When and how does photoinhibition matter for plant fitness?

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Abstract

The many biophysical factors that shape how plant species sort across environmental gradients may include photoinhibition, which I define broadly as oxidative damage that plants and other phototrophs risk incurring when they absorb excess light energy they cannot safely dissipate. Photoinhibition is seldom explicitly discussed as a potential driver of plant fitness and distributions. Here, I aim to show that it can be one by drawing on studies showing that natural gradients or experimental manipulations that increase the risk of photoinhibition thereby decrease plant fitness, or favor species with stronger photoprotective adaptations. A corollary is that alleviation of photoinhibition may be a common mechanism of facilitation. A large share of this research is set in stressful environments like alpine treelines or drylands, most likely because photoinhibition is most detrimental in the presence of other interacting stress factors. Nevertheless, knowing the specific role of photoinhibition may have practical value—for example, in understanding the uses of shading treatments in ecological restoration.

Much research assumes that photoinhibition alters fitness by reducing carbon assimilation. Nevertheless, a tension exists in ecological literature on photoinhibition: many kinds of stressful conditions that threaten oxidative damage to photosynthesis also directly constrain tissue expansion. If carbon sink strength declines more than source strength—as it often does—a carbon surplus may result and lead to feedback inhibition of photosynthesis. Under persistent carbon surplus, photoinhibition’s potential influence on carbon status may not matter much for fitness. This fact might be reconciled with photoinhibition’s known effects on plant fitness by considering its other consequences. Oxidative damage can have consequences far beyond photosynthesis—altering membranes, blocking phloem loading, and even triggering cell death. While such effects are harder to measure than photosynthesis, doing so may enrich our understanding of photoinhibition’s ecological consequences.

Keywords: fitness; photoinhibition; photoprotection; photosynthesis; reactive oxygen species (ROS); sink limitation

Introduction

The patterns of plant population and community ecology emerge from a few high-level processes, among which the best studied is ecological selection caused by variation in fitness across environmental gradients (Vellend 2016). One goal of plant ecophysiology is to explain how such variation emerges from the vast diversity of plant function at the level of tissues and cells. This knowledge is essential for predicting how global change will affect plant populations (Cabal et al. 2022).

Among the countless biophysical forces that may alter plant fitness, photoinhibition is among the most enigmatic. Here, I define photoinhibition as damage caused by non-thermal energetic consequences of light absorption. Kok (1956) provided some of the first evidence of photoinhibition by showing that algal cultures had lower photosynthesis after exposure to intense light. The study of photoinhibition gained momentum in the 1980s as researchers learned more about the structure and function of Photosystem II (PSII), whose D1 protein is particularly susceptible to inactivation by light (Anderson et al. 1998). Also around this time, the advent of tools like chlorophyll fluorescence made it easy to measure PSII efficiency. Light-induced damage is usually considered as a result of photosynthetically active radiation (PAR; 400-700 nm), although much of the ultraviolet (UV) range can also cause it (Takahashi et al. 2010). UV-B can also increase mutation rates by creating pyrimidine dimers in DNA (Schoen & Schultz 2019), which may also alter fitness in a way that is hard to extricate from effects on PSII, except perhaps by selectively filtering parts of the light spectrum (Lesser 1996; van de Poll et al. 2001).

Both PSII and Photosystem I (PSI) are susceptible to photoinhibition. Indeed, PSI damage can be more severe because it is harder to reverse, but it is also much rarer (Sonoike 2011), so lasting photoinhibition is most often taken to occur when the rate of PSII damage exceeds the rate of repair through D1 replacement (Long et al. 1994). This situation may occur when photosynthetic pigments absorb light energy in excess of the plant’s ability to dissipate it safely through either photochemical or non-photochemical quenching (e.g. through the xanthophyll cycle; Demmig-Adams et al. 1996). Because stresses like low temperatures or drought reduce photosynthesis, they increase the share of light in excess and exacerbate photoinhibition. The predominant mechanism(s) of this effect are still debated. Excitation energy transfer and electron transport generate reactive oxygen species (ROS) at both PSI and PSII. Damage to PSII may occur at either its acceptor or its donor side (Pospíšil 2016; Kale et al. 2017). Under an 'acceptor-side' mechanism, ROS are generated and cause D1 inactivation in proportion to the amount of excess light (Vass 2011). Under a 'donor-side' mechanism, D1 inactivation occurs in proportion to the *total* amount of light absorbed (Tyystjärvi & Aro 1996), but ROS generated by excess light inhibit D1 replacement (Takahashi & Murata 2008). Acceptor- and donor-side mechanisms produce different kinds of ROS, and perhaps at different levels depending on the quantity and spectrum of light and the degree of interacting stresses (Hakala et al. 2005; Pospíšil 2016), which may cause them to have different ecological consequences.

In defining photoinhibition as involving 'damage,' I distinguish it from biochemical mechanisms of photoprotection that protect against damage that is longer lasting and more costly to reverse. The line between sustained biochemical photoprotection and damage is blurry, since it is often ambiguous whether a given molecular process that indicates reduced electron transport function (like declines in functioning D1) is, within a certain environmental context, best interpreted as a result of photoinhibitory damage or as an adaptive mechanism that *averts* more severe consequences (Adams et al. 2013; Tikkanen et al. 2014; Malnoë 2018). Beyond just the biochemical scale, photoprotective mechanisms are incredibly diverse, including: positioning of leaves to reduce light absorption, reflective leaf structures, chloroplast movement, light-screening pigments like flavonoids and anthocyanins, reductions in chlorophyll antenna size, non-photochemical quenching (NPQ) by pigments, and ROS scavenging by antioxidants (Raven 2011; D'Alessandro 2020). Many of these mechanisms have known trade-offs; for example, all plants grow in environments where light fluctuates on some time-scale, but declines in light absorption or induction of NPQ under high light can reduce photosynthesis when light declines (Raven 2011; De Souza et al. 2022). Plants might thus be expected to evolve towards an optimal level of photoprotection for their growth environment.

Although the mechanisms of photoinhibition and photoprotection have become clearer through time, their relevance for ecology remains obscure. Here, I aim to describe what we know about photoinhibition's effects on fitness and to re-evaluate this knowledge in the context of our changing understanding of whole-plant function. I focus on land plants, although at times I draw examples from other photosynthetic organisms.

Can excess light reduce fitness?

Here, I try to establish that photoinhibition can damage plant fitness. For multiple reasons, I propose to avoid using biochemical or physiological indicators alone to infer that photoinhibition has ecological consequences. The first reason is the aforementioned ambiguity about when such indicators are best interpreted as photoinhibition or photoprotection. The second is that photosynthetic efficiency—as estimated by fluorescence-based measures like (dark- or light-acclimated) F_v/F_m—is not the same as photosynthesis. Given that light is not just a stressor but also an essential resource, an increase in light very often causes both a decline in photosynthetic efficiency and an increase in photosynthesis, and at high light photosynthesis is usually limited by RuBisCO kinetics rather than electron transport. The third reason is that photosynthetic carbon fixation is not always limiting for fitness—a point to which I return later.

So how can we show that photoinhibition does (or doesn't) matter? I focus on evidence about how excess light affects plant fitness and its consequences, like species distributions, drawing on physiological evidence only in a supporting role (Fig. 1). Such evidence would imply that fitness declines as incident light increases, all else held equal. This stipulation that all else be held equal is hard to meet exactly, since gradients of light (artificial or natural) are often confounded with factors like air temperature and humidity (Niinemets & Valladares 2004). While these other factors should be controlled as well as possible, experiments need not be done in the complete absence of other abiotic stresses. Indeed, most abiotic stresses are only dangerous in combination (Mittler 2006; Zandalinas et al. 2021). What *is* important is that the severity of other stresses stay relatively constant across light environments.

First, I note that if photoinhibition posed no threat, it would be hard to explain the ubiquity of photoprotective pathways like the xanthophyll cycle(s) (Esteban et al. 2009; Goss & Lepetit 2015). Likewise, many lineages have putative light avoidance 'behaviors' like chloroplast movement in plants (Howard et al. 2020) and whole organismal movement in phytoplankton (Raven 2011). Species found in bright environments are often better at avoiding or recovering from photoinhibition (Montgomery et al. 2008; Kothari et al. 2021; Fig. 1A). This pattern holds even when the plants are grown in common garden-like environments, which implies that it is not just an outcome of plasticity. Indeed, organisms in extremely bright, hot environments often have extraordinary mechanisms to avoid and dissipate excess light (Levin et al. 2021). It would require formal evidence synthesis to tell whether such patterns are truly consistent—but if so, it would imply that photoprotection is important for maintaining fitness under high light.

Another form of evidence comes from experiments that grow plants across light environments and show that high light causes declines in fitness (Fig. 1B). Researchers have long described how high light can suppress population growth in phytoplankton (Edwards et al. 2015; Croteau et al. 2022), and these experiments generally raise fewer concerns about confounding between light and other stress factors. Another simplified setting for detecting the influence of photoinhibition is with photoprotection-deficient mutants of species like *Arabidopsis*. Under natural conditions, mutants deficient in NPQ produce fewer seeds (Külheim et al. 2002) and mutants deficient in chloroplast movement grow less (Howard et al. 2020).

Interpretation can get more complicated among land plants in more natural settings. Appendix S1 summarizes many case studies that provide plausible evidence that increases in light can reduce growth or fitness. Many of these studies monitored the microclimate to test whether their treatments allowed them to isolate the effect of light. For example, as part of a much broader study of treelines (see also Germino & Smith 1999), Germino et al. (2002) found that survival in alpine spruce seedlings was halved when overtopping grasses were removed, even though the removal treatment reduced water and low-temperature stress. Velasco & Becerra (2020) found that artificial shading had a much more beneficial effect than irrigation on tree seedling survival in a semiarid grassland, which suggests that the effect of shading was not due to water status. Bader et al. (2006) used a series of shading and neighbor removal treatments to show that high light could account for much of the failure of trees to establish beyond a tropical alpine treeline. Many of the case studies summarized in Appendix S1 took place in typically 'stressful' settings like alpine treelines and drylands, where interacting stresses like low temperature or drought may make it more plausible that photoinhibition matters. Most studies on trees were also conducted using seedlings; this may be partly a matter of convenience, but it may also reflect a concern that early recruitment is an important stage where trees are particularly vulnerable to photoinhibition (Germino et al. 2002; Slot et al. 2005).

A corollary to the apparent importance of photoinhibition is that shading may be a common mechanism of facilitation. This point is again clear in phytoplankton, among which theoretical (Gerla et al. 2011) and empirical (Veraart et al. 2012; Faassen et al. 2015) research suggests that intraspecific facilitative amelioration of photoinhibition cause Allee effects. In trees, Kothari et al. (2021) found that interspecific facilitation of shade-tolerant species by larger neighbors contributed to whole-community overyielding. The importance of facilitation between adults and seedlings is also implicit in much of the research on recruitment at treelines or in canopy gaps (Ball et al. 1991; Egerton et al. 2000; Slot et al. 2005). In the context of facilitation research guided by the stress-gradient hypothesis (Bertness & Callaway 1994), amelioration of photoinhibition may be one of many mechanisms through which nurse plants aid their beneficiaries in stressful environments (Cabal et al. 2022).

Understanding that photoinhibition can reduce fitness can also help us make sense of the efficacy of certain ecological interventions. For example, reforestation experiments often find that experimental shading increases survival (Egerton et al. 2000; Velasco & Becerra 2020). While high light is usually most harmful in combination with other stresses like drought, it may be less expensive to reduce the intensity of light than to alleviate those other stresses.

A whole-plant perspective on photoinhibition

So far, I claim there is evidence that photoinhibition can harm plant fitness. Given that photoinhibition involves damage to thylakoid membrane complexes, many studies of photoinhibition implicitly assume that its main cost to fitness is to reduce photosynthesis. Indeed, most attempts at quantifying the costs of photoinhibition focus on energetic or other resource-related costs, both of foregone photosynthesis and of protein repair (Long et al. 1994; Raven 2011; Murchie & Niyogi 2011).

But is this assumption true? The answer depends on how carbon-limited fitness is. In our high-[CO_2] world, plant growth under moderate stress is often regulated less by carbon assimilation than by direct constraints on tissue expansion or carbon export from leaves (Cabon et al. 2022; Fig. 2). In other words, plants are often sink-limited, particularly under many of the conditions that promote photoinhibition: the intersection of high light with drought, nutrient limitation, or cold temperatures (Körner 2003). The result often manifests as a buildup of non-structural carbohydrates (NSCs) in tissues (Körner 2003). Such NSCs in apparent excess could still be useful as osmolytes that promote drought tolerance, or as insurance against future disturbance (Sala et al. 2012). Nevertheless, when plant fitness is not carbon-limited, the apparent importance of photoinhibition and photoprotection becomes a puzzle (Slot et al. 2005).

These considerations led Adams et al. (2013) to propose that photoinhibition is primarily a *consequence* of growth limitation, not a cause. Accumulation of NSCs causes plants to reorganize their metabolism to downregulate photosynthesis and promote sink activity (White et al. 2016; Fig. 2). Experimental stimulation of source activity or blockage of sink activity can cause many of the physiological hallmarks of photoinhibition, including declines in dark F_v/F_m and D1 activity (Adams et al. 2013). Many plants acclimate by upregulating photoprotective mechanisms (e.g. NPQ) enough to balance the decline in photochemical quenching, allowing them to avoid damage. Without taking a position on the prevalence of source- vs. sink-limitation under photoinhibitory conditions, I think this challenge should occasion a reconsideration of *how* photoinhibition matters for plant fitness.

On its own, this account lacks an explanation for how photoinhibition could be harmful for fitness. Ecophysiologists often refer to the easily measurable consequences of excess light-induced ROS generation in reducing photosynthetic function, but it may help to look toward other aspects of cellular function. In particular, molecular physiologists have mapped out a much wider range of consequences of excess light-induced ROS generation (D'Alessandro et al. 2020)—but primarily in a few model organisms and without having yet demonstrated their importance in nature.

It may be time for a synthesis: Could excess light-induced ROS generation have an ecological role in natural settings beyond its influence on carbon assimilation via electron transport? The species and quantity of ROS produced are dependent on the mechanism (acceptor-side, donor-side, or other) and intensity of photoinhibition. ROS species differ in their lifetimes, reactivities, and ability to cross membranes (Møller et al. 2007; Mittler 2017). In general, though, ROS like singlet oxygen produced along the electron transport chain can attack the unsaturated lipids in the thylakoid and produce lipid peroxides (Demmig-Adams et al. 2014; D'Alessandro et al. 2020). These in turn can break into reactive carbonyl species (RCS), which through their role as signaling molecules and their toxicity can—in sufficient quantities—damage other components and trigger pathways towards cell death (Møller et al.

2007; Chan et al. 2012; D’Alessandro et al. 2020). Even before this point, the signaling functions of ROS can also trigger other processes beyond the chloroplast, like callose deposition in phloem-loading complexes, which may serve to block the spread of pathogens (when present) but hinders the export of sugars and other compounds from leaves (Demmig-Adams et al. 2014).

Under certain circumstances, these consequences may be much more relevant than reductions in carbon assimilation. For example, although most research on PSII inhibition’s influence on mortality in seagrasses and algae focuses on the potential for carbon starvation, oxidative damage appears to be a stronger driver (King et al. 2021). Prescott et al. (2020) even suggest that sink-limited plants may dispose of surplus carbon to avoid feedback inhibition of photosynthesis and the resulting risk of photoinhibition—a proposal that could only make sense if photoinhibition does more than just reduce carbon assimilation.

Whether any of these adverse consequences occurs depends on the quantity of the potentially harmful molecules and on plants’ ability to contain them. Within a certain range, ROS and lipid peroxides are essential as redox signals that coordinate development, signaling, and acclimation to stressful conditions, including by upregulating photoprotection (Mittler 2006; Foyer 2018). The danger may come when plants are unable to stop runaway spirals of ROS production. For example, if unrepaired damage to photosynthetic machinery limits plants’ ability to dissipate light photochemically, the amount of light in excess may increase, which could increase ROS production and perhaps create a vicious cycle in which photoinhibition begets more photoinhibition. This possibility is implied by findings that PSII-inhibiting herbicides can, depending on their mechanism, steeply enhance ROS production (Fufezan et al. 2002; Chen et al. 2010). ROS and RCS may also attack and inactivate the enzymes that scavenge and detoxify them (D’Alessandro et al. 2020). Plants adapted to bright or fluctuating light conditions often have a strong capacity to acclimate and keep ROS within a safe range through protective mechanisms like NPQ or ROS scavenging, but plants adapted to shade may have more limited capacity (Fig. 2). Interacting stresses may also limit plants' abilities to keep ROS within a safe range. These phenomena may explain observations of photooxidative bleaching (Powles 1984) or leaf abscission (Egerton et al. 2000) under high light. Hence, it seems inapt to reach the Panglossian conclusion that ROS generation is always helpful or benign, or that symptoms like PSII inhibition are always protective rather than an indication of damage to fitness. Some researchers have suggested that photoinhibition may only be important in 'unrealistic' circumstances, as when plants are outside of their usual environmental niche (Adams et al. 2013). But this is no reason to dismiss its importance: part of the business of community ecology is to explain why plants don't grow where they don't grow.

One specific situation in which photoinhibition may reduce fitness other than through energetic costs is during senescence in winter- (and perhaps drought-) deciduous plants. Efficient nutrient resorption during senescence is critical for growth in the following year (El Zein et al. 2011) and consequently for fitness (May & Killingbeck 1992). Senescing leaves are highly vulnerable to light-induced damage (Kar et al. 1993; Merzlyak & Hendry 1994), and the reddish anthocyanins many species produce in the fall may serve to improve foliar nutrient resorption through photoprotection (Hoch et al. 2003; Renner & Zohner 2019). While failures of nutrient resorption could result from photoinhibitory carbon depletion (Hoch et al. 2001), they might also result from oxidative damage to proteins involved in breaking down nutrient-containing molecules, or from callose-induced blockage of phloem loading.

I close with some ideas for ecologists to explore the potential consequences of photoinhibition more fully. To establish whether photoinhibition matters at all for fitness, it is important to measure growth or demography rather than relying solely on physiological indicators. To establish whether photoinhibitory conditions deplete carbon reserves, it could help to measure NSCs (Slot et al. 2005), although this approach is best treated just as a heuristic (Weber et al. 2019). In general, photosynthetic and chlorophyll fluorescence indicators may be useful but should be chosen and interpreted with care. A particular parameter that may be useful for studying oxidative damage is the fraction of light not dissipated through either photochemistry or NPQ (sometimes denoted Φ_{NO}; Demmig-Adams et al. 1996; Kramer et al. 2004) may help indicate the potential for ROS generation (Fig. 2). Studying oxidative damage at the molecular level is tricky under field conditions, but lipid peroxidation may be a good candidate for measurement using the relatively simple TBARS assay (Hodges et al. 1999). Given the clear evidence that human activity is altering global light regimes (Norris et al. 2016; Lu et al. 2017), it is important to understand when and how photoinhibition matters—not just in the leaf, but across the whole plant.

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Author Contributions

Shan Kothari is the sole author of this paper.

Data Availability Statement

This is a synthesis article and contains no data.

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Figures

Figure 1: Two potential approaches to test the importance of photoinhibition and photoprotective adaptations for fitness. These approaches are respectively analogous to the ‘likelihood’ and ‘vital rates’ approaches described in a much more general context in Laughlin & Messier (2015). Here, we consider two species (i and ii). I depict species (i) with more yellowish leaves and steeper leaf angles to imply stronger photoprotective adaptations—high NPQ by carotenoids and light avoidance at midday, respectively. For simplicity, I assume these traits are not plastic. In reality, photoprotection can include an immense variety of mechanisms with no obvious common currency to summarize a plant’s total photoprotective capacity.

(A) One way to test the importance of photoinhibition is to observe whether photoprotective traits are correlated consistently with environmental gradients in the risk of photoprotection. Here, as light increases, species (i) comprises a greater fraction of community composition. As with all observational data, causal inference may be hard and interpretation requires special care to rule out competing explanations. For example, species (i) may be absent under high light due to environmental filtering caused by photoinhibition or other abiotic stresses, because it is outcompeted there by species (ii), or a combination. Nevertheless, if sites with higher light consistently have species with greater constitutive expression of photoprotective adaptations, it would imply that there is ecological selection for those adaptations. A more rigorous test might involve determining whether including photoprotective traits improves predictive models of community assembly (Laughlin & Messier 2015).

(B) Another way to test the importance of photoinhibition is to monitor vital rates across natural or (ideally) experimental gradients of light. Here, we see that species (i) has its greatest growth rates at high light, while species (ii)’s growth is reduced at high light levels. Dashed lines separate the individuals in each treatment to clarify that they are not directly interacting. This kind of experiment can be done with a single species/genotype or with multiple; in the latter case, researchers can test whether plants that are more shade-tolerant (and high light-intolerant) have fitness optima at lower light levels.

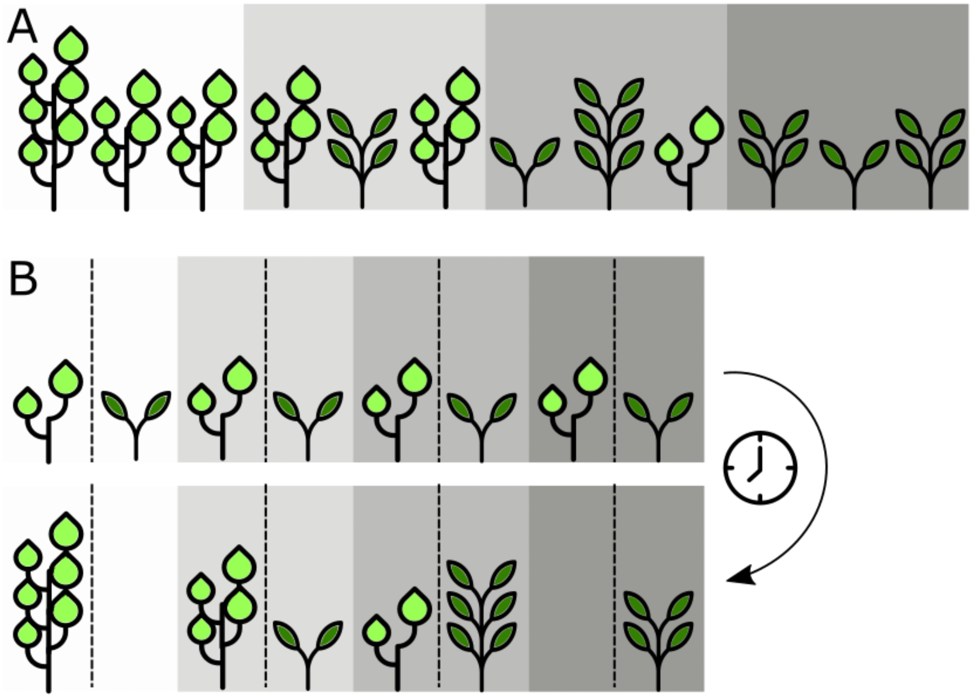
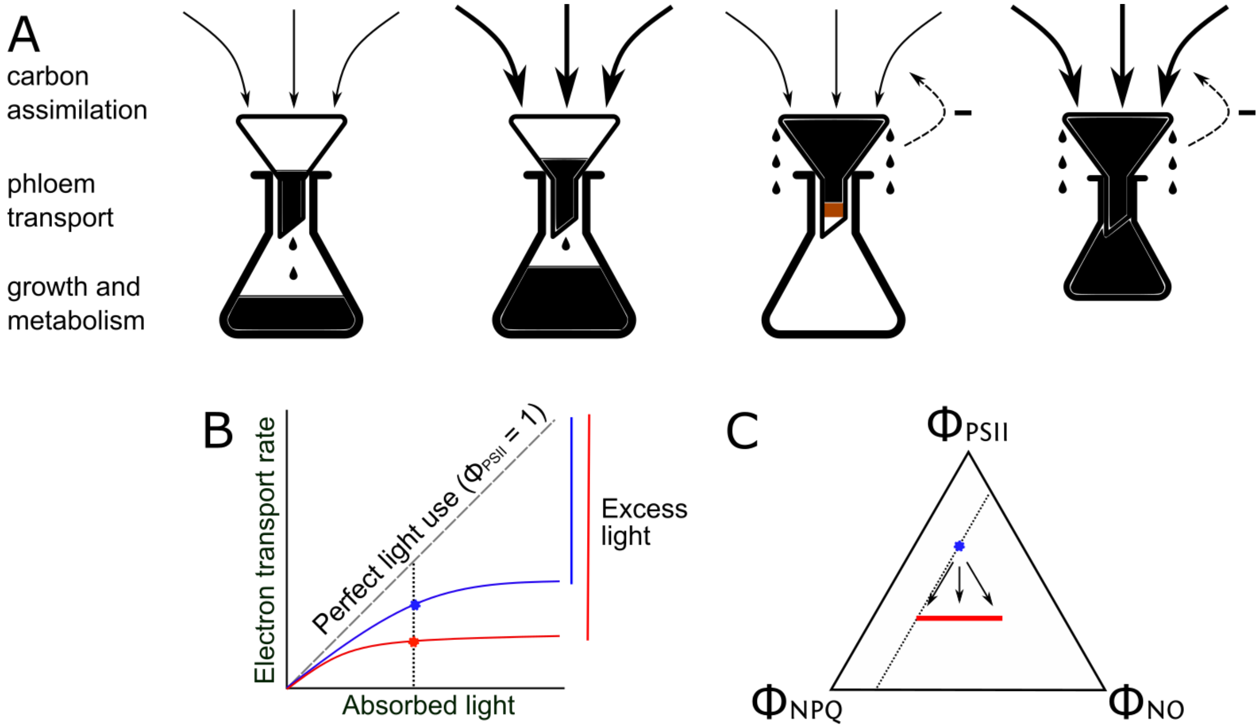

A
B

Figure 2: (A) As a rough analogy, the balance between carbon sources and sinks may be described as liquid being poured (photosynthesis) into a funnel (phloem transport) draining into a flask (carbon sinks). Here, the carbon that flows into the flask is available for metabolism and growth at the meristems, and in reality would be steadily consumed. When the funnel's spout is stopped (as when phloem transport is blocked) or when the flask is small (limited sink capacity), carbon can build up in the source tissues. Often, this buildup causes feedback inhibition of photosynthesis (dashed arrows), reducing the rate of inflow. This representation is inspired by Adams et al. (2013). (B) Feedback inhibition or more direct constraints on light use (e.g. low temperature) can reduce the electron transport rate at a given light level (red) compared to a healthy plant under conditions conducive to growth (blue). As a result, the fraction of absorbed light that is used to power electron transport (Φ_{PSII}) declines and a greater fraction of light is in excess. (C) Absorbed light energy can be partitioned into three quantum yields—Φ_{PSII}, Φ_{NPQ}, and Φ_{NO}. Φ_{NPQ} is the fraction of light dissipated through NPQ, while Φ_{NO} is the fraction that undergoes non-regulated dissipation—including through pathways that produce ROS. Under internal or external constraints to electron transport, Φ_{PSII} declines, but the share of consequent increase in Φ_{NPQ} vs. Φ_{NO} depends on how much the plant can induce NPQ, allowing a range of scenarios (red line). Plants with limited capacity for NPQ may have elevated ROS production.


A
carbon assimilation
phloem transport
growth and metabolism
-
-
B
Electron transport rate
Perfect light use (Φ_PSII = 1)
Excess light
Absorbed light
C
ΦPSII
ΦNPQ
ΦNO

Appendix S1

Table S1: A brief summary of studies that might be taken as evidence that photoinhibition due to excess light can have negative effects on plant fitness. These studies all report declines in some fitness-related variable (survival, growth, or reproductive output) in conditions with high light. I include some studies that report only distributions of existing individuals if there is a strong case that absences are due to mortality rather than other factors like dispersal limitation. In general, I omit studies that only compare fitness in across coarse natural gradients (e.g. understory vs. gaps) because such gradients often include changes in multiple environmental variables and cannot be used to isolate the importance of photoinhibition. However, I include a few examples where such contrasts are accompanied by physiological and/or microclimatic measurements that allow a more convincing attribution of fitness gradients to the effects of light. This table should not be mistaken for a rigorous, formal evidence synthesis, since I did not use a well-defined search procedure and I only summarize studies that appear to show some positive evidence that photoinhibition can affect fitness. Nevertheless, I hope that they convince the reader of the possibility that excess light can damage fitness.

Citation	Species	Ecosystem or setting	Treatment	Physiological response	Fitness response	Notes
Agyeman et al. 2003	Seedlings of 16 west African tree species	Shadehouses in Ghana	Trees were grown in one of six shadehouses with varying degrees of shade.	None reported	In many (but not all) species, whole-plant relative growth rate was highest at irradiances below the maximum growth irradiance. Shade-tolerant species showed the greatest inhibition of growth at high irradiance.	More severe shading treatments tended to reduce maximum air temperature and slightly increased relative humidity.
Akhalkatsi et al. 2006	*Betula litwinowii* seedlings	Alpine treelines in the country of Georgia	The number of seedlings was surveyed across a number of plots within sites that varied in slope, aspect, elevation, and overstory cover of *B. litwinowii* or the shrub *Rhododendron caucasium*	Seedlings in sun-exposed microsites had more red anthocyanic leaves.	More sheltered microsites beneath shrub or tree cover, or on the north-facing walls of soil depressions, had greater *B. litwinowii* seedling abundance.	The sheltered sites with greater seedling abundance had lower air and soil temperatures than more exposed sites.
Bader et al. 2006	Seedlings of six (in the observational component)	Alpine treelines in northern Ecuador	The number of sprouts was surveyed along transects that crossed the treeline from the	None reported	Out of the six species in the observational survey, four were almost completely absent beyond the treeline but the	Microclimatic monitoring revealed that the forest buffered temperature extremes, but the four páramo treatments were

	or eight (in the experimental component) tree species		cloud forest into the páramo. In addition, some seedlings were experimentally transplanted into either the forest or the páramo, and the latter were subjected to shading by shadecloth, clearing of neighbors, or both treatments		other two showed dramatic increases in abundance. In the experimental component, survival was greatest in the forest, then in the páramo under shadecloth, then in páramo controls. Clearing of neighbors also had a negative effect on survival.	similar. However, cleared and unshaded plots did have higher soil temperature and apparently lower soil moisture. The authors note several additional observations that suggest a role for photoinhibition. For example, the species that survive best in the páramo appear to have photoprotective adaptations like reflective leaves or specialized pigments. Also, in many species the light-exposed parts of the leaves were the only ones to show apparent damage.
Ball et al. 1991	*Eucalyptus pauciflora* seedlings	Alpine treelines in southeastern Australia	Plants were naturally growing on slopes in aspects either more protected or more exposed to sunlight during the winter; for physiological measurements, some trees were also shaded artificially	Trees on exposed sites had lower rates of photosynthesis under light-limited conditions, but not under high light.	Juvenile trees tended to be distributed close to the canopy margin and along an arc to the better-protected south of the canopy. Juvenile trees in exposed areas were often stunted.	
Ballestreri et al. 2021	Four subdominant or understory tree species	Restoration experiment in the Atlantic Forest of southern Brazil	Trees were grown in the varying degrees of shade provided by one of four overstory tree species	Deeper shading caused increases in chlorophyll content and dark-acclimated F_v/F_m, and decreases in stomatal density. All species appeared to show greater photosynthetic capacity under deeper shade.	One species (*Eugenia involucrata*) had a major increase in mortality under the greatest light level. Many species showed greatest growth in height or stem diameter under partial shade.	Because the treatment here involves interactions with neighbors, the outcome may result not just from shading but also from other sorts of mechanisms of interactions among neighboring plants.
Close et al. 2002	*Eucalyptus nitens* and *Eucalyptus globulus* seedlings	Alpine treelines in Tasmania, Australia	Plants were either left exposed or surrounded with open-top shadecloth shelters for the first fourteen weeks after planting	Unshaded *E. globulus* developed high leaf anthocyanin content, as well as severe leaf abscission and severe but transient declines in dark-acclimated F_v/F_m. Unshaded *E. nitens* had the same responses, but much more moderate. Shaded trees showed slight increases in anthocyanins and declines in dark-acclimated	Unshaded *E. globulus* suffered severe leaf abscission and had high mortality and reduced height growth compared to shaded *E. globulus*. However, unshaded *E. nitens* had much more modest levels of abscission and greater height growth than shaded *E. nitens*.	The researchers measured air temperature and light quality and found that the shelters had minimal effects on both.

				Fv/Fm after the shadecloth was removed.		
del Valle et al. 2020	*Silene littorea*	Greenhouse and experimental garden in Mediterranean southern Spain	Plants were grown either under a methacrylate filter that transmitted most UV or a polycarbonate filter that excluded most UV.	Plants under UV exclusion produced less anthocyanins and phenolics. They also had greater midday F_v/F_m, but the similar pre-dawn F_v/F_m.	Plants under UV exclusion had the same ovule and seed production per flower, but considerably lower pollen production and seed set.	
Egerton et al. 2000	*Eucalyptus pauciflora* seedlings	Treeless pasture in southeastern Australia	Plants were grown on either the exposed or sheltered sides of vertical screens that intercepted half of incoming light	Trees on the exposed side of the screens had lower dark-acclimated and midday F_v/F_m and lowered photosynthetic light-response curves. These trees also lost much of their leaf area to abscission during the winter.	Exposed trees had lower shoot and total biomass after the winter.	The researchers measured air temperature and soil moisture. They found that the shelters had no significant influence on air temperature, but caused a small increase of soil moisture on the exposed side.
Gatti et al. 2014	Saplings of the palm *Euterpe edulis*	Shadehouse and various sites in subtropical northern Argentina	Plants were grown in either high or low light in shadehouses or in natural canopy understories/gaps	Seedlings grown under higher irradiance had a smaller relative decline in F_v/F_m and faster recovery. High growth irradiance did not affect stem water potential but did cause substantial decreases in leaf water potential and increases in plant Huber value.	In the shadehouse, relatively high irradiance treatments are associated with somewhat lower growth and irradiance. In natural gaps, survival was much lower but growth was much higher than in understories.	In this study, the subtle but perhaps important influence of the treatments on water relations makes it hard to uniquely pinpoint an effect of photoinhibition, since high mortality at high irradiance could have been exacerbated by water deficits.
Germino & Smith 1999	*Picea engelmannii* and *Abies lasiocarpa* seedlings	Alpine treelines in Wyoming, United States	The position of plants was surveyed along four distinct transects. For physiological measurements, some potted plants were also experimentally subjected to nighttime warming (transparent plastic sheets), daytime	Potted *A. lasiocarpa* seedlings subjected to daytime shading had higher saturated photosynthetic rates than unshaded seedlings, both comparing shading to control and shading + warming to just warming. There was no major effect in *P. engelmannii*. Among natural seedlings, those	Both species were almost entirely found in the one transect with high tree cover. *A. lasiocarpa* in particular was largely missing from highly open microsites.	The authors measured light spectral quality and found that it was unaffected by the treatments.

			shading, or both	in exposed environments had more inclined and clustered needles.		
Germino et al. 2002	*Picea engelmannii* and *Abies lasiocarpa* seedlings	Alpine treelines in Wyoming, United States	Naturally occurring seedlings were surveyed repeatedly for survival as a function of factors that influence their exposure to stress. For some naturally occuring seedlings, neighboring grasses were removed. Some seedlings were also artifically sown among several sites with varying exposure to high light and other potential stress factors.	None reported	*P. engelmannii* seedlings (but not saplings or emergents) had greater survival close to the cover of the tree island. *P. engelmannii* emergents had greater mortality on more exposed south and east-facing slopes. In general, survival was greater when there were features upwind or overhead, or when trees were surrounded by moss or overtopped by grass.	Removal of neighbors alleviated water and low temperature stress but still increased mortality, which the authors attribute to photoinhibition due to increased light. Seedlings with removed neighbors also experienced greater wind speeds.
Gómez-Aparicio et al. 2006	Two evergreen and two deciduous late-successional tree species	Montane botanical garden in Mediterranean southeastern Spain	Plants were growing in pots either under full sunlight or under mild or severe shading treatments imposed by shadecloth.	Under shade, all species increased chlorophyll content and decreased carotenoid content. Shade also caused increases in F_v/F_m throughout the day, including before dawn. The two deciduous species had lowered photosynthetic light-response curves under high light, while the two evergreen species showed the opposite pattern. The authors report many other changes in plant allocation and physiology that are less relevant here.	One deciduous species (*Acer opalus*) experienced a very high rate of mortality at full sunlight, which was reduced by two-thirds under even a moderate shading treatment. No other species experienced negative survival or growth (total dry mass) consequences from high light.	Soil moisture was held constant across treatments. The moderate shade treatment had no major effect on air temperature, but the more intense shade treatment tended to reduce temperature substantially.

Holly et al. 1994	*Eucalyptus polyanthemos* seedlings	Treeless pasture in southeastern Australia	Plants were either grown in the open or in a series of shelters that excluded various fractions of incident light	Trees had the highest pre-dawn F_v/F_m under 50% or 30% of natural light, both in midwinter and in spring.	Trees showed the greatest stem elongation under 50% or 30% of natural light.	The researchers measured humidity, air temperature, and wind speed. While they found that while most shelter designs had minimal effects on humidity and temperature, shelters reduced wind speed in proportion to their shading intensity.
Howard et al. 2020	*Arabidopsis thaliana*—an NPQ-deficient mutant, a chloroplast movement-impaired mutant, three mutants deficient in chloroplast movement as well as other aspects of physiological function, and a wild-type	Growth chambers and an experimental garden in Massachusetts, United States	Plants were grown either outdoors or in a growth chamber with light fluctuating on an hour-long cycle	Under natural conditions, the chloroplast movement-impaired mutant had higher dark-acclimated F_v/F_m than the wild-type.	Under natural conditions, the chloroplast movement-impaired movement had smaller rosettes, smaller and fewer leaves, fewer siliques, fewer secondary inflorescences, and earlier bolting than the wild-type. The NPQ-deficient mutant was largely unaffected.	
Kothari et al. 2021	Eight temperate, winter-deciduous broadleaf tree species in the first eight years of growth	Densely planted tree diversity experiment in Minnesota, United States	Plants were grown either in monocultures, where they were generally unshaded, or in bicultures with faster-growing conifers that provided substantial shade	Plants grown in bicultures had substantially higher pre-dawn F_v/F_m and lower production of photoprotective pigments. The most shade-tolerant species had the greatest increase in pre-dawn F_v/F_m in biculture. At least in one species (*Tilia americana*), they also showed high photosynthetic rates under high light levels and delayed leaf senescence.	Two species (*T. americana* and *Acer negundo*) grew faster with larger neighbors; most of the others grew slower.	Because the treatment here involves interactions with neighbors, the outcome may result not just from shading but also from other sorts of mechanisms of interactions among neighboring plants. Trees under the shade of larger neighbors generally had more negative pre-dawn leaf water potential, but less negative midday water potential.

Külheim et al. 2002	*Arabidopsis thaliana*—two NPQ-deficient mutants and a wild-type	Growth chambers and an experimental garden in northern Sweden	Plants were grown in growth chambers with constant and fluctuating light conditions, as well as in the field.	The two mutants had lower midday F_v/F_m under field conditions, especially under high light.	In the field and under fluctuating light, the two mutants had fewer seeds and fruits per plant. Under constant light, there was no effect.	
Murray et al. 1993	Multiple species of *Sphagnum* mosses	Moist mountain slopes in northern Alaska	At one site, all shade-producing vascular plants were removed in several plots, which were compared to control plots. At another site without high vascular plant cover, shadecloth shelters were set up and compared to control plots. In addition, physiological measurements were taken in the laboratory from various Arctic and temperate mosses.	Mosses under high light had lower dark-acclimated F_v/F_m and lower photosynthetic capacity than those under lower light.	At both sites with shade experiments, mosses under shade (from shadecloth or vascular plants) had much greater growth in length.	Shaded treatments tended to have somewhat lower moss surface temperature.
Ronco 1970	*Picea engelmannii* seedlings	Nursery in the Central Rocky Mountains	Trees were grown in one of three shade treatments	Unshaded seedlings had much lower photosynthetic light-response curves than fully shaded seedlings. Unshaded and partially shaded seedlings had no major differences in their water deficit.	The paper relies on a 1961 research note by the same author, which is not widely available, to support the claim that light influences seedling survival. It reports that trees growing under full sun suffered from chlorosis and had greater mortality than those under partial shade. It also reports that drought, frost heaving, and herbivory are not major causes of mortality.	
Semchenko et al. 2012	46 herbaceous species from temperate grasslands	Common garden in Estonia	Plants were grown either in full sunlight or in three shading treatments of varying intensity	None reported	Moderate shade increased total plant biomass relative to full sunlight	The shading treatments moderately buffered air temperature and increased relative humidity, particularly the more intense ones. The authors attribute the positive effect of shade on growth to dynamic regulation of growth

						rather than amelioration of abiotic stress. However, it is unclear how this is possible, considering that plants cannot build tissue with material they have not acquired.
Slot et al. 2005	*Pinus sylvestris* juveniles	Glades with low tree density within forests in western Siberia	Plants were naturally growing on slopes in aspects either more protected or more exposed to sunlight during the winter. Some seedlings were also either left exposed or artifically shaded following removal of adult trees.	In the smaller size class across the growing season, more naturally exposed trees had lower pre-dawn and midday F_v/F_m and lower photosynthetic rates at equivalent light availability. These exposed small trees had greater non-photochemical quenching, xanthophyll pigment to chlorophyll ratios, and xanthophyll de-epoxidation state. Similar results held when comparing artificially exposed and shaded trees. The researchers found that more exposed and photoinhibited trees were not depleted in NSCs.	Seedlings recruited mainly within the crown projection area of adult trees, usually on the protected northern side.	Air temperature differed very little between the northern (protected) and southern (exposed) sides of adult trees, especially in autumn and winter. Southern trees had slightly less negative $\delta^{13}C$, which led the researchers to suggest tentatively that they may be more prone to desiccation. However, soil moisture content did not differ between northern and southern aspects during the summer.
van de Staaij et al. 1997	*Silene vulgaris*—a highland population adapted to higher UV-B, and a lowland population adapted to lower UV-B	Greenhouse in the Netherlands	Plants were grown in a greenhouse with either no additional UV-B, a low dose, or a high dose	None reported	The lowland population showed a large reduction in seed-producing flowers and seeds per plant under high UV, but the highland population showed an increase in seeds per plant under high UV. In each population, seed mass and germination were unaffected.	
Velasco & Becerra 2020	Seedlings of nine woody species	Pots in an open grassland in central Chile	Trees were grown together with one of eight different herb species (or control), under either shadecloth or control, and in either a wetter or drier simulated precipitation regime	None reported	The shade treatment had an overwhelmingly large positive impact on the recruitment (survival) of tree seedlings. Water and herb cover had much smaller effects.	

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