

photochemical reactions of photosynthesis are light saturable, when background irradiance increases, there is a decreased probability of finding an “open” photochemical target or “hole” for absorbed radiation. Thus, the change in fluorescence induced by an actinic source also decreases. This process is called photochemical quenching.

The photochemical target for excitation energy can be inferred from the rate of light saturation of fluorescence. This saturation profile, described by a cumulative one-hit Poisson function, reflects the effective absorption cross section for the photochemical reaction (Ley and Mauzerall, 1982; Falkowski and Kolber, 1995). All photosynthetic organisms have developed mechanisms to adjust these cross sections dynamically in response to background light (Long et al., 1994). Thus, as irradiance increases, the cross section can be made smaller to minimize photodamage to the reaction centers; conversely, when irradiance decreases, the cross sections can be made larger, to optimize light harvesting. There are two major strategies for altering cross sections. On short time scales (minutes), the adjustments are made by adding or removing pigments that dissipate the excitation as heat. These pigments, a set of taxonomically dependent carotenoids, are located within the light-harvesting systems and compete effectively with chlorophyll *a* for fluorescence. Thus, when irradiance is high, there is an overall reduction in fluorescence yield, reflecting a decrease in the effective cross section of the photochemical process (Olaizola et al., 1994). The reduction in fluorescence is a component of what is sometimes called nonphotochemical quenching (Falkowski and Kolber, 1995). On longer time scales, cells can increase or decrease the number of chromophores per unit cell through a feedback process coupled to sense irradiance levels (Escoubas et al., 1995).

Superimposed on the diel changes in fluorescence are short-term variations resulting from the passage of clouds across the sky and photodamage to the reaction centers resulting from overexposure to supraoptimal irradiance. The passage of clouds across the sky is slow enough to permit changes in the effective cross sections of the photosynthetic apparatus, leading to a change in fluorescence yields. This phenomenon is readily observed in stimulated fluorescence profiles or time series made under partially cloudy conditions (e.g., Abbott et al., 1982; Stramska and Dickey, 1992a, 1998). Under high irradiance levels, a fraction of the photochemical reaction centers can become “irreversibly” damaged; repair is accomplished by *de novo* protein synthesis. The damaged reaction centers act as nonphotochemical fluorescent quenchers, but recovery occurs on time scales of hours. Depending on the availability of nutrients (which are essential for protein synthesis), total repair is usually achieved overnight.

Physical turbulence is a primary mechanism responsible for bringing nutrients into the euphotic zone. Under nutrient-replete conditions, the maximum change in variable fluorescence is remarkably constant for a wide number of phytoplankton taxa (Kolber et al., 1988). As cells become nutrient limited, however, the quantum yields decline. Transects of variable fluorescence signals show large-scale variations in fluorescence yields that correspond to changes in water mass characteristics, especially to nutrient supply. Thus, as physical fronts or eddies develop, the associated changes in nutrient supply are manifested in photochemical energy conversion efficiency. The sensitivity and precision of variable fluorescence measurements can be used to infer mesoscale physical–biological interactions in real-time as well as from moored instrumentation.

The diel cycle is critically important as an evolutionary selection process in both phytoplankton and zooplankton in the context of vertical migrations. Because solar energy inputs are required for photosynthesis, yet lead simultaneously to stratification,