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Light alters the impacts of nitrogen and foliar pathogens on the performance of early successional tree seedlings

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Light limitation is a major driver of succession and an important determinant of the performance of shade intolerant trees. This shade intolerant habit may result from a resource allocation strategy characterized by rapid growth and high metabolic costs, which may make shade intolerant species particularly sensitive to nutrient limitation and pathogen pressure. In this study, we evaluated the degree to which nitrogen availability and fungal pathogen pressure interact to influence plant performance across different light environments. To test this, we manipulated nitrogen availability (high, low) and access by foliar fungal pathogens (sprayed with fungicide, unsprayed) to seedlings of the shade intolerant tree, *Liquidambar styraciflua*, growing for approximately three months across a gradient in light availability, from forest understory to adjacent old field. Foliar fungal damage varied with light and nitrogen availability; in low light, increasing nitrogen availability tripled foliar damage, suggesting that increased nutrient availability in low light makes plants more susceptible to disease. Despite higher foliar damage under low light, spraying fungicide to exclude pathogens promoted 14% greater plant height only under high light conditions. Thus, although nitrogen availability and pathogen pressure each influenced aspects of plant performance, these effects were context dependent and overwhelmed by light limitation. This suggests that regardless of environmental context, the spread of shade-intolerant species can be limited by light alone.

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Keywords: American sweetgum; foliar fungal pathogens; old field succession; *Pseudocercospora liquidambaricola*; shade tolerance; top-down, bottom-up

Author contributions: ANB and RWH designed and performed the experiment, analyzed the data and wrote the manuscript.

ABSTRACT

Light limitation is a major driver of succession and an important determinant of the performance of shade intolerant trees. This shade intolerant habit may result from a resource allocation strategy characterized by rapid growth and high metabolic costs, which may make shade intolerant species particularly sensitive to nutrient limitation and pathogen pressure. In this study, we evaluated the degree to which nitrogen availability and fungal pathogen pressure interact to influence plant performance across different light environment~~s~~. To test this, we manipulated nitrogen availability (high, low) and access by foliar fungal pathogens (sprayed with fungicide, unsprayed) to seedlings of the shade intolerant tree, *Liquidambar styraciflua*, growing for approximately three months across a gradient in light availability, from forest understory to adjacent old field. Foliar fungal damage varied with light and nitrogen availability; in low light, increasing nitrogen availability tripled foliar damage, suggesting that increased nutrient availability in low light makes plants more susceptible to disease. Despite higher foliar damage under low light, spraying fungicide to exclude pathogens promoted 14% greater plant height only under high light conditions. Thus, although nitrogen availability and pathogen pressure each influenced aspects of plant performance, these effects were context dependent and overwhelmed by light limitation. This suggests that regardless of environmental context, the spread of shade-intolerant species can be limited by light alone.

INTRODUCTION

Shade intolerant species are, by definition, unable to persist in low-light environments. This may result from fundamental trade-offs, where shade intolerant species in high-light, early successional environments tend to allocate resources toward rapid growth (Walters and Reich

1999, Myers and Kitajima 2007, Valladares and Niinem 2008). This rapid growth strategy, however, becomes disadvantageous in low-light, later successional environments, where high metabolic costs reduce the ability to tolerate light limitation and other stressors (Wright et al. 2003). This rapid growth strategy als ay depend critically on factors like soil nutrients and pathogen pressure (Augspurger 1984, Coley et al. 1985, Myers and Kitajima 2007, Pasquini et al. 2015, Griffin et al. 2016), that can alter plant performance in different light environments. In this way, shade intolerance may drive succession from herbaceous to forest communities (Loach 1967).

Shade intolerant and tolerant species exhibit different resource strategies, which are driven by a trade-off between resource acquisition in high resource environments and resource conservation in low resource environments (Wright et al. 2004, Reich 2014). In high resource environments (e.g., high light), the acquisitive strategy prioritizes growth of new tissue to acquire resources rapidly, resulting in plants with thin, high nutrient leaves that photosynthesize and respire rapidly (Wright et al. 2004). In low resource environments (e.g., low light), the conservative strategy prioritizes increased tissue longevity, resulting in plants with tough, low nutrient leaves that photosynthesize and respire slowly. This acquisitive, shade-intolerant strategy may also hinder growth under low nutrient conditions and increase susceptibility to pathogens and herbivores (Coley et al. 1985, Fine et al. 2004, Hahn and Maron 2016).

Pathogens are critical drivers of dynamics in plant communities (Mordecai 2011). Throughout forest and grassland systems, pathogens can limit seedling survival (Hersh et al. 2012) and ecosystem productivity (Mitchell 2003, Maron et al. 2011), promote diversity (Bever et al. 2015, LaManna et al. 2017), and limit species' ranges (Spear et al. 2015, Bruns et al. 2019). Pathogens can alter community composition through negative density dependent seedling survival (Comita et al. 2014, Bayandala et al. 2017), benefiting more resistant species (Welsh et al. 2016), and those that have escaped their specialist herbivores and pathogens (Heckman et al. 2016). Because pathogen impacts can also change with light and nutrient availability (e.g., Dordas 2009, Veresoglou et al. 2013, Heckman et al. 2016, Ballaré and Pierik 2017, Liu et al. 2017, Agrawal 2020), shade-intolerant species, which occupy habitats ranging from open fields to closed-canopy forests, may experience large differences in pathogen impacts throughout their range

The inability to persist in the shade may depend on the combined effects of light and other environmental factors, including soil nutrients and pathogen pressure (Augspurger 1984, Coley et al. 1985, Myers and Kitajima 2007, Pasquini et al. 2015, Griffin et al. 2016). In temperate forests, nitrogen is often a limiting nutrient (Baltzer and Thomas 2007, LeBauer and Treseder 2008). Nutrient limitation may be especially detrimental for species that exhibit rapid growth, like shade intolerant trees, because it can drastically reduce their ability to build photosynthetic machinery and some defensive compounds (Coley et al. 1985, Stamp 2003). When unable to defend against consumers, shade intolerant plants in low nitrogen habitats may lose more tissue to disease (Fine et al. 2004). Additionally, reduced photosynthetic capacity could reduce disease tolerance more when light and nutrients simultaneously limit growth (Baltzer and Thomas 2007, Myers and Kitajima 2007). Thus, susceptibility to pathogens among shade intolerant species may be particularly high when light and nutrients are limiting (Kitajima and Poorter 2010, Griffin et al. 2016, Griffin et al. 2017).

In this study, we simultaneously tested how light and nutrient limitation influenced the susceptibility of an early successional tree species to pathogens and how pathogens impacted plant performance. We evaluate this using an important pioneer species of old fields and early successional forests, *Liquidambar styraciflua* (Oosting 1942, Wright and Fridley 2010, Fridley and Wright 2018). In these early successional environments, *L. styraciflua* can experience severe foliar disease (McElrone et al. 2010) as well as varied nutrient and light conditions, making the interaction between pathogens and resource limitation important for understanding successional dynamics. To date, this interaction has been addressed in only a few studies (e.g., Griffin et al. 2016, Griffin et al. 2017). We predicted that:

1) Fungal disease will be highest when light and nitrogen are both limiting.
2) Pathogen impacts on plant performance will be highest when light and nitrogen are both limiting.

METHODS

Study syste

Liquidambar styraciflua, or American sweetgum, is common throughout the Southeastern US, where it is a shade intolerant, early successional deciduous tree and a key transitional species during succession, competing well in early successional systems but becoming less common when its seedlings are shaded out as succession proceeds (Clark et al. 2004, Wright and Fridley 2010, Hersh et al. 2012, Addington et al. 2015, Brown et al. 2020).

We examined the impact of resource limitation and pathogen pressure in Duke Forest Teaching and Research Laboratory, (Orange Co., NC) in an old field and adjacent forest. Since 1996, herbaceous dominance of the old field has been maintained through annual mowing. Throughout the old field, sweetgum occurs as seedlings and small saplings, which become larger and more abundant toward the forest edge. This 40 year-old forest is dominated by early successional trees such as loblolly pine (*Pinus taeda)*, tulip poplar (*Liriodendron tulipifera*) and

American sweetgum. Later successional species like *Acer rubrum* and *Quercus* spp. also occur throughout the forest.

Experimental manipulat

We conducted the study from July through mid-October 2014 using a split-plot design. At the whole plot level we manipulated light availability (high ~~light,~~ low light~~, three intermediate light~~ levels), and at the subplot level we manipulated nitrogen availability (high, low) and fungal pressure (sprayed, unsprayed). Each subplot was a single sweetgum seedling grown in its own pot; each whole plot was a cluster of four pots surrounded with a wire cage to exclude deer. These treatments were replicated 10× in the high light treatment, 10× in the low light treatment, and 4× at each of the 3 light levels along the light transect for a total of 128 subplots (i.e., pots) within 32 whole plots.

Light availability

At the whole plot level, we randomly assigned seedlings to levels of light (high, low, or a position along a light transect). Seedlings in the high light treatment were placed in the open field; seedlings in the low light treatment were placed under the forest canopy. Each light transect ran between the high light treatment and the low light treatment, with seedlings at one of three points along the gradient from high to low light availability: ~10m from the forest edge, ~5m from the forest edge, or at the forest edge.

To quantify differences in light availability between light treatments, in early October we attached one Onset HOBO pendant light logger (Onset Computer Corporation, Bourne, MA) to each whole plot replicate. The loggers measured and recorded light availability every 5 minutes for 10 (. At this time, overstory trees had not yet begun to noticeably senesce and no disturbances (e.g., tree falls) had occurred that would have substantially altered the light availability from what these plants would have experienced earlier in the growing season. Thus, we expect the differences in light availability between treatments in October to reflect differences in the relative, although not absolute, light availability throughout the duration of the experiment.

Nitrogen availability and fungal pressure

At the subplot level, seedlings growing in separate pots were grouped into replicated 2 × 2 factorial manipulations of nitrogen (high or low) and ene[illegible]damage (high or low) treatments. Within each light treatment, replicates of the four nitrogen × enemy damage treatment combinations (i.e., each whole plot replicate) were spaced ~5m apart.

Seedlings in each nitrogen treatment received five applications of aqueous ammonium nitrate solution ($NH_4^+NO_3^-$) over the course of ten weeks, from July 24, before being moved to the field, to September 18, three weeks before the end of the study. Seedlings in the high nitrogen treatment received 2 g N m^{-2} $application^{-1}$ (10 g N m^{-2} total), which corresponded to 92 mg $NH_4^+NO_3$- $plant^{-1}$ $application^{-1}$, and seedlings in the low nitrogen treatment received 0.2 g N m^{-2} $application^{-1}$ (1 g m^{-2} total), which corresponded to 9.2 mg $NH_4^+NO_3^-$ $plant^{-1}$ $application^{-1}$. This application rate was intended to alleviate N limitation in old fields and other grass-dominated communities (Borer et al. 2014, Fay et al. 2015) and substantially increased experimental soil N above baseline levels at this site (Stevens et al. 2015).

Seedlings in the sprayed treatment were sprayed biweekly with a foliar fungic[illegible] Mancozeb (Dithane DF, Dow AgroSciences, Indianapolis, IN), for the duration of the field study, while seedlings in the unsprayed treatment were not. Mancozeb is commonly used in ecological studies (e.g., Mitchell 2003, Parker and Gilbert 2007, Heckman et al. 2016, Heckman et al. 2017); it is a broad-spectrum non-systemic fungicide that has no known direct effects on photosynthesis, leaf longevity, shoot growth, or root growth (Lorenz and Cothren 1989, Kope and Trotter 1998, Parker and Gilbert 2007), nor does it affect mycorrhizal fungi when applied at recommended rates (Parker and Gilbert 2007). In the greenhouse, fungicide application reduced total biomass by ~ 10%, but this effect was only marginally significant ($P = 0.084$; Table S1a; Fig. S1a, Supplementary Methods 1).

Seedling propagation

We grew seeds purchased from Sheffield's Seed Co. (Locke, NY) in flats in the greenhouse at the University of North Carolina at Chapel Hill for 10 days, then transplanted individual seedlings into 2.84L pots filled with 3:1 mix of potting medium (Fafard 3B; Sun Gro) and sterilized sand. To ensure that other soil nutrients would not limit seedling growth, we added to the potting medium 10 g P m^{-2} as triple super phosphate, 10 g K m^{-2} as potassium sulfate, and 100 g m^{-2} micronutrients (Scotts Micromax, Marysville, OH), corresponding to 1 g triple super phosphate plant $^{-1}$, 0.45 g potash plant $^{-1}$, and 2 g micronutrients plant $^{-1}$ (Borer et al. 2014, Fay et al 2015; soil N from site: Stevens et al. 2015).

Measurements

In this study, we measured two responses—foliar damage and plant height—to determine whether light and nitrogen availability alter pathogen impacts on plants. Foliar damage by pathogens was quantified visually by referring to digitized images of known damage severity (James 1971, Mitchell et al. 2002, Mitchell et al. 2003). We measured foliar damage as the percent of leaf area visibly damaged on October 3, 2014 on five leaves per plant, including the youngest and oldest leaves as well as three leaves evenly spaced in age (e.g., on a seedling with 10 leaves, we selected leaves 1,3,6,8, and 10). For seedlings with five or fewer leaves, we measured damage on every leaf. Surveying leaves of different ages should best describe the mean level of damage across the entire plant, because damage typically increases with leaf age (Hatcher et al. 1995, Halliday et al. 2017, Heckman et al. 2019).

Plant height was measured every two weeks from July 25, 2014, one week after placing seedlings in the field, until October 3, 2014 (6 observations). Each time, we measured seedling height from the base of the stem through the end of the petiole of the highest leaf, which reflects the highest point at which the seedling can photosynthesize. Here, we report the accumulation of height in these plants by calculating the area under the curve of these biweekly height measurements using the 'auc' function in the MESS package in R (Ekstrøm 2016). Height accumulation accounts for the non-linear nature of plant growth trajectories, allowing us to avoid post hoc selection of dates for analysis.

Data Analysis

We analyzed these data with linear mixed effects models in the nlme package (Pinheiro et al. 2016) in R version 3.5.3 (R Foundation for Statistical Computing, Vienna 2019). Light was a categorical whole plot effect, while nitrogen and spraying treatments were categorical subplot effects. Because both maximal and total daily light availability were similar in transect and high light subplots ($P = 0.18$; Fig. S2), and because there were no significant differences in height between the transect and high light treatments, we combined transect subplots with high light subplots for all analyses. To meet the normality assumption for linear models, foliar fungal damage was cubed-root transformed. This transformation provided the best means of meeting the normality assumption because it is more strongly normalizing than the square root transformation, but less so than the log transformation. To reduce heteroscedasticity of residuals in the height analysis, we used the varIdent function in 'lme' to allow variances to differ between light treatments (Zuur et al. 2009, Pinheiro et al. 2016).

RESULTS

Impacts of light and nitrogen on efficacy of spraying

Light and nitrogen availability jointly altered the effect of spraying on visible foliar fungal damage (Light × Nitrogen × Spraying; P = 0.03; Tab[illegible]2): in high light, fungal damage was unaffected by spraying or nitrogen treatment; in low light, fungal damage was near zero for all sprayed plants in both nitrogen treatments (Tukey HSD: P = 0.48), but fungal damage was 3× greater for unsprayed plants in the high nitrogen treatment than the low nitrogen treatment (Tukey HSD: P = 0.04). Averaged across all light and nitrogen treatments, spraying reduced fungal damage by 83% (Spraying, P < 0.001; Fig[illegible]).

Impacts of light and nitrogen on foliar fungal damage

Among only unsprayed plants, light availability altered the effect of nitrogen on foliar fungal damage (Nitrogen × Light, P = 0.01; Table S3; Fig. 1): in high light, fungal damage did not differ between nitrogen treatments (Tukey HSD: P = 0.078); in low light, however, fungal damage was over 3× higher on high nitrogen than low nitrogen plants (Tukey HSD: P = 0.039). This is contrary to our prediction that damage would be highest under low light and low nitrogen.

Impacts of light, nitrogen, and pathogens on plant height

Light availability altered the effect of spraying on plant height (Damage × Light, P = 0.002; Tab[illegible]4; Fig. 2): in high light, sprayed plants grew 14% taller than unsprayed plants, but did not differ in low light (High light, Tukey HSD: P = 0.002; Low light, Tukey HSD: P = 0.22). This suggests that spraying reduced the deleterious effects of fungal disease on plant performance, even though it did not significantly reduce visible damage. Light availability also altered the effect of nitrogen on height (Light × Nitrogen, P = 0.004; Table S4). In high light, plants grew 17% taller in the high nitrogen treatment than the low nitrogen treatment (Tukey HSD: P < 0.001). Height did not differ across nitrogen treatments in low light (Tukey HSD: P = 0.[illegible] Contrary to expectation, light and nitrogen did not interact with spraying to influence plant height (P = 0.72; Table S4).

DISCUSSION

Light, nitrogen, and pathogens additively and interactively influenced foliar damage and plant height. Foliar fungal damage unexpectedly increased with increasing nitrogen availability only in low light, suggesting that increased nitrogen availability under low light makes plants more susceptible to enemies (Dordas 2009, Zhou et al. 2015, Ballaré and Pierik 2017). Despite the fact that damage was lower under high light, plant height was more heavily impacted by pathogens under high light conditions. This is contrary to other studies showing either greater impacts of pathogens and herbivores in low light or no difference in impacts between light environments (e.g., Augspurger 1983, Myers and Kitajima 2007, Bayandala et al. 2017). Together, these results demonstrate the importance of light and nitrogen for modulating pathogen impacts on plant performance.

Increasing nitrogen availability increased pathogen damage in the shade, but not in the sun. Although this result could be attributable to differences in fungal inoculum between light environments, it is unlikely that differences in inoculum were solely responsible for variation in damage. First, this effect was mediated by nitrogen (Veresoglou et al. 2013). If inoculum load had differed systematically between high and low light, a strong main effect of light would be likely. Second, there is a biologically plausible mechanism specifically relating nitrogen and light availability to enemy damage: plants in the shade may have lacked energy to synthesize defense compounds, leaving their nitrogen-rich leaves more susceptible to pathogen infection (Stamp 2003, Zhou et al. 2015). Additionally, shade intolerant species often downregulate the jasmonic acid pathway in low light, reducing their ability to resist pathogens (Ballaré and Pierik 2017). Moreover, seedlings in low light may resist shedding their leaves, even when heavily damaged, because abscission would lead to greater carbon loss than pathogen damage (Russo and Kitajima 2016). These results also highlight potential influences of soil nutrients on consumer pressure across different stages of succession (Griffin et al. 2016, Griffin et al. 2017): high nitrogen supply may reinforce the dominance of shade intolerant species in early stages of succession (i.e., high light environments) by contributing to growth without increasing damage, but may undermine performance of shade intolerant species in later successional stages by increasing damage without increasing growth (Reinhart et al. 2010).

Interactive effects of light and nutrients on seedling disease may help explain patterns of species occurrence in forests. For instance, in the forest understory, seedlings of shade intolerant species like *L. styraciflua* do not aggregate as often as shade tolerant species, indicating conspecific negative density dependence (Clark et al. 2004, Brown et al. 2020), which may result from foliar disease (Hersh et al. 2012). This may prevent shade intolerant species from maintaining large enough seedling and sapling populations to exploit infrequent tree falls and result in their exclusion from forest understories (O'Hanlon-Manners and Kotanen 2004, Wulantuya et al. 2020). Thus, pathogens may provide important regulation of species in lower light environments. This may be especially true of shade-intolerant species, which typically exhibit acquisitive strategies characterized by rapid growth and little defense investment (Kitajima and Poorter 2010, Brown et al. 2020).

Increasing both light and nitrogen availability considerably increased plant height, a key measure of seedling performance. However, the effect of nitrogen depended on light availability: nitrogen addition had no effect on seedling height in low light, while nitrogen addition increased plant height in high light. This indicates that light was more limiting than nitrogen to growth in the understory, but that nitrogen was more limiting than light in the open field. Despite interactions between light and nitrogen on plant height, these resources did not simultaneously interact with pathogen pressure. Instead, spraying increased plant height only in high light, which was contrary to our prediction that pathogen impacts on plant performance would be higher under low light (Augspurger 1983, Stamp 2003, Myers and Kitajima 2007). This effect indicates that fungal pathogens were negatively impacting plant performance in high light, even without visible differences in fungal damage. This may have occurred because visible fungal damage symptoms include both the actual effect of the pathogen and the plant's immune response to the pathogen (Agrios 2005). If leaf damage caused by pathogens had larger negative impacts on plant growth than damage caused by plant immune responses, then visible damage symptoms may not correspond one-to-one to impacts on fitness (Aldea et al. 2006) and spraying still could have reduced the deleterious effects of fungal pathogens on plant performance. Additionally, fungal pathogens may not have impacted plant height in low light because seedling growth was severely light-limited regardless of damage.

Although this study demonstrates important impacts of light, nutrients, and pathogens on *L. styraciflua* performance, there are several limitations. First, this study was short. This short duration highlights a critical life history stage, survival and growth of establishing tree seedlings (De Steven 1991, Fridley and Wright 2018), but we cannot account for differences in overwinter survival or impacts of light, nutrients, and pathogens beyond this critical window. Second, by growing seedlings alone in pots, we eliminated interspecific competition, which may have been more important in herbaceous-dominated old fields (Flory and Clay 2010, Fridley and Wright 2012) than in the more sparsely vegetated forest understory. Thus, growing plants in pots versus directly into field soil may have had a larger impact on the results in herbaceous-dominated fields than in the forest understory. Third, the fungicide could have had different impacts in the field and greenhouse, which may have resulted from environmental differences between the greenhouse and the field. Under field conditions, ultraviolet radiation degrades fungicide and rainfall washes fungicide off leaves, necessitating frequent spraying to exclude pathogens (Parker and Gilbert 2007, Heckman et al. 2016). Using this spraying frequency in the greenhouse, where fungicide may not degrade as rapidly, may have exposed these plants to higher fungicide concentrations. But, if the fungicide treatment had also had direct negative effects on plant performance in the field, the positive effects of spraying on plant height would indicate an even stronger indirect positive effects of fungicide on plant performance (e.g., growth facilitated by reduced pathogen infection).

These results have important implications for the longer-term survival of seedlings across light environments. If seedlings in low light use belowground carbon stores to compensate for immediate damage rather than overwinter survival (Piper et al. 2015), it could reduce longer-term survival and reproduction in ways that cannot be captured in a single-season study. Seedlings growing under high nitrogen already often allocate less biomass to root growth than leaf and stem growth because aboveground tissue can acquire the new limiting resource, light (Walters and Reich 1999, Shipley and Meziane 2002). However, this resource allocation strategy may leave fewer resources available for recovery from damage later in the growing season when deciduous trees increase carbon stores in preparation for large carbon expenditures the following spring (Klein et al. 2016). Under these conditions, plants growing in low light are faced with the possibility of compensating for current tissue loss or maintaining carbon stores for the following spring.

Establishment and growth of shade-intolerant species in old fields is an important stage of secondary succession (Meiners et al. 2015). The rapid rate of succession in southern US old fields relative to northern old fields is primarily driven by temperature (Fridley and Wright 2018), but within regions, succession can also be driven by nutrients and consumers (Wright and Fridley 2010, Fridley and Wright 2012, Meiners et al. 2015). Here, foliar disease reduced the performance of *L. styraciflua* under high light conditions, suggesting that pathogens may be able to modestly slow the early stages of succession from fields to forests. Thus, herbaceous dominance of communities may last longer when *L. styraciflua*, one of the primary early successional trees of the region, experiences strong consumer pressure (Gill and Marks 1991). High disease on *L. styraciflua* may also explain why *Pinus taeda*, the other major pioneer species, is often the fastest growing tree in these old fields (R.W. Heckman, unpublished data). However, once young forests establish a closed canopy, increased nitrogen availability can increase foliar disease, but this effect appears too small to impact sweetgum regeneration in the understory—light limitation is too severe, even when pathogen pressure and nitrogen limitation are alleviated, to allow rapid seedling growth.

In conclusion, we found that nitrogen and light interact to impact fungal damage, with the highest levels of damage at high nitrogen and low light. Despite this, spraying had larger impacts on plant height under high light, indicating that pathogen pressure was higher when light was abundant and that fungal pathogens exerted negative impacts on plant performance beyond what was visible on leaves. Overall, though, light limitation had the largest influence on plant performance, overwhelming both nitrogen limitation and pathogen pressure. Given this, it appears that the shade intolerant species *L. styraciflua* can be excluded from later successional habitats solely through reduced light availability—high pathogen pressure and nitrogen limitation may exacerbate this, but are not required.

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FIGURE LEGENDS

Fig. 1 Effects of nitrogen and light availability on mean foliar fungal damage for plants not sprayed with fungicide, calculated using linear mixed models and back transformed from a cubed root transformation. Dashed lines represent plants growing in low light and solid lines represent plants growing in high light. Error bars represent 95% confidence intervals (N = 32 whole plots; N = 64 subplots).

Fig. 2 Effects of nitrogen and light availability, and damage treatment on height accumulation in the field from 8 days after beginning the field experiment (73 days), calculated using linear mixed models. Dashed lines represent plants growing in low light and solid lines represent plants growing in high light. Error bars represent 95% confidence intervals (N = 32 whole plots; N = 128 subplots).

Figure 1

Effects of nitrogen and light availability on mean foliar fungal damage

Effects of nitrogen and light availability on mean foliar fungal damage for plants not sprayed with fungicide, calculated using linear mixed models and back transformed from a cubed root transformation. Dashed lines represent plants growing in low light and solid lines represent plants growing in high light. Error bars represent 95% confidence intervals (N = 32 whole plots; N = 64 subplots).

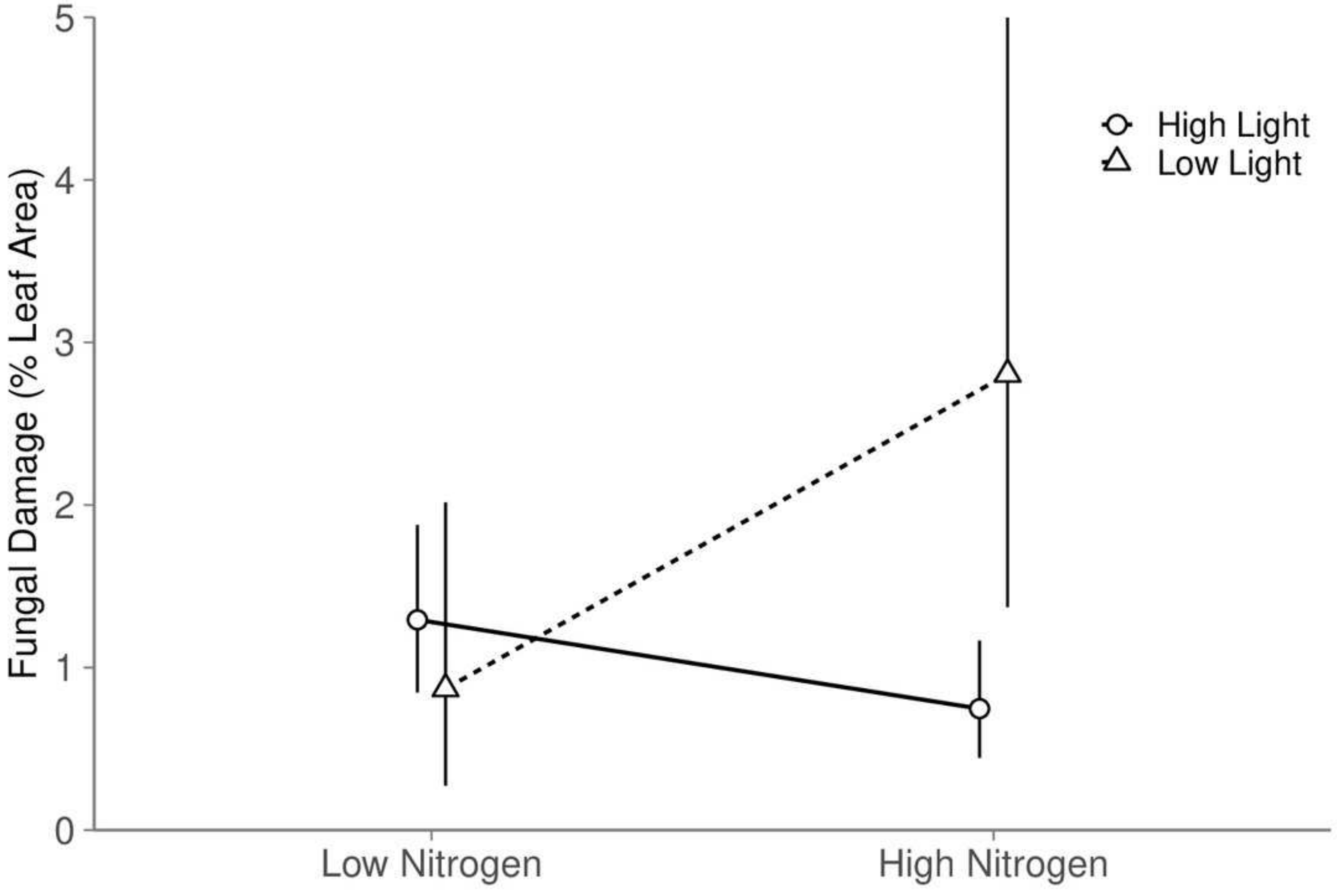

Figure 2

Effects of nitrogen and light availability, and damage treatment on height accumulation in the field

Effects of nitrogen and light availability, and damage treatment on height accumulation in the field from 8 days after beginning the field experiment (73 days), calculated using linear mixed models. Dashed lines represent plants growing in low light and solid lines represent plants growing in high light. Error bars represent 95% confidence intervals (N = 32 whole plots; N = 128 subplots).