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 as oxidative damage that photosynthetic organisms 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. I draw 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. One implication 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—as, for example, in understanding the uses of shading treatments in ecological restoration.

Much research assumes that photoinhibition diminishes fitness by reducing photosynthesis and causing carbon depletion. Nevertheless, a tension exists in ecological literature on photoinhibition: many kinds of stressful conditions that threaten oxidative damage to photosynthesis also directly constrain the use of carbon for tissue expansion. As a result, conditions that cause photoinhibition may often cause carbon reserves to remain steady or even increase. This fact might be reconciled with photoinhibition's demonstrated influence on plant fitness by considering its other consequences. Oxidative damage can

have consequences far beyond photosynthesis—altering proteins and membranes, blocking phloem loading, and triggering cell death. While such effects are harder to measure in the field 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

One goal of plant ecophysiology is to explain how patterns of variation in fitness across environmental gradients emerge from the vast diversity of plant function at the level of tissues and cells. This knowledge is essential for predicting how plant communities will be reshaped by global change factors. Such factors include the quantity and quality of light, which is changing due to decadal trends in cloud cover (Norris et al. 2016) and aerosol emissions (Wild et al. 2009), and at smaller scales due to trends in forest overstory cover (Landuyt et al. 2019). These trends may alter plant fitness because light serves as both a resource essential for photosynthesis and a potential cause of stress due to photoinhibition.

Here, I define photoinhibition narrowly as damage caused by non-thermal energetic consequences of light absorption. Kok (1956) provided early 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 investigated the structure and function of Photosystem II (PSII), whose D1 protein is particularly susceptible to inactivation by light (Long et al. 1994). Around the same time, new tools like portable chlorophyll fluorometers made it easier to measure PSII efficiency (Schreiber et al. 1975). Photoinhibition is best studied as a result of oxidative damage from photosynthetically active radiation (PAR; 400-700 nm), although it can also be caused by much of the ultraviolet range (UV; Takahashi et al. 2010; Mattila et al. 2023). UV-B can also increase DNA mutation rates by creating pyrimidine dimers (Britt 2004). The effects of UV-related mutational load on fitness are variable (Llorens et al. 2015) and hard to extricate from light's effects on PSII, except perhaps by selectively filtering parts of the light spectrum (Lesser 1996; van de Poll et al. 2001).

In light-exposed leaves, reactive oxygen species (ROS) are produced mainly in chloroplasts and peroxisomes (Foyer & Noctor 2003). In chloroplasts, ROS like singlet oxygen ($^1O_2$) are generated during the transfer of excitation energy at both PSII and Photosystem I (PSI), rendering both susceptible to damage. Indeed, PSI damage is harder to reverse but also rarer (Sonoike 2011), so lasting photoinhibition is most often taken to occur when the rate of PSII damage exceeds the rate of repair (Long et al. 1994). This situation can occur when 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 & Adams 2006). There remains debate about the main mechanism(s) of this effect. In general, excess light causes the PSII plastoquinone pool to become overreduced, and the resulting limitation in electron transport increases the formation of excited triplet chlorophyll. Next, triplet chlorophyll can interact with O_2 to create $^1O_2$ (Mattila et al. 2023), which can either damage PSII (acceptor-side inhibition; Vass 2011) or inhibit repair of PSII that has been damaged directly by light (donor-side inhibition; Hakala et al. 2005; Takahashi & Murata 2008). Stresses like low temperatures or drought tend to exacerbate photoinhibition by reducing photochemical dissipation of light energy, perhaps among other mechanisms (Fig. 1; Hutchison et al. 2000; Takahashi & Murata 2008). Growing evidence suggests that multiple mechanisms contribute to PSII damage under natural conditions, with the balance determined by the amount and spectrum of light and by other environmental conditions like temperature (Kono et al. 2022; Mattila et al. 2023). Acceptor- and donor-side mechanisms often produce different ROS (Kale et al. 2017), which differ in their lifetime, reactivity, and ability to cross membranes (Møller et al. 2007; Mittler 2017). Whether their ecological consequences differ is largely unexplored.

In defining photoinhibition as involving 'damage,' I distinguish it from biochemical mechanisms of photoprotection that prevent damage, which would last longer and be more costly to reverse. The line between sustained biochemical photoprotection and damage is blurry, since it is often ambiguous whether an indicator of reduced electron transport function (like declines in functioning D1 protein) is best interpreted as a result of damage or an adaptive mechanism to *avert* more severe consequences when other factors constrain photochemical dissipation (Adams et al. 2013; Tikkanen et al. 2014). Beyond just the biochemical scale, photoprotective mechanisms include diverse ways to reduce light reaching the chloroplast, dissipate excess energy, or scavenge reactive species (Raven 2011; D'Alessandro 2020), but many of these mechanisms have known drawbacks. For example, all plants grow in environments where light fluctuates on some time-scale; but while reduced light absorption or non-photochemical quenching (NPQ) induction may be advantageous under high light, they may also 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 typical growth environment.

Although the mechanisms of photoinhibition and photoprotection have become clearer through time, their relevance for population and community ecology remains the subject of debate. Here, I aim to re-evaluate photoinhibition's influence on fitness 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.

Photoinhibition and source-sink interactions

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 harm of photoinhibition focus on estimating energetic or other resource-related costs of foregone photosynthesis and protein repair (Murchie & Niyogi 2011; Raven 2011), and using these estimates to project the loss in plant productivity or growth (Ögren & Sjöstrom 1990; Long et al. 1994; Werner et al. 2001; Burgess et al. 2015; Kothari et al. 2021).

But do these costs explain how photoinhibition may reduce fitness? 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. 1). In other words, plants are often sink-limited, particularly under many of the conditions that also cause photoinhibition: the combination of high light and moderate drought, nutrient limitation, or cold temperatures (Körner 2003; Muller et al. 2011). The result often manifests as a buildup of non-structural carbohydrates (NSCs) in tissues (Körner 2003). Elevated NSCs may be mobilized as osmolytes that promote drought tolerance, or as insurance against future disturbance, which are useful for long-term growth and survival (Sala et al. 2012). However, accumulation of NSCs (especially osmotically inactive ones like starch) suggests that carbon is at least not limiting in the short term.

Although studies of photoinhibition often estimate reductions in photosynthesis, they seldom measure NSC reserves. In those studies that have, hallmarks of photoinhibition are often accompanied by NSC accumulation rather than depletion, consistent with the idea that photoinhibitory conditions are often sink-limiting (Hogewoning & Harbinson 2007; Adams et al. 2013). If the consequences of photoinhibition are described mainly in terms of carbon limitation, in many cases it becomes a puzzle how it could influence fitness (Slot et al. 2005).

These considerations led Adams et al. (2013) to propose that photoinhibition is mainly 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. 1). Thus, 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 photoprotection (e.g. NPQ) enough to balance the decline in photochemical quenching, allowing them to avoid damage. Indeed, Adams et al. (2013) question "whether there is any situation in which photoinhibition could be construed as damage or could be limiting plant productivity"—except under conditions seldom found in nature. Without taking a position on the general prevalence of source- vs. sink-limitation, I argue that this challenge should cause us to reconsider *how* photoinhibition matters for plant fitness.

Can excess light reduce fitness?

Here, I try to establish that despite the challenge posed above, photoinhibition can reduce plant fitness. In doing so, I avoid using biochemical or physiological indicators alone. The first reason is the ambiguity about when such indicators are best interpreted as photoinhibition or photoprotection. The second is that many common indicators—including fluorescence-based measures like (dark- or light-acclimated) F_v/F_m—estimate the efficiency of electron transport, which is not the same as photosynthesis. Because light is both a stressor and an essential resource, an increase in light often causes both a decline in photosynthetic efficiency and an increase in actual photosynthesis. Furthermore, photosynthesis under high light is often limited by RuBisCO kinetics rather than electron transport. The third reason is that, as mentioned earlier, photosynthetic carbon fixation need not always be limiting for fitness.

So how can we show that photoinhibition does (or doesn't) matter? I focus on how excess light affects plant fitness (or proxies) and its consequences, like species distributions, drawing on physiological indicators only in a supporting role. The question is: all else held equal, does increasing available light beyond a certain point cause fitness to decline and/or favor species with stronger photoprotective adaptations (Fig. 2)? The 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, studies of light stress need not be done in the complete absence of other abiotic stresses. Indeed, most stresses are only harmful in combination (Mittler 2006; Zandalinas et al. 2021). What *is* important is that the severity of other stresses stays relatively constant across light environments.

From an evolutionary perspective, it would be hard to explain the ubiquity of photoprotective pathways like the xanthophyll cycle(s) if photoinhibition posed no potential threat (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 naturally found in bright environments are often better at avoiding or recovering from photoinhibition (Montgomery et al. 2008; Kothari et al. 2021; Fig. 2A). This pattern holds even in common garden-like environments, which implies that it is not just a result of plasticity. Indeed, organisms in extremely bright, hot environments often have extraordinary mechanisms to avoid and dissipate excess light (Levin et al. 2021). Mutants of species like *Arabidopsis* also provide a simple system for revealing the importance of photoprotection: 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). These findings imply that optimal allocation to photoprotection is important for maintaining fitness across light environments.

Other evidence comes from experiments that grow plants across light environments (Fig. 2B). Researchers have long described how high light can suppress population growth in phytoplankton (Edwards et al. 2015; Croteau et al. 2022). Among land plants, interpretation is often complicated due to potential confounding between light and other microclimatic factors. Appendix S1 summarizes more than 20 case studies that provide evidence that increases in light can reduce plant growth or fitness. Many of these studies implemented treatments to disentangle light from other factors and monitored the microclimate to confirm their effectiveness. For example, Bader et al. (2006) and Baumeister & Callaway (2006) each crossed shading with other treatments to show that high light could account for much of the failure of trees to establish beyond (respectively) tropical and temperate treelines. Elevated daytime leaf temperature may be among the factors most susceptible to confounding with high light since the absorption of shortwave radiation is part of the leaf energy budget (Muir 2019). However, many case studies found that high light is detrimental to survival and growth even in cold environments, where increased leaf temperature would be expected to be beneficial (e.g. Ball et al. 1991; Close et al. 2000; Akhalkatsi et al. 2001; Egerton et al. 2002). Likewise, Germino et al. (2002) found that survival among spruce seedlings at alpine treelines was halved when overtopping grasses were removed, even though the removal treatment ameliorated water and nighttime low-temperature stress. Other studies ruled out other factors by manipulating them directly. For example, Velasco & Becerra (2020) found that artificial shading provided a much stronger benefit than irrigation on tree seedling survival in a semiarid grassland, which suggests that the seedlings were not strongly water-limited and the effect of shading was not due mainly to reduced transpiration.

Many of the case studies in Appendix S1 are from settings like alpine treelines and drylands, where interacting stresses like low temperature or drought may make photoinhibition more salient. 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 trees are most vulnerable to photoinhibition during recruitment (Germino et al. 2002; Slot et al. 2005).

One implication of this research 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 facilitative amelioration of photoinhibition can produce alternative stable states and allow light-sensitive species to establish. In trees, Kothari et al. (2021) also found that fast-growing, shade-intolerant species reduced photoinhibition in their light-sensitive neighbors. Much of the research on recruitment at treelines or in canopy gaps emphasizes facilitation between adult trees and seedlings (Ball et al. 1991; Egerton et al. 2000; Slot et al. 2005). In the context of research guided by the stress-gradient hypothesis (Bertness & Callaway 1994), amelioration of photoinhibition may be one of the mechanisms through which nurse plants aid their beneficiaries in stressful environments (Cabal et al. 2022).

Understanding that photoinhibition can reduce fitness can also help explain the uses 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 reduce plant fitness. Perhaps in part because photosynthesis is easily measured in the field, ecophysiological studies often explain this influence in terms of reductions in carbon assimilation. However, the critiques described above raise doubts about the generality of such explanations, and it may help to look toward other aspects of plant function. Molecular physiologists have mapped out a much wider range of consequences of excess light-induced ROS generation, which may lead to cellular damage or even death (D'Alessandro et al. 2020)—but primarily in a few model organisms and without yet having demonstrated their importance in nature.

It may be time for a synthesis: Could excess light-induced ROS generation have a role in natural settings beyond its influence on carbon assimilation via electron transport? Besides attacking thylakoid proteins like D1, species like $^1O_2$ produced along the electron transport chain can also react with the unsaturated lipids in the thylakoid and produce lipid peroxides, which in turn break into reactive carbonyl species (RCS). The products of these cascading reactions can cause further damage and, at high enough levels, trigger pathways towards cell death (Møller et al. 2007; Chan et al. 2012; D'Alessandro et al. 2020). This damage may help explain observations of bleaching and necrosis (Powles 1984; Hogewoning & Harbinson 2007) or leaf abscission (Egerton et al. 2000; Close et al. 2002) under high light. Even at more modest levels, the signaling functions of ROS and their products can initiate other changes beyond the chloroplast. For example, oxidative stress causes callose deposition in phloem-loading complexes, which may have the adaptive role of blocking the spread of pathogens (when present), but also hinders the export of sugars and other compounds from leaves (Demmig-Adams et al. 2014).

These broader consequences of oxidative damage may often matter more than reductions in carbon assimilation. For example, although most research on PSII-inhibiting herbicides in seagrasses and algae focuses on reductions in photosynthesis, other sorts of oxidative damage may cause greater harm (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 which would require that photoinhibition have potential effects besides reducing carbon assimilation.

Whether any of these adverse consequences occurs depends on whether the plant can acclimate to its environment. In general, ROS and their diverse products are essential as redox signals that coordinate development, signaling, and acclimation to stressful conditions, including upregulation of photoprotection (Mittler 2017). This fact has been taken to imply that elevated ROS production under photoinhibitory conditions is generally not harmful (Foyer 2018). However, the danger may arise when there are runaway spirals of ROS production that plants cannot control. For example, if unrepaired damage to photosynthetic machinery limits photochemical light dissipation, the share of light in excess may rise, which could increase ROS production (Fig. 1) and perhaps create a cycle in which photoinhibition begets more photoinhibition. This possibility is implied by findings that depending on their mechanism, PSII-inhibiting herbicides can steeply enhance ROS production (Fufezan et al. 2002; Chen et al. 2010). ROS and RCS may also inactivate the enzymes that scavenge and detoxify them (D'Alessandro et al. 2020). Plants adapted to bright or fluctuating light often have a strong capacity to acclimate and maintain homeostasis through protective mechanisms like NPQ or ROS scavenging. However, plants adapted to shade or subject to interacting stresses may have more limited capacity (Foyer et al. 1994). Hence, it seems premature to conclude that the physiological consequences of excess light exposure are necessarily benign; such conclusions can only be drawn by observing fitness. Some researchers have suggested that photoinhibition may only matter in unrealistic circumstances, as when plants are beyond their usual niche (Adams et al. 2013). But this is scant 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 and fitness in following years (May & Killingbeck 1992; El Zein et al.

2011). Senescing leaves are highly vulnerable to light-induced damage (Kar et al. 1993; Merzlyak & Hendry 1994), and the red anthocyanins many species produce in the fall may serve to improve nutrient resorption by screening light (Renner & Zohner 2019). While failures of nutrient resorption could result if photoinhibition causes carbon depletion (Hoch et al. 2001), they might also result from oxidative modifications to proteins involved in breaking down nutrient-containing molecules, or from callose-induced blockage of phloem loading.

On the other hand, one might ask when photoinhibition could be more likely to cause or exacerbate carbon limitation. One example is the combination of high light and low or fluctuating [CO_2], which constrains photochemistry and carbon uptake without directly constraining sink strength (Durchan et al. 2001) and may affect many aquatic producers (Ibelings & Maberly 1998). Likewise, while species adapted to strongly fluctuating light often have high capacity for flexible NPQ (Demmig-Adams & Adams 2006), any damage incurred during transient periods of high light could cause carbon limitation under low light. More speculatively, this question may depend on the relative sensitivity of plants' carbon sources and sinks to environmental stresses. For example, under water limitation, species whose stomatal regulation keeps water potential more stable (i.e. 'isohydric' species) may have lower photosynthesis while more often maintaining the turgor required for tissue growth. This situation may cause carbon depletion, which could worsen if the decline in photochemical dissipation also causes photoinhibition (McDowell et al. 2008). In practice, however, the relationship between stomatal regulation and carbon balance is more complicated (Martínez-Vilalta & Garcia-Forner 2017). As our understanding develops of how plants regulate carbon assimilation and allocation, so too may our understanding of when and how photoinhibition matters.

Considering photoinhibition's role beyond just photosynthesis may require a broadened range of methods. To establish whether photoinhibition has consequences for fitness, it is important to measure growth or demographic rates and to include light treatments high enough for those consequences to manifest.

Indeed, those studying photoinhibition or light limitation as factors in community assembly should consider exposing plants to light regimes beyond those experienced by (but found within dispersal distance of) existing populations, since a major goal of community ecology is to explain what excludes species beyond their niche (Cadotte & Tucker 2017). Physiological indicators should be chosen and interpreted with care. Measuring NSCs could help establish whether photoinhibition is depleting carbon reserves (Slot et al. 2005; Hogewoning & Harbinson 2007; Adams et al. 2013), but this approach is best treated only as a heuristic of carbon limitation (Weber et al. 2019). To disentangle flexible photoprotection from potential damage, one fluorescence parameter that may be useful is the fraction of light energy not dissipated through either photochemistry or NPQ (sometimes denoted Φ_{NO}; Demmig-Adams et al. 1996; Kramer et al. 2004; Fig. 1). Measuring the consequences of oxidative damage at the molecular level is tricky under field conditions, but the relatively simple TBARS assay for lipid peroxidation may be a good candidate (Hodges et al. 1999). When these indicators are coincident with variation in fitness, they may provide support for causal claims about photoinhibition's influence.

In summary, we can describe two hypotheses for how photoinhibition may influence plant fitness: (1) by reducing carbon assimilation, and (2) by causing oxidative damage that may lead to cell death (King et al. 2021). These two hypotheses are not mutually exclusive—in fact, they are intertwined—but focusing on the first alone limits our understanding of how photoinhibition affects fitness. These hypotheses may bear different implications under global change: if sink limitation is growing in prevalence (Cabon et al. 2022), focusing on carbon assimilation alone may lead researchers to conclude prematurely that photoinhibition is declining in relevance. Given the scope of human alteration of light regimes, it is essential to understand when and how photoinhibition matters—not just in the leaf, but across the whole plant.

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Shan Kothari was responsible for conceptualizing, writing, and revising this article.

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Figures

Figure 1: (A) The balance between carbon sources and sinks may be compared to liquid being poured (photosynthesis) into a funnel (phloem transport) draining into a flask (carbon sinks). The carbon that flows into the flask is available to be consumed by metabolism and growth. When the spout is stopped (blockage of phloem transport) or the flask is smaller (limited sink capacity), carbon can build up in source tissues. Often, this buildup causes feedback inhibition of photosynthesis (dashed arrows), reducing the inflow rate. This representation is adapted from Adams et al. (2013). (B) Feedback inhibition or external constraints on light use (e.g. low temperature) reduce the electron transport rate at a given light level (red) compared to a healthy plant under favorable conditions (blue). As a result, the fraction of absorbed light used to power electron transport (Φ_{PSII}) declines and a greater fraction 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 dissipated through NPQ. Φ_{NO} is the fraction that undergoes non-regulated dissipation—including through pathways that produce ROS—and generally does not decline below ~0.16 (dashed line; Kono et al. 2022). Under internal or external constraints to electron transport, Φ_{PSII} declines, but the resulting share of increase in Φ_{NPQ} vs. Φ_{NO} depends on how much the plant can induce NPQ, allowing a range of scenarios (red line). When evaluating the risk of damage, it may help to consider whether Φ_{NO} is elevated rather than whether Φ_{PSII} is reduced.

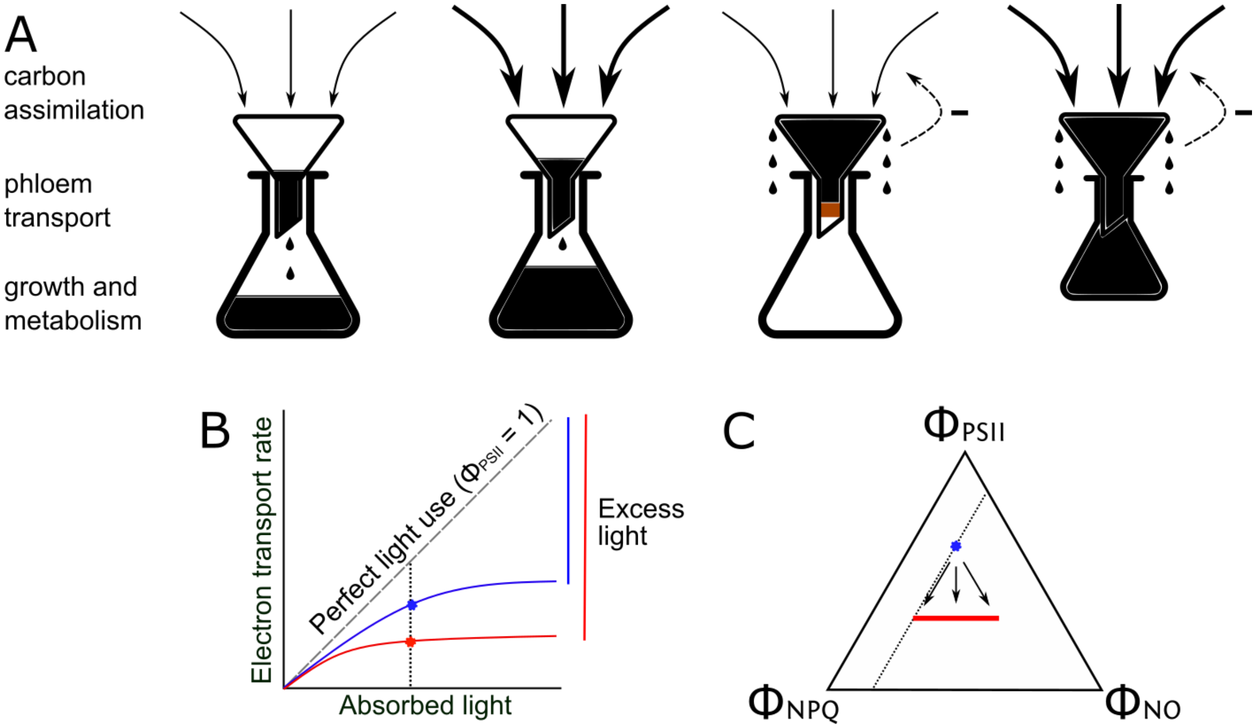
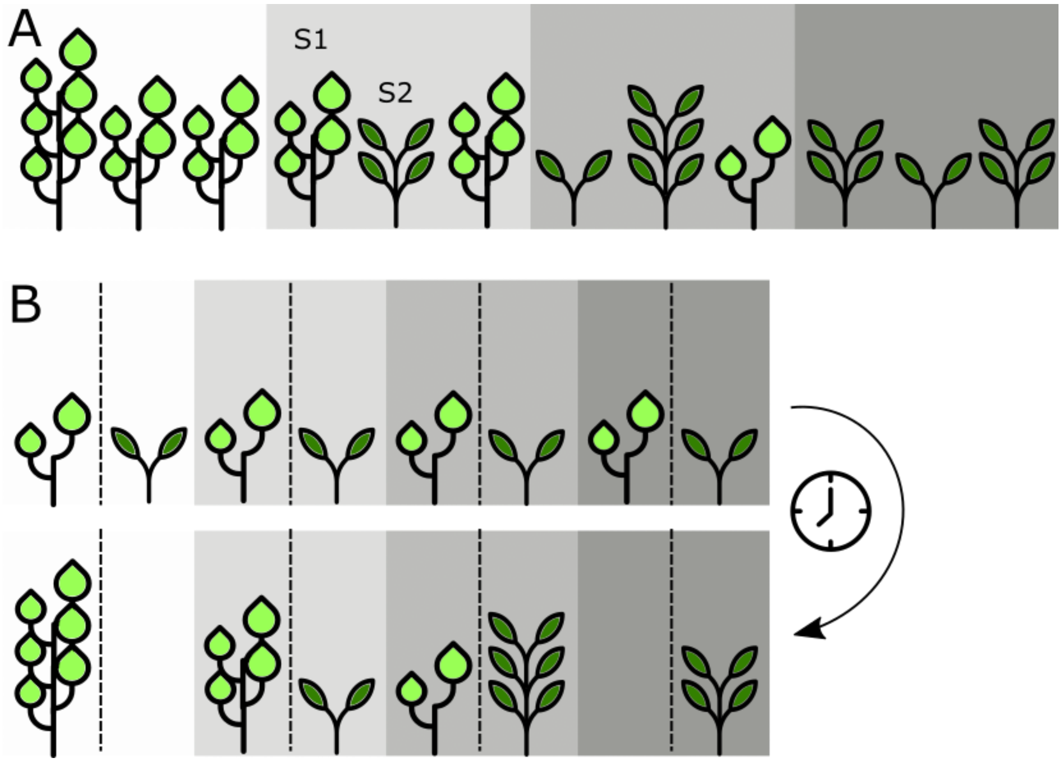

A
carbon assimilation
phloem transport
growth and metabolism
-
-
B
Electron transport rate
Absorbed light
Perfect light use (Φ_{PSII} = 1)
Excess light
C
Φ_{PSII}
Φ_{NPQ}
Φ_{NO}

Figure 2: Two potential approaches to test the importance of photoinhibition and photoprotective adaptations for fitness, similar to the general ‘likelihood’ and ‘vital rates’ approaches described by Laughlin & Messier (2015). I consider two species (S1 and S2), depicting S1 with more yellowish leaves and steeper leaf angles to imply stronger photoprotective adaptations—high NPQ by carotenoids and reduced light absorption at midday, respectively. For simplicity, I assume these traits are not plastic. (A) One approach is to observe whether photoprotective traits are correlated consistently with environmental gradients in the risk of photoprotection. As with all observational data, causal interpretation requires care to rule out competing explanations. For example, S1 may dominate under high light because S2 is filtered out by abiotic stresses like photoinhibition, outcompeted by S1, or a combination. Nevertheless, if species found in brighter sites consistently have greater constitutive photoprotective adaptations, it would imply that those adaptations help maintain fitness under high light. (B) Another approach is to monitor vital rates across gradients of light. Here, S1 has its greatest growth rates at high light, while S2’s growth is reduced at high light levels. Dashed lines separate individuals in each treatment to clarify that they are not directly interacting. This kind of experiment can be done with one or multiple species/genotype(s). If there are multiple, researchers can test whether more light-sensitive plants have fitness optima at lower light levels.


A
S1
S2
B

Appendix S1

Table S1: A brief summary of studies that provide 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. Most of these studies are experimental, but 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 provide physiological evidence that photoinhibition is occurring without testing whether it influences fitness or resulting population/community-level consequences. I also 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 variation in fitness to be attributed more convincingly to the effects of light. This table should not be considered a formal evidence synthesis, since I only aim to summarize various studies that appear to show some positive evidence that photoinhibition can reduce 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	Alpine treelines in northern	The number of sprouts was surveyed along	None reported	Out of the six species in the observational survey, four were	Microclimatic monitoring revealed that the forest buffered

	observational component) or eight (in the experimental component) tree species	Ecuador	transects that crossed the treeline from the 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		almost completely absent beyond the treeline but the 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.	temperature extremes, but the four páramo treatments were 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.	Trees on more exposed sites did also tend to have slightly lower nighttime leaf temperature.
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.
Baumeister & Callaway 2006	*Pseudotsuga menziesii* and *Ribes cereum* seedlings	Forest-grassland ecotones in Montana, United States	The number of natural recruits was surveyed in relation to wind exposure whether they were growing under an adult *Pinus flexilis* crown. In one experiment, seedlings were planted under *P.*	None reported	Natural seedlings were disproportionately found growing under *P. flexilis* crowns. In the first experiment, survival was increased by shade and by protection from wind. In the second experiment, shade had a strong primary influence on survival and seedling height,	Plant-available N and P were not significantly different between *P. flexilis* crowns and the open. Litter depth was greater under the crowns. Soil moisture was lower at 10 cm under *P. flexilis* and in shade treatments, and equivalent at 20 cm. Soil moisture was also

			flexilis or in the open, and at windward or leeward sites. In a separate experiment, seedlings were grown in the open under one of six treatments that include shade, increased snow, and wind protection		and additional benefits of snow accumulation and wind protection for survival only appeared in the shade. In both experiments, *Ribes* mortality in the open was highest during the late summer, but *Pseudotsuga* mortality was highest over the winter.	greater in spring and early summer in the snowdrift plots. Based on the seasonal pattern of mortality, the authors suggest that the facilitative effect of shade on *Ribes* (but not *Pseudotsuga*) had more to do with moisture than photoinhibition.
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 Fv/Fm after the shadecloth was removed.	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.
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 higher 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	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	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

				substantial decreases in leaf water potential and increases in plant Huber value.	higher than in understories.	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 shading, or both	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 in exposed environments had more inclined and clustered needles.	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.
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.	Neighbor removal alleviated water and low temperature stress but still increased mortality, which the authors attribute to photoinhibition due to increased light. Neighbor removal also caused greater wind stress.
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	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.

				pattern. The authors report many other changes in plant allocation and physiology that are less relevant here.		
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 growth in height 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.
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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