diatoms (Goss and Lepetit 2015). For comparison, in the plants data we found, QE for Z and A+Z was 0.19 ± 0.04 mol Chl *a* · (0.01 mol Z)$^{-1}$ (SE, n=3) and 0.39 ± 0.11 mol Chl *a* · (0.01 mol Z+A)$^{-1}$ (SE, n=7), respectively (Table S5 in the Supporting Information). The lower QE in V-containing microalgae can be explained by the fact that in many species, a significant portion of NPQ can develop without Z and/or A synthesis (explaining the $Y_0 > 0$ values observed in several species, Table S3), and for some species only when grown under excess light (Finazzi and Minagawa 2014, Quaas et al. 2015, Christa et al. 2017). In fact, in V-containing microalgae, the NPQ mechanism appears very heterogeneous and can be achieved by different processes beyond the XC at the molecular level (reviewed in Finazzi and Minagawa 2014). In the most recent studies (Bonente et al. 2012, Lunch et al. 2013, Quaas et al. 2015), it has been emphasized how V-containing microalgae show a great diversity in XC and NPQ extents, kinetics and relationship, with no obvious reason(s) for such diversity.

Interestingly, the giant kelp *Macrocystis pyrifera,* which has a V cycle together with a protein composition and spatial organization of its LHC antenna system closer to the diatoms (they both belong to the Stramenopiles; Lavaud and Goss 2014, Goss and Lepetit 2015), showed a QE similar to the highest values reported for Dd-containing microalgae (Table S3). Therefore, not only the nature of the XC (i.e., one vs. two de-epoxidation steps) but also the composition and organization of the LHC

antenna system determines the efficiency of XC pigments in NPQ as well as its induction kinetics and maintenance over a range of light conditions (see Goss and Lepetit 2015, Kuthanová Trsková et al. 2018 for further details).

Studies specifically investigating the link between the natural light climate of species/ecotypes and QE amplitude in V-containing microalgae are scarce. A first study compared two ecotypes of the Prasinophyceae *Ostreococcus* (Six et al. 2008), respectively adapted to high irradiance and fluctuating light (*Ostreococcus tauri* isolated from a South of France lagoon) and to stable low irradiance (*Ostreococcus* RCC809, isolated from Atlantic Ocean deep-chlorophyll maximum). While NPQ capacity was similar in the two strains, *O. tauri* showed a higher V de-epoxidation and a lower QE (Table S3). A second study compared four species and ecotypes of the freshwater green microalga *Cosmarium* sp. (Charophyceae) isolated from different latitudes (Stamenković et al. 2014). All of them displayed very similar QE (Table S3) but *C. crenatum* (ca. 2x higher) probably due to the fact that in this species, the XC mostly leads to the accumulation of A (Stamenković et al. 2014). No latitudinal adaptation of NPQ-related XC was observed for *Cosmarium* sp. (in contrast to Dd-containing microalgae, see Laviale et al. 2015), which might partly be due to the fact that all clones were isolated from similar shallow freshwater habitats exposed to occasional high light exposure. Obviously two studies are not enough to raise any conclusion on an apparent loser link between QE and adaptation of V-containing microalgae to their light niche. It could be that, XC-related NPQ might not be a major player of their photoadaptive strategy, and QE would not be as good of a fingerprint as it is in Dd-containing microalgae. Therefore, one should look at other relevant processes, such as alternative electron pathways (Cardol et al. 2008, Saroussi et al. 2019) and the PSII repair cycle (Ni et al. 2017), to gain deeper insights on the role of photoprotection in the ecophysiology of V-containing microalgae.

Finally, studies included in our meta-analysis did not allow to state on an effect of growth irradiance on QE (i.e., comparison of QE under several growth Es for a given species; Table S3).

NPQ in a growth and ecophysiological strategy

In order to conceptualize our findings, we related the proportion of absorbed energy that is dissipated as heat (Φ_{NPQ} as calculated by Hendrickson et al. 2004; see Fig. S7 in the Supporting Information)

and the growth rate (μ/μ_m) to the energetic pressure during light-acclimated growth (E/K_E) in two diatoms that are known to show very different quenching efficiencies (see Table S2): *Cyclotella meneghiniana* (low NPQ and QE diatom) and *P. tricornutum-P. t.2* strain (high NPQ and QE diatom; Fig. 6). Our model, the construction of which is described in Figure S8 and Appendix S1 in the Supporting Information is based on the relationships between Dt and E/K_E (Fig. 2), between QE and E (Fig. 5), and between XC-mediated Φ_{NPQ} and NPQ in diatoms (Fig. S7). We only selected data from these two diatoms, as they were the most complete set that allowed us this modeling procedure.

The fine-tuned NPQ XC-related photoprotection is generally presented as a mechanism limiting photoinhibitory damages during fast and short-term increases in irradiance (Demmig-Adams et al. 2014). As a consequence, under a given and stable light environment (i.e., fixed growth irradiance and E/K_E), one would expect microalgae to modify their photosynthetic machinery in order to exploit in the most optimal manner the actual irradiance (see Geider 1987, MacIntyre et al. 2002, Raven and Geider 2003), and thus minimize fast dissipative processes, such as XC-mediated NPQ, which induction could appear futile and even detrimental. In contrast, Figure 6 (and Fig. 2) clearly shows that diatoms acclimated to a given energetic pressure corresponding to a certain growth irradiance still dissipate a significant proportion of the light energy they absorb. With our modeling, at $3K_E$, i.e., at growth irradiance that nearly saturates growth (corresponding to $\mu = 0.95\ \mu_m$), diatoms dissipate between 30 % ($\Phi_{NPQ} = 0.30$; low NPQ-QE diatom) and 61% ($\Phi_{NPQ} = 0.61$; high NPQ-QE diatom) of the absorbed light energy at the PSII-associated LHC sites. It means that in conditions of steady-state growth, in a fully photoacclimated state, and despite adjustments of the photosynthetic machinery, diatoms maintain a capacity to absorb light which is higher than their needs and from which a significant (excessive) part of absorbed energy is dissipated as heat via XC-NPQ.

Interestingly, this photoadaptive strategy has first been described in overwintering evergreen plants and trees (Demmig-Adams et al. 2014b). While annuals and deciduous plants lower their Chl *a* content in response to environmental stresses ('annual growth strategy'), evergreens tend to maintain their Chl *a* content and induce large NPQ (i.e., qZ; Verhoeven 2014) based on the maintenance of a high Z content ('evergreen growth strategy'). The benefit for maintaining excessive harvesting capacity was proposed to support the relatively prompt resume of C fixation and growth when conditions become favorable for photosynthesis upon spring warming (Demmig-Adams et al. 2014).

In diatoms, and maybe Dd-containing microalgae, a similar strategy under excess growth irradiance and/or low temperature (Figs. 3, 6), would possibly allow to anticipate a decrease in ambient irradiance (and/or increase in temperature), for remaining performant under a wide range of irradiances, and especially well above their K_E. The benefits of this strategy are clear if NPQ relaxation is faster (timescale: minute) than the building of the light harvesting machinery (timescale: hours) and also faster or in the same range than the light/temperature fluctuations (MacIntyre et al. 2002). We recently reported an extreme of this photoadaptative strategy in a polar diatom (Lacour et al. 2018). It maintains its light harvesting capacity and growth rate at 0°C when grown under an excess irradiance (ca. 50 K_E), and it dissipates most of the absorbed energy via a sustained NPQ triggered by a high and permanent Dt content.

Therefore, instead of disentangling their LHC system to face any prolonged, and potentially unfavorable, change in irradiance and/or temperature, diatoms, and possibly Dd-containing microalgae, maintain their LHC system and tune their photosynthetic efficiency with, at least, XC-related NPQ. At the molecular level, this is possible because the XC-mediated NPQ process can rapidly modify and maintain the function(s) of the LHC system, i.e., absorption under stable irradiances lower or close to K_E, absorption and dissipation for stable irradiances over K_E. In such a framework, the modification of the function of the LHC needs to be fast in both ways, i.e. on one hand fast XC-mediated NPQ induction should allow the LHC to rapidly enter and maintain a dissipative state under stable high light conditions, and on the other hand it should be able to rapidly relax to avoid limitation of light absorption and photochemical efficiency upon return to stable more favorable light conditions. This balanced and flexible interplay needs a fine-tuned partnership between many actors (LHC pigments and proteins, regulatory partners of NPQ and XC, etc.) which central node could be the redox state of the plastoquinone-PQ pool (Lepetit et al. 2013, Wilhelm et al. 2014). Indeed, the PQ redox state is the cross-road of irradiance/light dose changes and energetic pressure which influences, at different timescales, a feedback and interrelated triggering of the photochemical electron transport rate, the transthylakoïdal ΔpH, the Dd de-epoxidation into Dt, the Dd+Dt pool size and the LHC protein synthesis via the retrograde signaling pathway (Lepetit and Dietzel 2015).

Contrary to light and temperature response, under moderate N limitation (see Fig. 4), Dd-

containing microalgae seem to use the 'annual' strategy: they adjust their light-harvesting capacity to their growth capacity (Halsey et al. 2010) so that the need for NPQ is restricted. One possible explanation is based on the N cost of maintaining the LHC system in the 'evergreen' strategy. Indeed, the protein-rich LHC system is very demanding in N, which is, by definition, an unaffordable element under N limitation. This explanation is also in agreement with the fact that nutrient availability is less variable than irradiance and temperature in the natural environment, making the 'evergreen' strategy less efficient, at least for Dd-containing microalgae.

The growth strategy of photoautotrophs depends on the relative benefit/cost balance in a specific environment and/or lifestyle. For planktonic diatoms and microalgae inhabiting a mixed water column, the 'evergreen' strategy could well support its ability to acclimate to the mean irradiance around which the light environment constantly fluctuate. This photoadaptative strategy clearly differs from acclimating to the highest potential irradiance which allows avoiding the harmful effect of light stress but which strongly reduces photosynthetic efficiency under low/moderate light conditions (Falkowski and Raven 2007). Overall, the hypothesis we propose here (Figs. 6, S8) supports how the diatoms, and possibly the Dd-containing microalgae, can exploit a large range of irradiance changes, coupled with a large range of temperatures (including close to 0°C) and nutrient availability, and over various time scales. This portrait fits well with the ability of diatoms i) to thrive in very different marine ecosystems and habitats, typically coastal vs. open ocean and temperate *vs*. polar systems (Mock and Medlin 2012, Lacour et al. 2017), and ii) to dominate in habitats with extreme light climate (in terms of high average irradiance and/or high light fluctuations) such as turbulent water columns (i.e., upwelling areas for instance), estuarine intertidal flats, polar sea-ice margins, etc. (Lavaud and Goss 2014, Lyon and Mock 2014, Wilhelm et al. 2014). The general light-response flexibility of diatoms, as well as its diversity (see Table S2; Lepetit et al. 2012, Lavaud and Goss 2014, Wilhelm et al. 2014), might also well explain, in part, how they (and in general Dd–containing microalgae) have become essential primary producers of our contemporary oceans (Benoiston et al. 2017, Tréguer et al. 2018).

Future directions

The molecular regulation of NPQ is complex, it shows a high diversity among autophototrophs, and, although this is a dynamic field of research, it is not yet fully understood (Demmig-Adams et al. 2014, Goss and Lepetit 2015, Ruban 2016, Wobbe et al. 2016, Magdaong and Blankenship 2018, Pinnola and Bassi 2018). Various aspects of NPQ regulation were not integrated to this study, especially the induction and relaxation kinetics of XC-related NPQ. They are thought to be an important adaptive trait that could explain, in part, the ecological niche distribution of growth forms and species in the aquatic (Dimier et al. 2007, 2009b) and terrestrial habitats (Demmig-Adams et al. 2014). Obviously, further studies are needed to better understand the respective roles of environment and genetics on XC-related NPQ regulation with a coupled effort in using genetic manipulation, natural biodiversity and field experiments. Thanks to the fact they can now be easily genetically and experimentally manipulated (Gruber and Kroth 2017, Moejes et al. 2017, Tirichine et al. 2017), microalgae have been often used to understand the influence of growth environmental conditions on the functional diversity of XC-related NPQ processes. On the contrary, and as pointed out in our study, investigations of XC-related NPQ in plants under several light conditions are too few, and often with no quantitative evaluation of the energetic state of the whole organism for a more integrated picture to emerge (see Demmig-Adams et al. (2017). More quantitative comparisons of plants and trees adapted and acclimated to different growth conditions are needed to further decipher the diversity of the regulation of XC-related NPQ in multicellular systems (see for instance the recent work by Míguez et al. 2017).

Studies on NPQ in microalgae have also clearly focused on Dd cycle organisms, and especially on diatoms, at the expense of other groups (Lavaud and Goss 2014, Goss and Lepetit 2015), obviously because of their ubiquity, high diversity and major role in the global marine primary production (Mock and Medlin 2012, Malviya et al. 2016, Benoiston et al. 2017). Light-dependent XC pigment content, NPQ and quenching efficiency data in conjunction with growth rate in non-diatom species remain scarce, especially in V-containing and green representatives for which many XC-NPQ studies have been performed using the model organism *Chlamydomonas reinhardtii* (Erickson et al. 2015, Wobbe et al. 2016). Nevertheless, recent studies examined the XC-related NPQ in diverse green representatives (Lunch et al. 2013, Stamenković et al. 2014, Quaas et al. 2015, Christa et al. 2017) as well as including new, ecologically relevant, models such as *Ostreococcus* (Finazzi and Minagawa 2014). In general, the recent explosion of genome sequencing of many species from different algal

groups now allows to better explore at the molecular level the functional diversity of the light-response regulation in microalgae (Finazzi et al. 2010, Brodie et al. 2017). The fact that these species represent a broad diversity of growth forms (planktonic, benthic, tychoplanktonic, etc.) and originate from different ecosystems and habitats (open ocean, coast, estuarine flats, sea-ice, temperate *vs*. polar system, etc.) will additionally support the study of the XC-related NPQ as a potentially significant functional adaptive trait.

At last, in plants, the improvement of photoprotection in a fluctuating light environment is one of the most promising research path for both enhancing the stress resistance and improving the productivity of future genetically-modified crops (Cardona et al. 2018), with genetic manipulation of the XC-related NPQ being at the forefront (Kromdijk et al. 2016, Murchie 2017). A better knowledge of the impact of XC-NPQ on metabolism and growth, and its functional diversity in microalgae (Goss and Lepetit 2015) will likely provide benefit to industrial microalgal production (Moejes et al. 2017) and to the generation of engineered cells for the bioproduction of molecules of interest such as biofuels (Hess et al. 2017, Wagner et al. 2017).

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Figure 1: Diadinoxanthin + Diatoxanthin (Dd + Dt) content for different species and taxa as a function of growth light conditions. (Dd+Dt)/Chlorophyll (Chl *a*) vs. growth irradiance (E) (panels A, B, C) and vs. growth irradiance normalized to light saturation parameter for growth (K_E; E/K_E, panels D, E, F) in diatoms (panels A, D), in other diadinoxanthin-containing microalgae (panels B, E) and in both merged groups (panels C, F). For panels C and F, linear regressions are shown with 95% confidence and prediction intervals, and corresponding R^2 and equations provided. Data sources are described in Table S1; the logarithmic scale version of panel F can be found in Figure S2A. Species abbreviations: *T. w.* (A), *Thalassiosira weissflogii* (Actin); *T. w.* (G), *Thalassiosira weissflogii* (Grunow); *T. g.*, *Thalassiosira gravida*; *C. n.*, *Chaetoceros neogracilis*; *S. c.*, *Skeletonema costatum*; *N. p.*, *Nitzschia palea*; *F. c.*, *Fragilariopsis cylindrus*; *E. h.*, *Emiliania huxleyi*; *H. c.*, *Hymenomonas carterae*; *A. c.*, *Amphidinium carteri*; *P. a.*, *Phaeocystis antarctica*.

Figure 2: Diatoxanthin (Dt) content for different species and taxa as a function of growth light conditions. Dt/ Chlorophyll (Chl *a*) vs. growth irradiance (E) (panels A, B) and vs. growth irradiance normalized to light saturation parameter for growth (K_E) (E/K_E, panels C, D) in diatoms (panels A, C) and in other microalgae (panels B, D). For panels C and D, linear regressions are shown with 95% confidence and prediction intervals, and corresponding R^2 and equations are provided. Data sources are described in Table S1; the logarithmic scale version of panels C and D can be found in Figure. S2, B and C, respectively. Species abbreviations: *T. w.* (A), *Thalassiosira weissflogii* (Actin); *T. w.* (G), *Thalassiosira weissflogii* (Grunow); *T. g.*, *Thalassiosira gravida*; *C. n.*, *Chaetoceros neogracile*; *S. c.*, *Skeletonema costatum*; *N. p.*, *Nitzschia palea*; *F. c.*, *Fragilariopsis cylindrus*; *E. h.*, *Emiliania huxleyi*; *H. c.*, *Hymenomonas carterae*; *A. c.*, *Amphidinium carteri*; *P. a.*, *Phaeocystis antarctica*.

Figure 3: Effect of temperature on the Diadinoxanthin + Diatoxanthin (Dd + Dt) and Diatoxanthin (Dt) content in species showing different sensitivity to light. **(**Dd+Dt)/ Chlorophyll (Chl *a*) (panels A, B) and Dt/ Chlorophyll (Chl *a*) (panels C, D) vs. growth irradiance (E) (panels A, C) and vs. growth irradiance normalized to (K_E) (E/K_E, panels B, D) in the polar diatoms *Chaetoceros neogracile* and *Thalassiosira gravida* acclimated at 0°C and 5°C. For panels B and D, linear regressions are shown with 95% confidence and prediction intervals, and corresponding R^2 and equations are provided. Each

data point is the mean of 3 independent cultures. In panels A and C, error bars represent standard deviations. Data sources are described in Table S1; the logarithmic scale version of panels B and D can be found in Figure S3, A and B, respectively.

Figure 4: Diadinoxanthin + Diatoxanthin (Dd + Dt) content in relation to growth under nutrient limitation. Normalized (Dd+Dt)/Chlorophyll (Chl *a*) vs. μ/μ_m in species exposed to various levels of nutrient limitation (nitrogen-N or phosphate-P). μ/μ_m increases as nutrient limitation decreases; when $\mu/\mu_m = 1$, cultures are replete and growth is optimal. For each species, (Dd+Dt)/Chl *a* was normalized by its the maximum value. Each data point was generated from a culture acclimated to a given level of nutrient limitation in a chemostat system; see the text for further details. Data were extracted from two studies: Goericke and Montoya (1998) and Stolte et al. (2000).

Figure 5: Quenching efficiency (QE) vs. growth irradiance (E) in different species. In both panels, QE is the slope of the NPQ *vs.* Diatoxanthin (or Zeaxanthin + Antheraxanthin) relationship. Only the species for which QE was reported for several Es are shown. Species abbreviations: *C. m.*, *Cyclotella meneghiniana*; *S. c.*, *Skeletonema costatum*; *P. t.2 and P. t.4, Phaeodactylum tricornutum* strains 2 and 4; *A. e.*, *Alexandrium excavatum*; diatoms are shown with open symbols and the dinoflagellate *A. e.* with closed symbols. Note that two plants (grey symbols), *Hedera helix* (*H. h.*) and *Zea mays* (*Z. m.*) were included (see Table S5) for the sake of comparison and a logarithmic scale was used. Data sources are described in Table S2.

Figure 6: Illustration of potential energy dissipation in diatoms with low and high NPQ ability. Modelled Φ_{NPQ} (proportion of absorbed energy dissipated as heat by NPQ in black) and μ/μ_m (in grey) as a function of growth irradiance (E) normalized by the light saturation for growth (E/K_E) in *Cyclotella meneghiniana* (low NPQ, dotted black line; Lavaud and Lepetit 2013) and *Phaeodactylum tricornutum-P. t.2* strain (high NPQ, continuous black line; Lavaud and Lepetit 2013). The computation of Φ_{NPQ} is based on the relationships between E, Diatoxanthin content and NPQ evidenced in this study (see the supplementary material for details and Fig. S8). μ/μ_m was modelled as proposed by MacIntyre et al. (2002) ($\mu/\mu_m = 1\text{-}\exp[-E/K_E]$, see the Methods).

Table S1: Data sources for the xanthophyll cycle (XC) datasets shown in Figures 1, 2, 3, S2, S3 and S5. The selected data include measurements of XC pigments and growth rates of unialgal cultures acclimated to several growth irradiances and one temperature (T, °C). n is the number of distinct irradiances.

Table S2: Data sources for the quenching efficiency (QE) dataset in diadinoxanthin (Dd)-containing species. The selected data included measurements of NPQ and diatoxanthin (Dt) content during short term light treatments of unialgal cultures at different irradiances. E is the growth irradiance, a is the slope of the NPQ vs. Dt relationship, Y_0 is the y-intercept, and n is the number of data points for each species (see the Methods section and Fig. S1).

Table S3: Data sources for the quenching efficiency (QE) dataset in violaxanthin (V)-containing species. The selected data included measurements of NPQ, and zeaxanthin (Z) and antheraxanthin (A) contents during short term light treatments of unialgal cultures at different irradiances (but for *Macrocystis pyrifera*). E is the growth irradiance, a is the slope of the NPQ *vs*. Z relationship, Y_0 is the y-intercept, and n is the number of data points for each species.

Table S4: Data sources for the xanthophyll cycle (XC) datasets shown in Figure S4. The selected data include measurements of xanthophyll pigments in land plants acclimated to several growth irradiances. n is the number of distinct irradiances.

Table S5: Data sources for the quenching efficiency (QE) dataset in land plants. The selected data include measurements of NPQ, Zeaxanthin (Z) and Antheraxanthin (A) contents in land plants during short term light treatments at different irradiances.

Figure S1: Parametrization of the non-photochemical quenching (NPQ) vs. Diatoxanthin (Dt) or Zeaxanthin (Z) + Anteraxanthin (A) relationship as shown in Tables S2 and S3- an example with the diatom *Phaeodactylum tricornutum.* Relationship between NPQ and Dt in *P. tricornutum-P. t.2*

acclimated to 50, 500 and 1000 µmol photons · m^{-2} · s^{-1} (Panel A). Linear fits were adjusted on the linear portion of the relationships. The slopes (a) and the Y intercept (Y_0) are provided (panels B, C, D). Saturation was observed for cells acclimated at 500 and 1000 µmol photons · m^{-2} · s^{-1} (panels C and D).

Figure S2: Diadinoxanthin + Diatoxanthin (Dd + Dt) and diatoxanthin (Dt) contents for different species and taxa as a function of growth light conditions**.** (Dd+Dt)/Chlorophyll (Chl *a*) vs. growth irradiance normalized to the light saturation parameter for growth (E/K_E) in Dd-containing microalgae (panel A). Dt/Chl *a* vs. E/K_E in diatoms (panel B) and in other Dd-containing microalgae (panel C). Regressions are shown with 95% confidence and prediction intervals. Data sources are described in Table S1. Note that the E/K_E axis is in logarithmic scale. Symbols are the same as in Figures 1 and 2.

Figure S3: Effect of temperature on the Diadinoxanthin + Diatoxanthin (Dd + Dt) content in species showing different sensitivity to light. Dd+Dt/Chl *a* (panel A) and Dt/Chl *a* (panel B) vs. growth irradiance normalized to the light saturation parameter for growth (E/K_E) in the polar diatoms *Chaetoceros neogracile* (circles) and *Thalassiosira gravida* (triangles) acclimated to 0°C (open symbols) and 5°C (closed symbols). Regressions are shown with 95% confidence and prediction intervals. Each data point is the mean of 3 independent cultures. Note that the E/K_E axis is in logarithmic scale. Symbols are the same as in Figure 3.

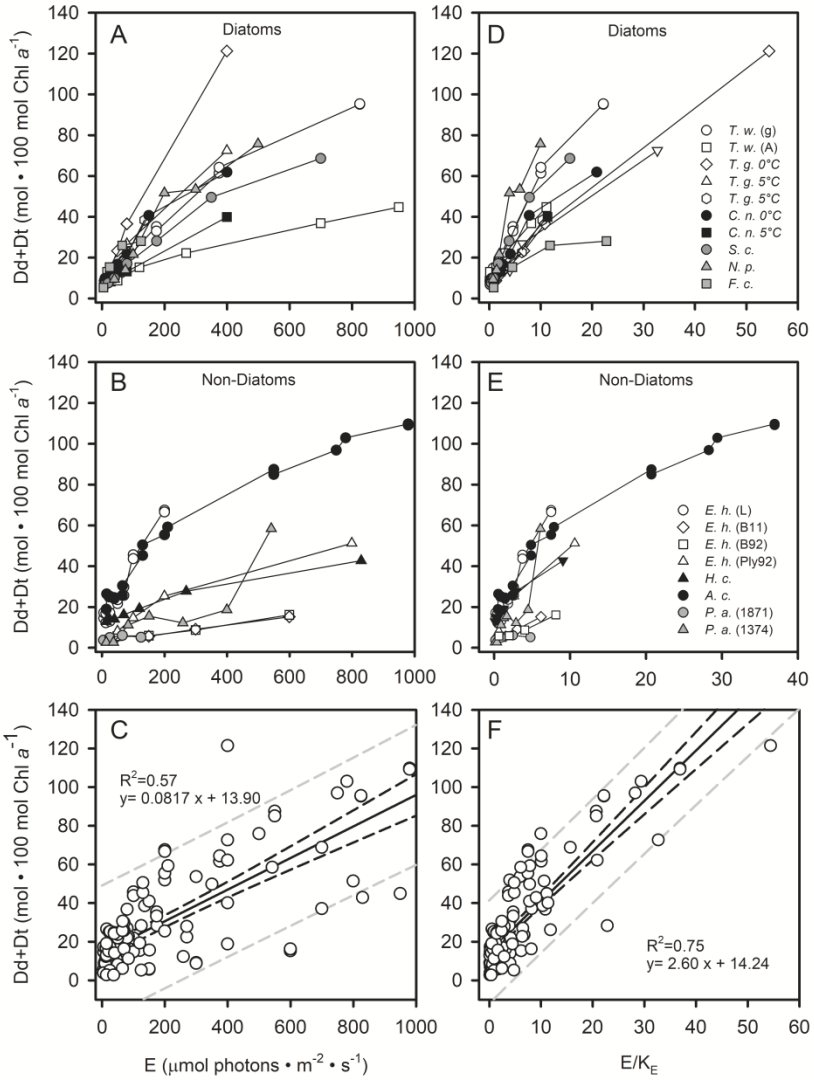
Figure S4: Zeaxanthin (Z) + antheraxanthin (A) + violaxanthin (V) pigments content in land plants as a function of growth light conditions. (Z+A+V)/Chlorophyll *a* (Chl *a*) (panel A), Z+A/Chl *a* (Panel B) and Z/Chl *a* (panel C) vs. growth irradiance (E). Data sources are described in Table S1.

Figure S5: Zeaxanthin (Z) + antheraxanthin (A) + violaxanthin (V) pigments content in V-containing microalgae as a function of growth light conditions. (Z+A+V)/Chlorophyll *a* (Chl *a*) (panel A), Z+A/Chl *a* (Panel B) and Z/Chl *a* (panel C) vs. growth irradiance (E). In panels A, B, C, linear regressions are shown and corresponding R^2 and equations are provided. Data sources are described in Table S1.

Figure S6: Quenching efficiency (QE) in different species. In both panels, QE is the slope of the NPQ vs. Diatoxanthin (or Zeaxanthin + Antheraxanthin) relationship. Panel A: Same as Figure 5 including all our dataset (see data sources in Tables S2 and S3). Panel B: Box plot diagram showing QE in Diadinoxanthin (Dd)- and Violaxanthin (V)-containing species.

Figure S7: Relationship between Φ_{NPQ} (proportion of absorbed energy dissipated as heat by NPQ, see the Methods section) and NPQ in *Thalassiosira gravida* and *Chaetoceros neogracile* exposed to various levels of irradiances (from 0 to 2000 µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}).

Figure S8: Illustration of potential energy dissipation in diatoms with low and high NPQ ability. Quenching efficiency-QE (A) and NPQ (B) vs. growth irradiance normalized to the light saturation parameter for growth (E/K_E) in *Cyclotella meneghiniana* (low NPQ diatoms) and *Phaeodactylum tricornutum-P. t.2* (high NPQ diatoms). μ/μ_m was modeled as proposed by MacIntyre et al. (2002) ($\mu/\mu_m = 1-\exp[-E/K_E]$, see the Methods section). In panel B, NPQ was modeled from equations 2, 3, 4 and 5 given above. The combination of both allowed to build the relationship shown in Figure 6.



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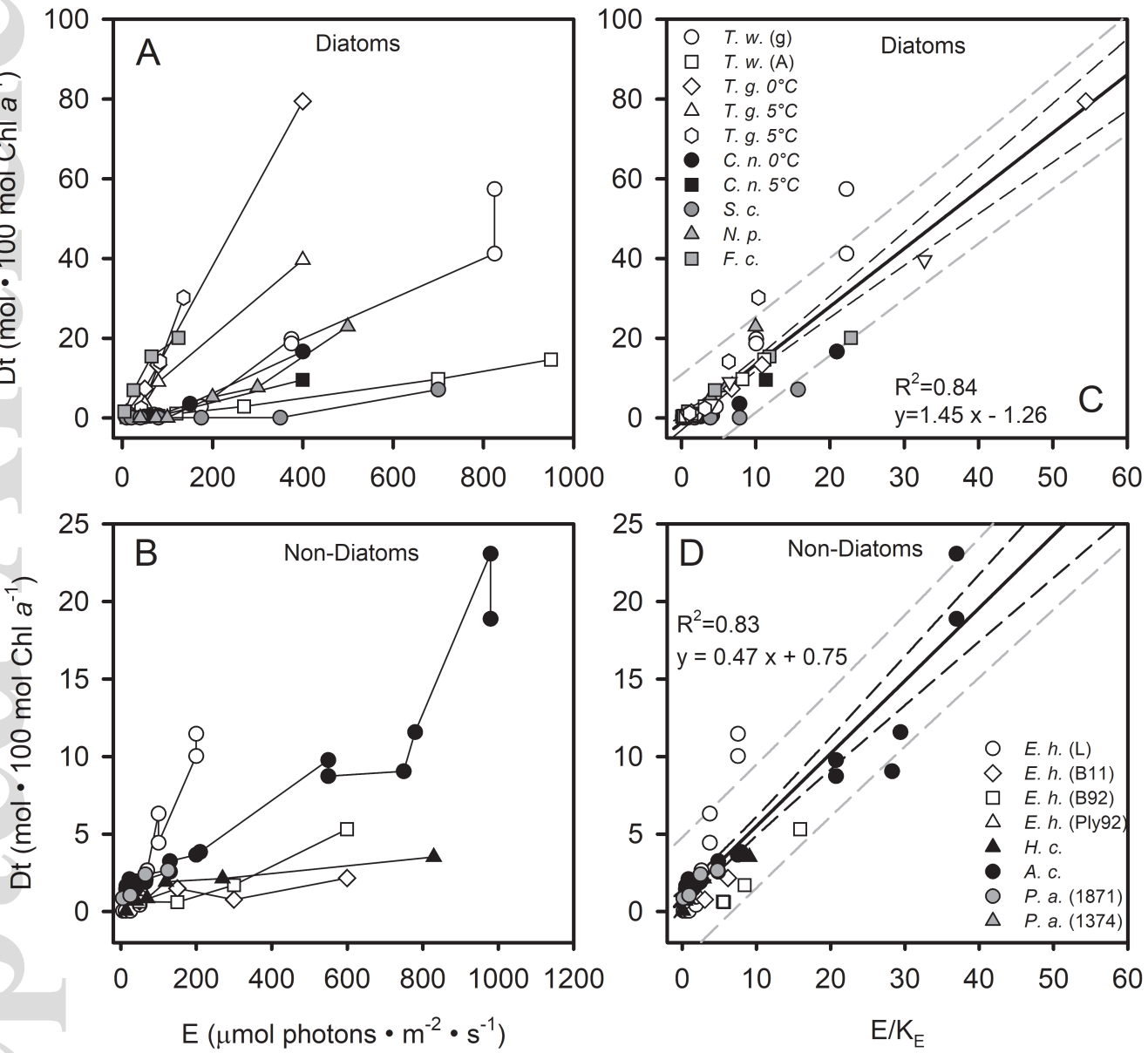

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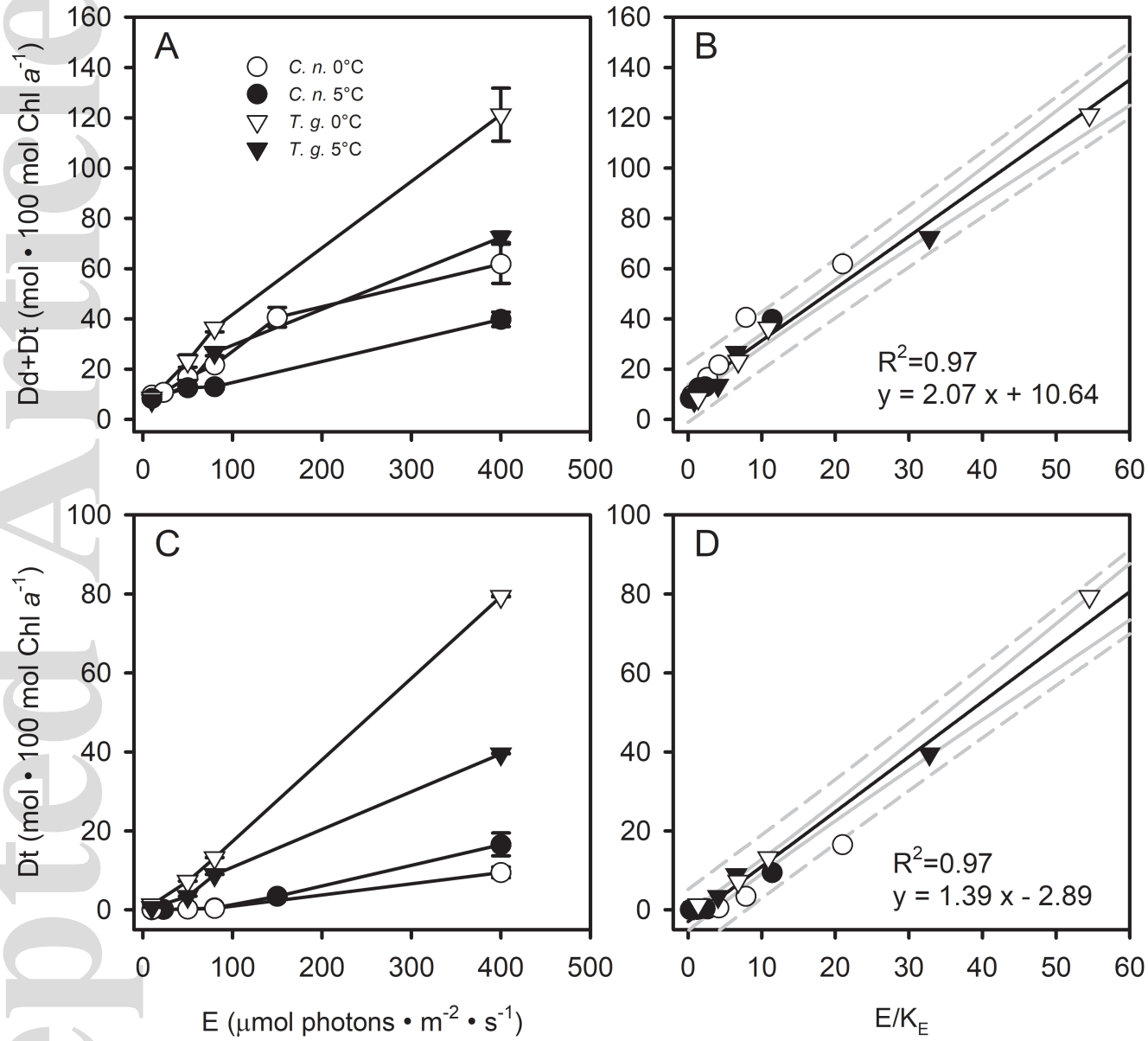

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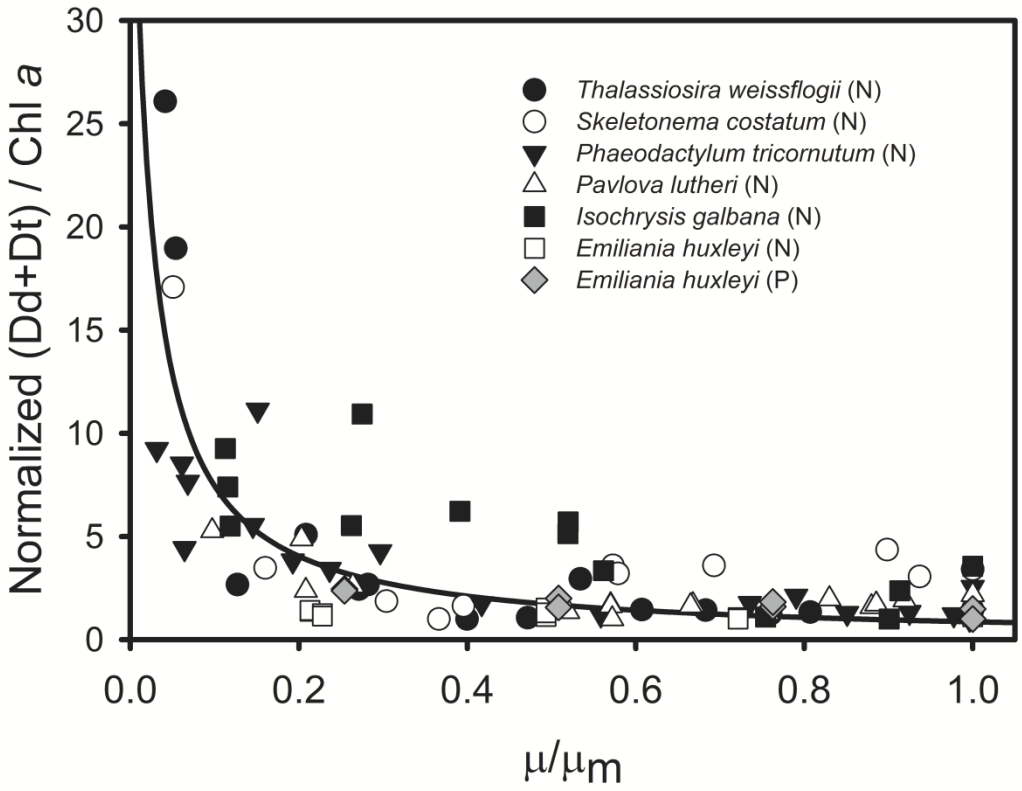

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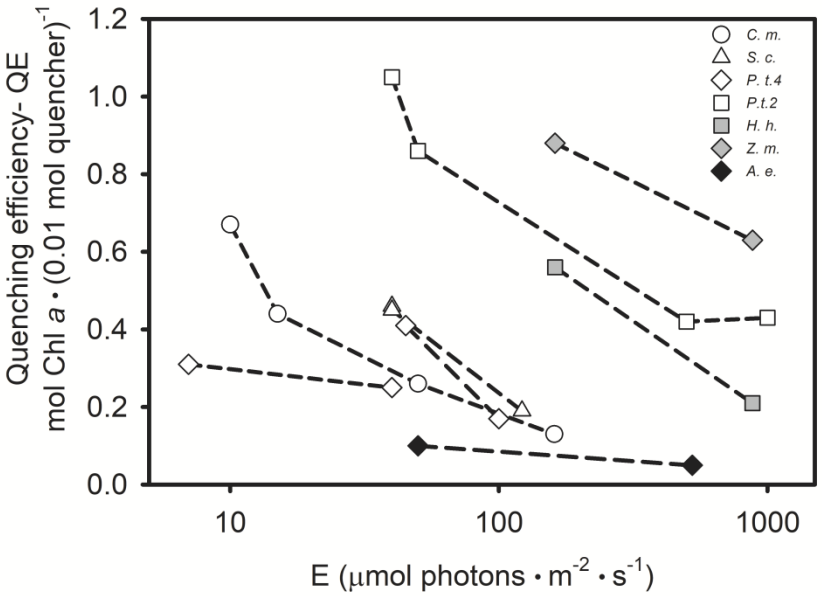

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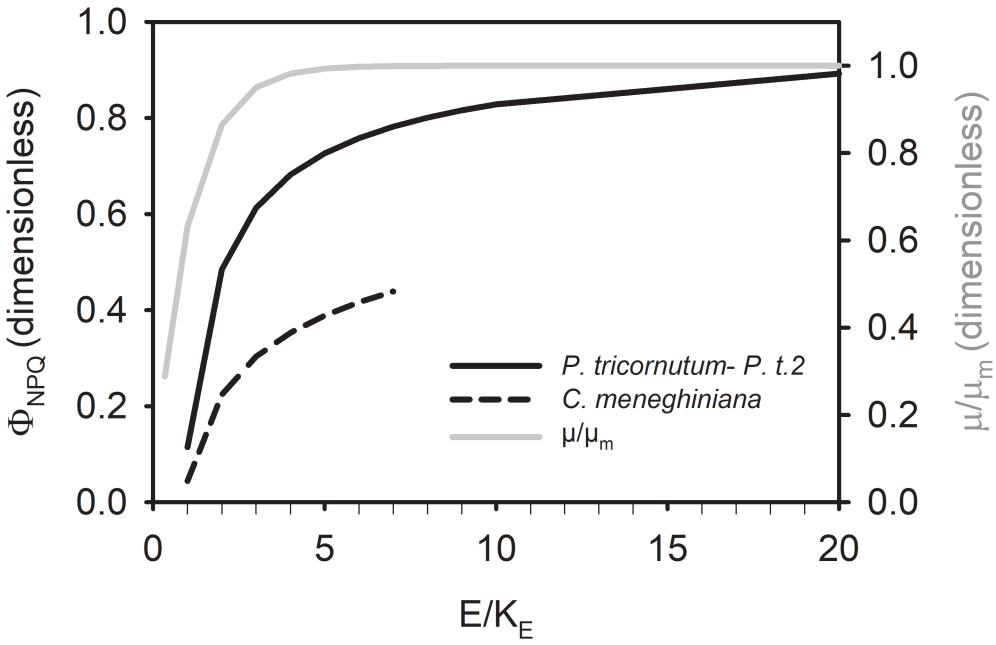

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