Spring phenology dominates over light availability in affecting seedling performance and plant attack during the growing season

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A B S T R A C T

Climate change can have important effects on plant performance by altering the relationship between spring temperature and other abiotic factors, such as light availability. Higher temperatures can advance plant phenology so that seedling germination takes place when days are shorter, and affect light availability for understory plants by altering the relative timing of seedling germination and canopy closure. To predict the effects of climate-induced changes in phenology and light availability on plant performance and species interactions during the growing season, we need to determine i) how effects of plant phenology on plant performance and the plant-associated community depend on light availability, and ii) to what extent effects of phenology and light availability on plant performance are direct vs. mediated by changes in the plant-associated community. We conducted a multifactorial field experiment to test for the effect of germination timing and light availability on *Quercus robur* seedling traits and performance, as well as attack by specialist plant pathogens, insects, and small mammals. Germination timing strongly affected seedling performance whereas light availability's effects were limited. Likewise, germination timing strongly affected herbivore and pathogen attack, whereas light availability and its interaction with germination timing explained a minor part of the variation. Small mammals preferentially attacked later germinating seedlings, which strongly affected plant survival, while insect herbivores and pathogens did not mediate the effect of germination timing and light availability on plant performance. The results showed that the effect of germination timing can have greater influence than light availability on plant performance and plant attack, and that small mammal herbivores can play a larger role than diseases and insect herbivores in mediating the effect of spring phenology on plant performance. Together, these findings advance our understanding of the consequences of climate-induced changes in spring phenology and the abiotic environment on plant performance within a community context.

1. Introduction

Climate change can have important effects on plant performance, species interactions and food web structure by altering the relationship between spring temperature and other abiotic factors (Parmesan and Hanley, 2015; Thackeray, 2016; Kharouba et al., 2018). As one important abiotic factor, light availability in the understory varies both spatially and temporally, with species composition and density of canopy trees and the seasonal closing and opening of the canopy creating a spatiotemporal mosaic of light availabilities (Vazquez-Yanes et al., 1990; Daws et al., 2002). Climate-induced shifts in the timing of events can affect daylight length experienced during seedling development,

and climate warming may affect the relative timing of germination and canopy closure, leading to changes in light availability for understory plants (Hamilton et al., 2016; Heberling et al., 2019). These changes in phenology and light availability might also affect the interactions between plants, pests and pathogens (Donnelly et al., 2011; Forrest, 2016). Disentangling the joint effects of spring phenology and the abiotic environment on plant performance and plant-associated food webs is therefore key to predicting the effects of climate change, as well as for understanding differences in plant performance and species interactions within heterogeneous landscapes more generally.

Spring phenology and light availability during the growing season might both independently and interactively influence plant

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performance. Earlier spring phenology has been reported to either increase (Seiwa, 1998, 2000; Benard and Toft, 2007) or decrease plant performance (Shevtsova et al., 2009; Gioria et al., 2016). For example, early germinating walnut seedlings (*Juglans ailanthifolia*) grew larger than their later germinating conspecifics as a result of a longer growing season (Seiwa, 2000), whereas later budburst in Finnish downy birch (*Betula pubescens*) may be selected against to avoid late frost damage (Bennie et al., 2010). In contrast, low light availability generally decreases plant performance (Welander and Ottosson, 1998; De Lombaerde et al., 2020). For example, seedlings of the tree species *Quercus robur* and *Fagus sylvatica* showed reductions in dry mass of leaves, stem and roots and increased mortality risk when growing under light conditions simulating a fully closed canopy conditions as compared to conditions with higher light availability (De Lombaerde et al., 2020). Interactive effects of spring phenology and light availability might also be important. As one mechanism for such interactive effect, the ability to assimilate may depend on both the mean temperature and light availability at a given phenological stage.

Spring phenology and light availability may also affect plant performance by influencing the presence and abundance of organisms associated with plants. Pathogen infection is well-known to be directly affected by abiotic environmental conditions such as temperature, humidity and light availability (Newsham et al., 2000; Elad et al., 2007; Austin and Wilcox, 2012; Suthaparan et al., 2016), but also requires synchrony between susceptible plant tissue and spore release (Guest and Brown, 1997; Desprez-Loustau et al., 2010). Light availability also affects levels of herbivory, with herbivory sometimes being higher under more open conditions (Louda and Rodman, 1996) and sometimes higher under shade (Muth et al., 2008). Spring phenology has been shown to affect insect herbivory in contrasting ways, with early bud-burst being associated with both lower (Pearse et al., 2015b; Barber and Fahey, 2015) and higher (Crawley and Akhteruzzaman, 1988; Heimonen et al., 2017) levels of herbivory. Disentangling the direct and indirect (i.e. mediated by pathogens and herbivores) nature of the joint effects of spring phenology and the abiotic environment on plant performance seems particularly relevant, as both plants and their attackers are known to respond to changes in spring phenology, the abiotic environment and their interaction (Ibáñez et al., 2010; Vautard et al., 2014). Despite evidence for the important effects of spring phenology and light availability, we lack studies on how these factors interact to influence plant performance and attacks by pathogens and herbivores, especially during the plant's first growing season.

The overarching aim of this study was to identify the impact of spring phenology (germination timing) and light availability on the performance of tree seedlings, as well as to assess the extent to which such effects were mediated by pathogens and herbivores. To achieve this, we conducted a multifactorial field experiment with pedunculate oak, *Quercus robur,* manipulating date of seedling germination and light availability, and measured plant traits, performance, and rates of attack by fungal pathogens, herbivorous insects and small mammals. More specifically, we addressed the following questions:

(1) How do germination timing and light availability affect seedling performance?
(2) How do germination timing and light availability affect the incidence and severity of plant attack?
(3) Does attack by pathogens and herbivores mediate the effect of germination timing and light availability on seedling performance?

We hypothesized that germination timing and light availability would affect both plant performance and rates of herbivory and infection. Specifically, we expected that seedlings with early spring germination and high light availability would have the highest survival and growth rates, and that late germinating seedlings growing under lower light availability may have a disproportionate reduction in performance.

We also expected that late germinating seedlings, which develop when pathogen spore loads are higher, would have higher levels of pathogen infection (Desprez-Loustau et al., 2010). Germination timing will likely impact synchrony with herbivores, whilst higher light availability will increase herbivory and decrease pathogen infection (Newsham et al., 2000; Muth et al., 2008). Germination timing and light availability may interactively shape plant attackers, such as higher light availability decreasing pathogen infection in more exposed late germinating seedlings. We further predicted that germination timing and light availability affect plant performance both directly, and through effects on plant attackers.

2. Materials and methods

2.1. Study system

The pedunculate oak, *Quercus robur* L., is a deciduous tree species belonging to the family Fagaceae. The pedunculate oak is common throughout Europe and reaches the northern limit of its range in southern Norway, Finland and Sweden (Zanetto, Roussel, & Kremer, 1994). The phenology of the pedunculate oak varies strongly within and among populations and between years (Bacilieri et al., 1995; Kremer et al., 2010).

The pedunculate oak hosts numerous pathogens (Horst, 2013) and herbivorous insects (Ranius and Hedin, 2001). In Europe, the most common fungal pathogens on the pedunculate oak are powdery mildews. In Sweden, the oak powdery mildew complex is dominated by two species belonging to the genus *Erysiphe.* The two species are spatially separated across the leaf surface: *E. alphitoides* mainly infects the upper leaf surface, and *E. hypophylla* is restricted to the lower leaf surface (Desprez-Loustau et al., 2018). Infection may cause tissue necrosis and is potentially devastating for young oak seedlings in natural systems and in tree nurseries (Marçais & Bréda, 2006). Infection in spring starts from overwintering sexual spores. During the growing season, the pathogen produces wind-dispersed, asexual spores (Marçais & Desprez-Loustau, 2014). The pedunculate oak also harbors a large number of herbivorous insects, including several species of Lepidoptera (Southwood, 1961). Further, oak acorns and seedlings are regularly browsed upon by various small mammals such as mice, voles and hares (Jensen et al., 2012).

2.2. Experimental design

To identify how variation in spring phenology and light availability can impact *Q. robur* seedling performance, as well as its associated pathogens and herbivores, we manipulated germination timing and light availability in a multifactorial design (Fig. S1). In order to create phenological differences between oak seedlings that correspond to the natural period of germination of oak (Nilsson et al., 1996; De Lombaerde et al., 2020), acorns were planted at three-week intervals: i) early germinating acorns were planted on 22 April 2018; ii) medium germinating acorns were planted on 15 May 2018; and iii) late germinating acorns were planted on 3 June 2018. Acorns were planted in plastic pots (7 cm × 7 cm × 18 cm) in potting soil (Krukväxtjord, SW Horto, Hammenhög, Sweden), covered with a thin layer of potting soil, and placed in a greenhouse (21 °C day/18 °C night). Seedlings were translocated to the field directly after germination to ensure natural exposure to infection and herbivory during their entire growth period. Thus, the environment experienced by seedlings at the same developmental stage differed based on our manipulation of germination timing, and when seedlings were translocated to the field. Seedlings were kept within the pots to prevent the confounding effect of spatial variation in soil types, and pots were buried into the ground to prevent heat damage from sunlight. A ground sheeting (Fågelskrämma, Stockholm, Sweden) was placed around the pots to prevent competition with other plants. In the field, seedlings from each phenology treatment were divided equally

into high light (55% of natural light) and low light (35% of natural light) treatment groups, via shade nets (Meyer, Frankfurt, Germany) creating six blocks (5 m × 3 m) for each light availability treatment. The field site was near the Bergius Botanical Garden (N 59°22′3.023″, E 18°3′3.907″). An electric fence (Gallagher, Stockholm, Sweden) was established around the field site to exclude large herbivores. The seedlings were watered *ad libitum* throughout the experiment, taking care to keep soil moisture constant across treatment combinations.

2.3. Data collection

To study how seedling traits and performance were influenced by germination timing and light availability, we measured several responses related to plant physiology and size. We measured leaf thickness (recorded with an IP-54 Electronic Outside Micrometre, Helios Pressier, Germany) and leaf chlorophyll (recorded as chlorophyll content index [CCI], with a CCm-200+ chlorophyll meter, Optisciences, Hudson, USA) on 8 August 2018, seedling height on 15 August 2018, leaf size on 20 August 2018 and the total number of leaves on 23 August 2018.

To study how germination timing and light availability affect attack by pathogens and herbivores, we measured powdery mildew infection on four occasions (25 June, 4 July, 17 July and 31 July 2018), and leaf herbivory on two occasions (25 June and 19 July 2018). For all seedlings, we recorded the presence or absence of powdery mildew and herbivore damage on each leaf (referred to as "infection incidence" and "herbivory incidence" respectively). We estimated powdery mildew severity as the percentage of each leaf on a seedling covered by the pathogen, with the upper and lower surfaces of the leaf measured separately. Likewise, we scored leaf herbivory severity as the percentage damage per leaf (Johnson et al., 2016). Severity scores were then averaged among all the seedling's leaves to get an average severity of herbivore and pathogen attack per seedling.

To investigate the impact of germination timing and light availability on attack by small mammal herbivores, we recorded feeding marks. Small mammal feeding marks were easy to identify and were characterized by heavy feeding on the acorn and/or seedling, often with the consumption of the entire seedling. The date and causes of seedling mortality were recorded throughout the experiment in 2018. In the following year (2019), we revisited the seedlings from May to June to record overwintering survival rates.

2.4. Statistical analyses

Statistical analyses were performed using R v 3.6.1 (R Core Team, 2019). Model structures, response variables and transformations are summarized in Table S1. Models were implemented with the *lmer* and *glmer* functions in the *lme4* package (Bates et al., 2014), and we tested for significance with the *Anova* function in the *car* package (Fox and Weisberg, 2019).

Effects of germination timing and light availability on seedling performance – To assess the impact of germination timing and light availability on seedling traits and performance, we used linear mixed effect models. More specifically, we used separate models for leaf chlorophyll, leaf thickness, seedling height, leaf area, leaf number, survival (in 2018) and overwintering survival (spring 2019), and modelled each response variable as a function of the fixed effects *'germination timing'*, *'light availability'* and *'germination timing × light availability'*. To account for variation between blocks, the random factor *'block'* was included in the models.

Effects of germination timing and light availability on plant attack – To assess the impact of germination timing and light availability on the leaf-level incidence of powdery mildew and herbivory, we used repeated-measures generalized linear mixed effects models with a binomial distribution. To assess the impact of germination timing and light availability on the average severity of powdery mildew and leaf herbivory per seedling, we used repeated measures linear mixed effects

models. We modelled the incidence and severity of powdery mildew (separately for the lower and upper leaf surface) and herbivory as a function of the fixed effects *'germination timing'*, *'light availability'* and *'date'*. To account for any changes in treatment effects through time, we included interactions between date, germination timing and light availability. For incidence models, we included the random effect *'plant ID'*, as incidence of attack was recorded for multiple leaves from the same seedling. We further included the random factor *'block'*.

As the treatment effects changed through time (i.e., there were significant *'germination timing × date'* and/or *'light availability × date'* interactions), we created date-specific models. More specifically, we modelled the date-specific incidence and severity of infection and herbivory as a function of the fixed effects *'germination timing'*, *'light availability'*, the interaction *'light availability × germination timing'*, the random factor *'block'*, and, for the incidence models, the random factor *'plant ID'*.

Effects of germination timing and light availability on seedling performance as mediated by plant attack – To test whether the effects of germination timing and light availability were mediated by plant attack, we compared models with vs. without the covariates powdery mildew infection and herbivory. Powdery mildew damage on the upper and lower leaf surface was expressed as the area under the disease progression curve (AUDPC), which gives a quantitative summary of disease intensity over time (Madden et al., 2017). For herbivory, we averaged the percentage of leaf herbivory across the two recording dates. We modelled the seedling performance traits leaf chlorophyll, leaf thickness, seedling height, leaf area, leaf number and survival as a function of the fixed effects *'germination timing'*, *'light availability'*, *'light availability × germination timing'*, *'upper leaf AUDPC', 'lower leaf AUDPC'* and *'herbivory'*. To account for variation between blocks, the random factor *'block'* was included in the model. Differences in the estimated effects of germination timing and light availability between the models with and without the covariates (i.e. powdery mildew infection and herbivory) would provide support for the hypothesis that the effects of germination timing and light availability on seedling physiology and growth are mediated by powdery mildew infection and/or leaf herbivory. To directly test how leaf traits affect plant attack from pathogens and herbivores, we modelled upper leaf AUDPC, lower leaf AUDPC and herbivory as functions of the leaf traits *'leaf thickness'* and *'leaf chlorophyll'*.

3. Results

3.1. Effects of germination timing and light availability on seedling performance

Germination timing affected seedling performance and leaf traits, with the exception of leaf thickness (Table 1). Intermediate and late germinating seedlings had higher levels of chlorophyll and were taller (Fig. 1AB). Leaf area increased between early to late germinating seedlings, and intermediate germinating seedlings had the most leaves (Fig. 1CD). Light availability only affected chlorophyll and leaf thickness (Table 1), with seedlings under higher light having lower chlorophyll levels and greater leaf thickness than seedlings under lower light (Fig. 1EF). The effect of germination timing on plant performance and leaf traits did not differ among light availabilities (i.e., there were no significant *'germination timing × light availability'* interactions; Table 1). Seedling mortality in spring strongly increased between early to late germinating groups, with 1.1% mortality in the early germinating group, 9.8% mortality in the intermediate germinating group, and 25.1% mortality in the late germinating group (Fig. 2A; Table 1). Seedlings in the low light availability group had slightly higher mortality rates over the winter (Fig. 2B, Table 1).

Table 1

The impact of germination timing, light availability, and the interaction light availability × germination timing on performance and survival measures of oak seedlings (*Quercus robur*). Shown are the results of (generalized) linear mixed effects models described in text. Significant estimates (p < 0.05) are shown in bold.

| Response variable	Germination timing			Light availability			Light availability × Germ. timing		
	Df	F/χ²	P	Df	F/χ²	P	Df	F/χ²	P
Leaf thickness	2	1.21	0.55	1	5.22	**0.022**	2	0.69	0.72
Chlorophyll	2	33.33	**<0.0001**	1	7.4	**0.006**	2	3.6	0.16
Seedling height	2	56.52	**<0.0001**	1	0.56	0.45	2	2.13	0.34
Leaf area	2	54.27	**<0.0001**	1	0.78	0.38	2	0.17	0.92
Leaf number	2	140.32	**<0.0001**	1	0.02	0.89	2	3.01	0.22
Spring survival	2	35.19	**<0.0001**	1	0.55	0.46	2	0.08	0.96
Overwintering survival	2	0.14	0.78	1	4.72	**0.03**	2	0.14	0.93
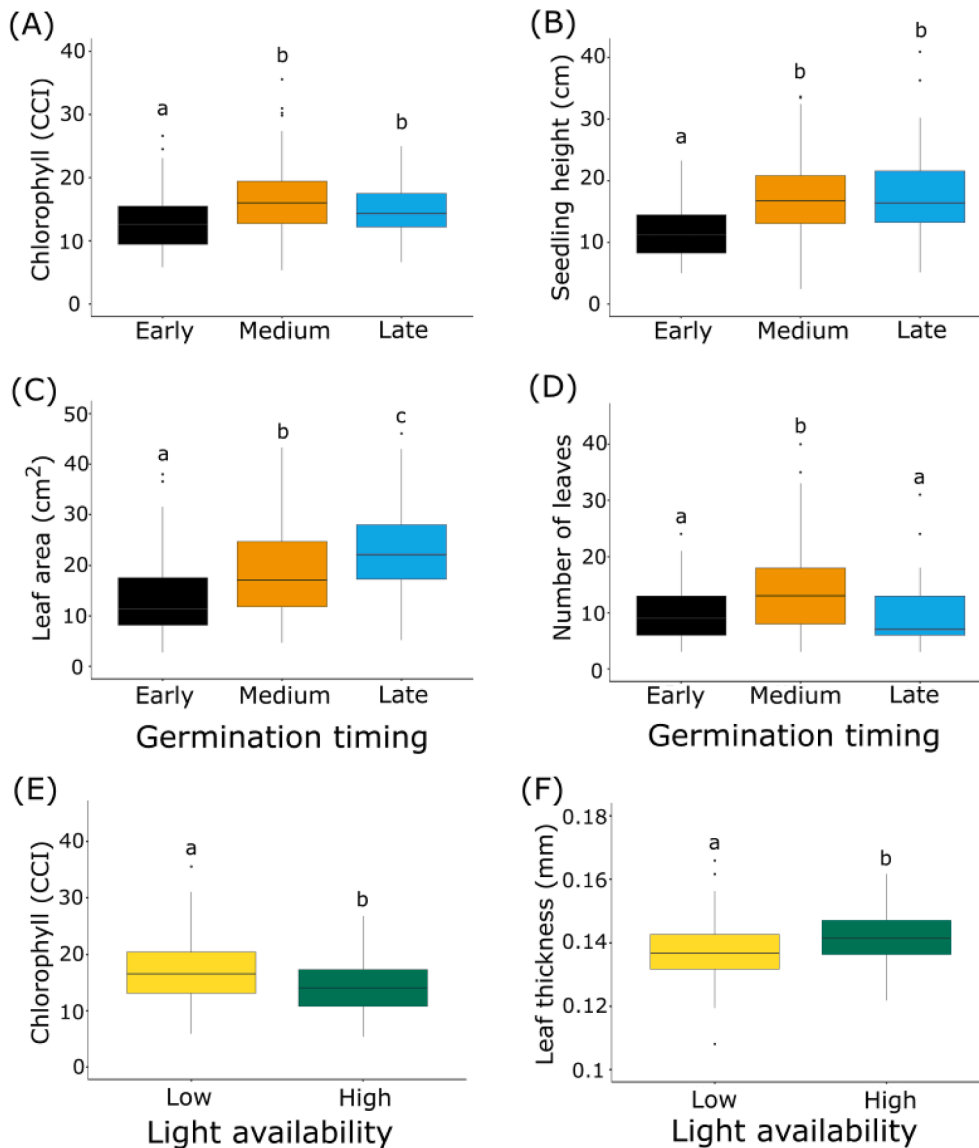
Fig. 1. The impact of germination timing and light availability on performance traits of *Quercus robur* seedlings. Shown are the impact of germination timing on (A) chlorophyll (recorded as chlorophyll content index [CCI]), (B) seedling height (C) leaf area and (D) number of leaves, and the impact of light availability on (E) chlorophyll and (F) leaf thickness. The lowercase letters identify which groups are significantly different from each other (p < 0.05) as based on post-hoc pairwise comparisons.

3.2. Effects of germination timing and light availability on plant attack

Plant attack by small mammals was higher for the later germinating seedlings: small mammals attacked 0% of the early germinating seedlings, 8.7% of the intermediate germinating seedlings, and 24.4% of the late germinating seedlings. Plant attack by small mammals was not affected by light availability or its interaction with germination timing (Table 2).

Germination timing affected powdery mildew infection incidence on the upper and lower surface of the leaves, though the effect varied through time (Table S2). Directionality of this effect was inconsistent through time for the powdery mildew on the upper leaf surface: in week 2, late germinating seedlings had the lowest infection incidence, whereas by week 6 infection incidence was lowest for the early germinating seedlings (Fig. 3A, Table 2). On the lower leaf surface, infection incidence was consistently higher for later germinating seedlings
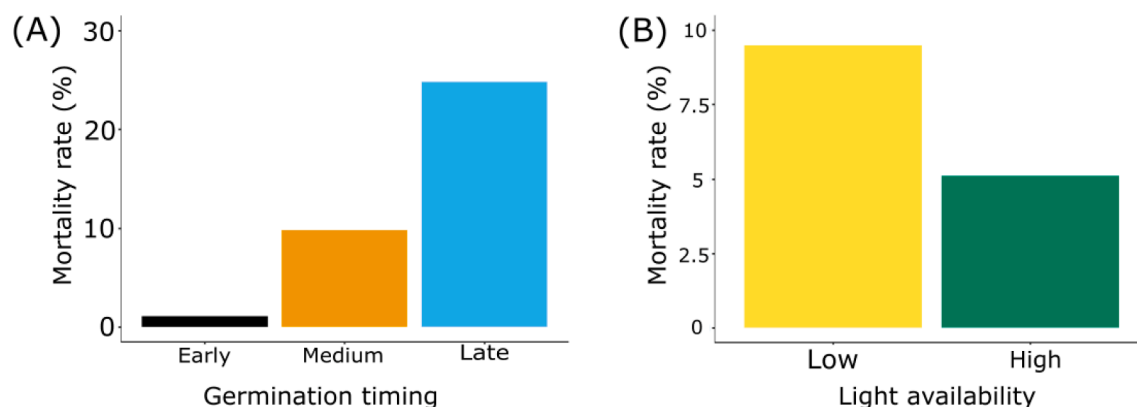
Fig. 2. The impact of germination timing and light availability on mortality rates of *Quercus robur* seedlings. Shown are (A) the relationship between germination timing and the percentage of seedlings that died during the first growing season (2018), and (B) the relationship between light availability during the first growing season on subsequent overwintering mortality.

Table 2

The impact of germination timing, light availability and their interaction on small mammal attacks, the proportion of a seedling's leaves infected with powdery mildew on the upper leaf surface, the proportion of a seedling's leaves infected with powdery mildew on the lower leaf surface, and leaf herbivory, on *Quercus robur* seedlings. Shown are the results of (generalized) linear mixed effects models described in text. Significant estimates (p < 0.05) are shown in bold.

Response variable	Week Number	Germination timing			Light availability			Light availability × Germination timing		
		DF	F/χ^2	P	DF	F/χ^2	P	DF	F/χ^2	P
Small mammal attack	N/A	2	32.8	**<0.0001**	1	1.07	0.59	2	0.2	0.9
Upper leaf surface powdery mildew incidence	Week 1	2	2.49	0.29	1	0.13	0.72	2	0.93	0.63
	Week 2	2	41.85	**<0.0001**	1	0.11	0.74	2	2.5	0.29
	Week 4	2	3.4	0.18	1	4.87	**0.027**	2	1.58	0.45
	Week 6	2	7.05	**0.029**	1	2.4	0.12	2	1.84	0.4
Lower leaf surface powdery mildew incidence	Week 4	2	67.12	**<0.0001**	1	0.29	0.59	2	0.58	0.75
	Week 6	2	60.15	**<0.0001**	1	0.16	0.69	2	2.45	0.29
Herbivory incidence	Week 1	2	36.87	**<0.0001**	1	0.9	0.34	2	7.35	**0.025**
	Week 4	2	6.08	**0.048**	1	1.03	0.31	2	3.74	0.15

(Table 2, Fig. 3C). Infection severity on the lower leaf surface, but not the upper leaf surface, was affected by germination timing (Table S2, Fig. 3BD). In week 4, infection severity was higher for early germinating seedlings, but this pattern was no longer statistically significant by week 6 (Table S3, Fig. 3D). Towards the end of the experiment, infection incidence was highest under high light availability, while severity was higher under low light availability (Tables 2, S2 and S3, Fig. 3EF). The effect of germination timing on powdery mildew incidence and severity was not affected by light availability (i.e., the '*germination timing × light availability*' interactions were not significant; Tables 2 and S3).

Germination timing affected herbivory incidence, but the pattern varied through time: herbivory was highest on intermediate germinating seedlings in week 1, and highest for late germinating seedlings in week 4 (Table 2, Fig. 4A). Moreover, the effect of germination timing on herbivory differed between the two light treatments during week 1 (Table 2). Late germinating seedlings had greatly reduced herbivory incidence under low light availability, compared to the same germination group under higher light (Fig. 4B). There were no effects of germination timing or light availability on herbivory severity (Table S3).

3.3. Effects of germination timing and light availability on seedling performance as mediated by plant attack

Small mammal herbivory was the major cause of seedling mortality: out of the 116 seedlings that died during the experiment, 109 seedlings died due to herbivory by small mammals. From those seedlings that were attacked by small mammals, only two individuals survived.

Powdery mildew and leaf herbivory did not mediate the effects of germination timing and light availability on any of the seedling performance traits in 2018, as indicated by the lack of change in

significance, and very minor change in effect estimates, of the terms '*germination timing*' or '*light availability*' when adding the covariates '*upper leaf AUDPC*', '*lower leaf AUDPC*' and '*herbivory*' to the model (cf. Table 1 and Table S4). However, the slight change in significance of the effect of light availability when the levels of pathogen and herbivore attack were included in the overwintering survival model, suggests that herbivory and pathogen infection might have mediated some of the effects of light conditions on overwintering survival of seedlings (Fig. 2B, Tables 1, S4). Leaf herbivory was only weakly positively related with leaf thickness, whereas powdery mildew infection was not associated with any of the seedling performance traits (Tables S4 and S5).

4. Discussion

Our study is among the first to quantify the impact of spring phenology (i.e., germination timing) and environmental variation (i.e., light availability) on plant performance and plant attack directly after germination and during the remainder of the growing season. We found that germination timing had a major impact on seedling performance, whereas under the range of experimental conditions we imposed light availability only affected leaf thickness and chlorophyll. Likewise, germination timing had a major impact on plant attack, while the effects of light availability on herbivory and pathogen infection were minor. While small mammals had a major effect on plant survival by preferentially attacking later germinating seedlings, insect herbivores and pathogens did not mediate the effect of germination timing and light availability on plant performance during the growing season. Taken together with the results of previous studies, our findings indicate that while abiotic factors like light availability can have a major impact on spring phenology and leaf traits, germination timing plays a more
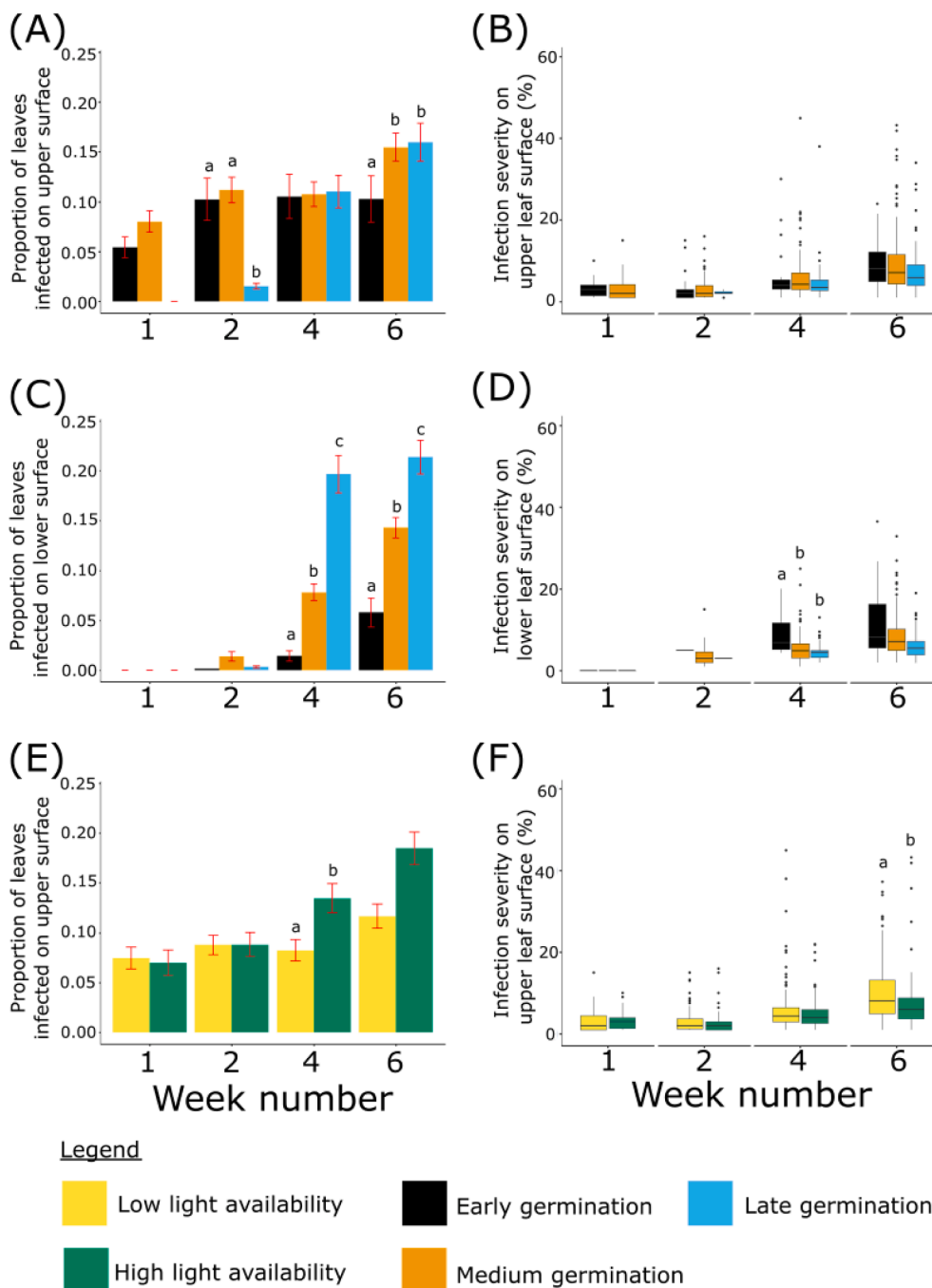
Fig. 3. The impact of early, medium and late germination timings and low and high light availability treatments on *Quercus robur* seedlings. The impact of germination timings on the proportion of leaves infected and severity of powdery mildew on (AB) the upper surface and (CD) lower surface of the leaf. The impact of light availability on (E) the proportion of leaves infected by and (F) severity of powdery mildew on the upper surface of the leaf under low and high light availability. The letters above the treatment levels identify which groups are significantly different from each other (p < 0.05) as based on post-hoc pairwise comparisons.

important role in shaping seedling growth and plant attack during the remainder of the growing season.

4.1. Effects of germination timing and light availability on seedling performance

We found that seedlings were larger in the intermediate and late germinating groups, but that mortality was lowest for early germinating seedlings. Our finding of reduced growth of early germinating seedlings contrasts with previous studies that show earlier spring germination enhances growth and survival of tree seedlings (Seiwa and Kikuzawa, 1996; Seiwa, 1997, 1998; Verdú and Traveset, 2005). One explanation for this difference may be the experimental exclusion of plant-plant competition in our experiment: under natural conditions, early germinating seedlings may gain a competitive advantage by growing before

canopy closure and escape competition from other plants. Our experimental seedlings had shade nets and ground sheeting, which removed the potential for this competitive advantage (DePamphilis & Neufeld, 1989; Miller, Winn, & Schemske, 1994; Seiwa, 2000). As expected, seedlings under low light availability produced thinner leaves with higher levels of chlorophyll, most likely as a strategy to more efficiently capture the sparser light available (Jackson, 1967; Valladares et al., 2000). One intrinsic caveat of the experimental design is that moving germinated acorns from a constant temperature regime (21 °C day/ 18 °C night) into the varied conditions of the field trial could have resulted in physiological shock (Close et al., 2005). Yet, temperature was high in spring 2018 (mean high: 23 °C/mean low: 12 °C during the planting period), and we did not detect a significant temperature trend in either the minimum or maximum daily temperature across the planting period (τ = 0.075, P = 0.47 and τ = -0.148, P = 0.15).
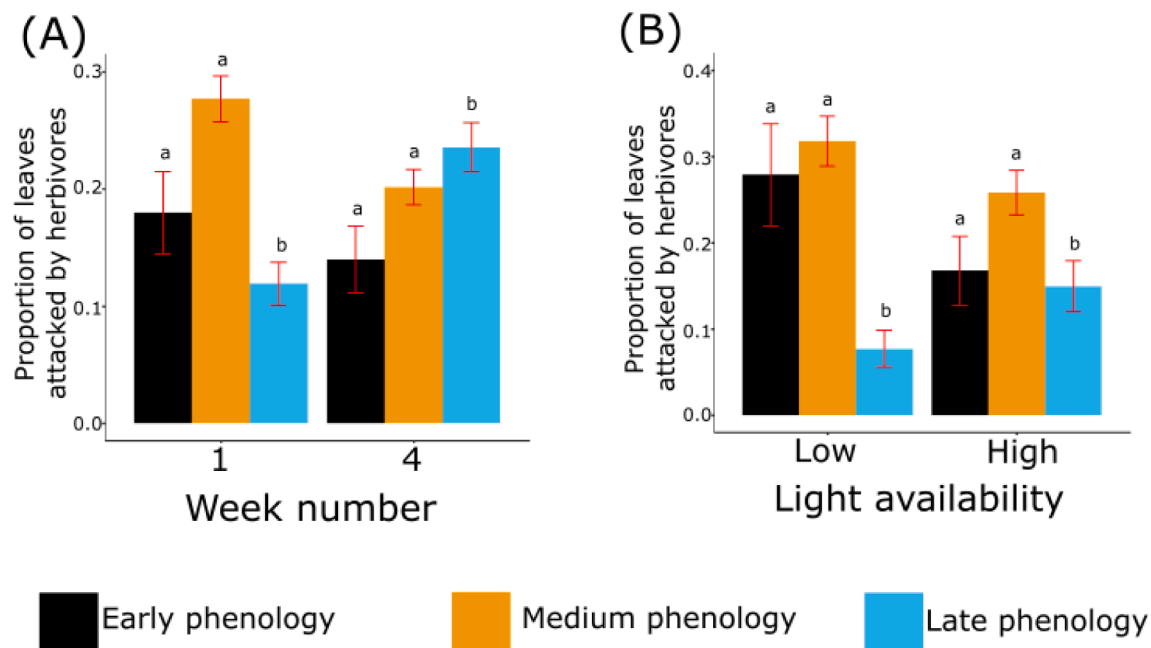
Fig. 4. The impact of germination timing and light availability on leaf herbivory incidence of *Quercus robur* seedlings. Panel (A) shows the impact of germination timing on the proportion of leaves attacked by herbivores in week 1 and 4. Panel (B) shows the interaction of germination timing and light availability on the proportion of leaves attacked for the first week of the experiment. The lowercase letters identify which groups are significantly different from each other (p < 0.05) as based on post-hoc pairwise comparisons.

4.2. Effects of germination timing and light availability on plant attack

Germination timing had a major impact on seedling attack by small mammal herbivores, powdery mildew and herbivorous insects, whereas light availability and its interaction with germination timing only explained a minor part of the variation. The apparent preference of small mammals for later-germinating seedlings may be explained by seasonal shifts in the diet of small mammals depending on the availability of alternative food resources (Soininen et al., 2013; Sunyer et al., 2014): most of the attacks occurred during the middle of the growing season, when the early germinating acorns had already started to shrivel due to extraction of resources from the acorn by the seedling.

Late germinating seedlings had the lowest disease levels on the upper leaf surface during the early part of the season, whereas infection levels on both the lower and upper surface were highest on the later-germinating seedlings towards the end of the experiment. The higher disease levels on early germinating seedlings observed early in the season may be due to a time lag between leaf colonization and the appearance of the symptoms, or due to differences in our ability to detect infection (i.e., early infections on the young developing leaves of late-phenology seedlings may have gone undetected). The findings of higher disease levels on the later-germinating seedlings at the end of the experiment matches our a priori prediction and previous research (Desprez-Loustau et al., 2010) that plants developing their leaves when the pathogen spore load in the air is already high would experience higher infection levels. Seedlings growing under lower light availability experienced higher infection severity on the upper leaf surface in the end of July. This disagrees with previous studies showing that higher light levels increased infection levels of multiple powdery mildew species (Newsham et al., 2000; Kelly, 2002), but matches field observations on higher infection levels on oaks in forest habitats when compared with unshaded open fields (Ekholm et al., 2017). Importantly, this finding suggests that low light availability may more strongly affect pathogens on the upper leaf surface, which makes sense given the fact that pathogens on the lower surface are already buffered from high surface temperatures, low relative humidity and UV radiation (Hewitt, 1974; Aust and Huene, 1986; Marçais and Desprez-Loustau, 2014).

Herbivory incidence was highest in early and intermediate-germinating seedlings at the start of the experiment, especially for those under low light availability. This pattern changed towards the end of the experiment in late July, when herbivory incidence was highest on later germinating seedlings and was similar among light availability treatments. In contrast to our findings of lower levels of cumulative herbivory on early germinating seedlings at the end of the season, Pearse et al. (2015a,b) found that earlier budburst resulted in increased levels of herbivory of adult oak trees at the end of the season. The difference between these findings suggests that selection on spring phenology may act in opposite directions during different life stages. In contrast to an earlier study (Muth et al., 2008), we did not find an independent effect of light availability on herbivory. Future studies may explore the mechanistic underpinning of the interactive effect of light availability and phenology in determining herbivory of seedlings. For example, seasonality, plant ontogeny, and light availability may each affect a seedling's defenses and nutritional profile, and therefore its quality as a resource to insect herbivores.

4.3. Effects of germination timing and light availability on seedling performance as mediated by plant attack

Small mammals mediated the effect of germination timing on plant survival: early germinating seedlings largely escaped attack, intermediate germinating seedlings had average rates of attack, and nearly one out of four late germinating seedlings died due to feeding by small mammals. Matching our findings on a phenological preference, Seiwa (1998) previously demonstrated in a natural forest that seedling attack by small mammals was lower for early germinating seedlings. Interestingly, this would suggest there is an advantage for early phenology seedlings to emerge from deeper underground, for example after being buried by squirrels, as this might reduce attack rates. As nearly every plant attacked by small mammals died, small mammals did not affect other aspects of seedling performance.

In contrast to the strong effect of small mammal herbivory on seedling survival, pathogen infection and insect herbivory had negligible effects on seedling survival and performance, and thus did not

mediate the effects of germination timing and light availability. The limited effect of pathogens and leaf herbivory on plant performance contrasts with other studies on both seedlings (Norghauer and Newbery, 2014; Solé et al., 2019) and adult oaks (Marçais & Bréda, 2006; Pearse et al., 2015b). While levels of infection and infestation in our study were well within the natural range found in Sweden and Europe, infection and infestation are also well known for their high variance, and may be affected by microclimate and distance to neighbouring oak trees (Seiwa et al., 2008; Deniau et al., 2017; Ekholm et al., 2017; Moreira et al., 2018; Demeter et al., 2021). In particular, major effects of powdery mildew on oak performance may only occur when seedlings, saplings or mature trees are severely infected (Bert et al., 2016; Dillen et al., 2016; Demeter et al., 2021). An interesting avenue for future research would thus be to explore the generality of our findings across environmental and geographic contexts, for example by establishing multiple common gardens where seedlings are tracked across multiple years. Such studies could also take into account the possible mediating role of beneficial microorganisms in the patterns observed. For example, mycorrhizal fungi are known to have a distinct phenology (Johnson-Green et al., 1995) and can have a profound impact on plant physiology, herbivory and disease levels (Idoia et al., 2004; Koricheva et al., 2009; Deniau et al., 2018).

Another explanation for the lack of an effect of pathogens and insects on seedling performance may be the availability of stored seed reserves, which could offset any immediate costs of infection and herbivory (Grime and Jeffrey, 1965). Although drawing upon stored reserves can affect future survival and performance (Sala et al., 2012; Pearse et al., 2015b), we found no effect of infection or herbivory on overwinter survival of our experimental seedlings, although we are unable to say if there would have been an effect on future plant performance. Taken together, while small mammals directly kill seedlings and thereby are likely to exert strong selection for seedling phenology, the seedling may be able to compensate the effect of pathogen and insect attack on plant performance by tapping into the stored resources in the acorn, at least in the short term.

5. Conclusions

With a changing climate, many organisms in seasonal environments will advance their spring phenology, and as a result experience different light conditions at a given developmental stage. Our study is among the first to investigate the simultaneous effects of germination timing and light availability on seedling performance and antagonists during the growing season. We found that the effect of spring phenology (i.e., germination timing) outweighs the effect of the abiotic environment (i. e., light availability) on seedling performance and several types of plant attack. Interestingly, our results suggest that sometimes small mammals, and not herbivorous insects and pathogens, mediate the effects of spring phenology on plant performance. Despite the previously demonstrated importance of light availability for creating spatial variation in spring phenology, we found that seedling performance and attack were largely unaffected by light availability. Hence, we conclude that abiotic factors like light availability may contribute to variation in phenology early in the season, but that spring phenology is more important than light availability for plant performance and attack during the growing season.

Author contributions

RWM, AJMT, JE and LJAvD conceived and designed the experiment. RWM conducted the empirical work. RWM analyzed the data. RWM wrote the first draft, and all authors contributed to the final manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data accessibility

Data associated with this manuscript will be archived in the Dryad Digital Repository upon acceptance.

References

Aust, H.J., Huene, J., 1986. Microclimate in relation to epidemics of powdery mildew. Annu. Rev. Phytopathol. 24, 491–510. https://doi.org/10.1146/annurev. py.24.090186.002423.

Austin, C.N., Wilcox, W.F., 2012. Effects of sunlight exposure on grapevine powdery mildew development. Phytopathology 102, 857–866. https://doi.org/10.1094/ PHYTO-07-11-0205.

Bacilieri, R., Ducousso, A., Kremer, A., 1995. Genetic, morphological, ecological and phenological differentiation between *Quercus petraea (Matt.) LIEBL.* and *Quercus robur L.* in a mixed stand of northwest of France. Silvae Genetica 44, 1–10.

Barber, N.A., Fahey, R.T., 2015. Consequences of phenology variation and oxidative defenses in *Quercus*. Chemoecology 25, 261–270. https://doi.org/10.1007/s00049-015-0194-5.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

Benard, R.B., Toft, C.A., 2007. Effect of Seed Size on Seedling Performance in a Long-Lived Desert Perennial Shrub (*Ericameria nauseosa* : Asteraceae). Int. J. Plant Sci. 168, 1027–1033. https://doi.org/10.1086/518942.

Bennie, J., Kubin, E., Wiltshire, A., et al., 2010. Predicting spatial and temporal patterns of bud-burst and spring frost risk in north-west Europe: the implications of local adaptation to climate. Glob. Change Biol. 16, 1503–1514. https://doi.org/10.1111/j.1365-2486.2009.02095.x.

Bert, D., Lasnier, J.-B., Capdevielle, X., et al., 2016. Powdery Mildew decreases the radial growth of oak trees with cumulative and delayed effects over years. PLoS ONE 11, e0155344. https://doi.org/10.1371/journal.pone.0155344.

Close, D.C., Beadle, C.L., Brown, P.H., 2005. The physiological basis of containerised tree seedling 'transplant shock': a review. Australian Forestry 68, 112–120. https://doi.org/10.1080/00049158.2005.10674954.

Crawley, M.J., Akhteruzzaman, M., 1988. Individual variation in the phenology of oak trees and its consequences for herbivorous insects. Funct. Ecol. 2, 409–415. https://doi.org/10.2307/2389414.

Daws, M.I., Burslem, D.F.R.P., Crabtree, L.M., et al., 2002. Differences in seed germination responses may promote coexistence of four sympatric Piper species. Funct Ecol. 16, 258–267. https://doi.org/10.1046/j.1365-2435.2002.00615.x.

De Lombaerde, E., Blondeel, H., Baeten, L., et al., 2020. Light, temperature and understorey cover predominantly affect early life stages of tree seedlings in a multifactorial mesocosm experiment. For. Ecol. Manage. 461, 117907 https://doi.org/10.1016/j.foreco.2020.117907.

Demeter, L., Molnár, Á.P., Öllerer, K., et al., 2021. Rethinking the natural regeneration failure of pedunculate oak: The pathogen mildew hypothesis. Biol. Conserv. 253, 108928 https://doi.org/10.1016/j.biocon.2020.108928.

Deniau, M., Jung, V., Le Lann, C., et al., 2017. Janzen-Connell patterns are not the result of Janzen-Connell process: Oak recruitment in temperate forests. Perspect. Plant Ecol., Evol. Systematics 24, 72–79. https://doi.org/10.1016/j.ppees.2016.12.001.

Deniau, M., Jung, V., Le Lann, C., et al., 2018. Janzen-Connell patterns can be induced by fungal-driven decomposition and offset by ectomycorrhizal fungi accumulated under a closely related canopy. Funct. Ecol. 32, 785–798. https://doi.org/10.1111/1365-2435.13003.

DePamphilis, C.W., Neufeld, H.S., 1989. Phenology and ecophysiology of *Aesculus sylvatica*, a vernal understory tree. Can. J. Bot. 67, 2161–2167. https://doi.org/10.1139/b89-274.

Desprez-Loustau, M.-L., Massot, M., Toïgo, M., et al., 2018. From leaf to continent: the multi-scale distribution of an invasive cryptic pathogen complex on oak. Fungal Ecol. 36, 39–50. https://doi.org/10.1016/j.funeco.2018.08.001.

Desprez-Loustau, M.-L., Vitasse, Y., Delzon, S., et al., 2010. Are plant pathogen populations adapted for encounter with their host? A case study of phenological synchrony between oak and an obligate fungal parasite along an altitudinal gradient. J. Evol. Biol. 23, 87–97. https://doi.org/10.1111/j.1420-9101.2009.01881.x.

Dillen, M., Verheyen, K., Smit, C., 2016. Identity rather than richness drives local neighbourhood species composition effects on oak sapling growth in a young forest. For. Ecol. Manage. 380, 274–284. https://doi.org/10.1016/j.foreco.2016.09.004.

Donnelly, A., Caffarra, A., O'Neill, B.F., 2011. A review of climate-driven mismatches between interdependent phenophases in terrestrial and aquatic ecosystems. Int. J. Biometeorol. 55, 805–817. https://doi.org/10.1007/s00484-011-0426-5.

Ekholm, A., Roslin, T., Pulkkinen, P., Tack, A.J.M., 2017. Dispersal, host genotype and environment shape the spatial dynamics of a parasite in the wild. Ecology 98, 2574–2584. https://doi.org/10.1002/ecy.1949.

Elad, Y., Messika, Y., Brand, M., et al., 2007. Effect of colored shade nets on pepper powdery mildew. Phytoparasitica 35, 285–299. https://doi.org/10.1007/BF02981163.

Forrest, J.R., 2016. Complex responses of insect phenology to climate change. Curr. Opin. Insect Sci. 17, 49–54. https://doi.org/10.1016/j.cois.2016.07.002.

Fox, J., Weisberg, S., 2019. An {R} companion to applied regression.

Gioria, M., Pyšek, P., Osborne, B.A., 2016. Timing is everything: does early and late germination favor invasions by herbaceous alien plants? JPECOL 11, 4–16. https://doi.org/10.1093/jpe/rtw105.

Grime, J.P., Jeffrey, D.W., 1965. Seedling establishment in vertical gradients of sunlight. J. Ecol. 53, 621–642. https://doi.org/10.2307/2257624.

Guest, D., Brown, J., 1997. Plant defences against pathogens. In: Plant Pathogens and Plant Diseases. pp 263–286.

Hamilton, J.A., El Kayal, W., Hart, A.T., et al., 2016. The joint influence of photoperiod and temperature during growth cessation and development of dormancy in white spruce (*Picea glauca*). Tree Physiol. 36, 1432–1448. https://doi.org/10.1093/treephys/tpw061.

Heberling, J.M., McDonough MacKenzie, C., Fridley, J.D., et al., 2019. Phenological mismatch with trees reduces wildflower carbon budgets. Ecol. Lett. 22, 616–623. https://doi.org/10.1111/ele.13224.

Heimonen, K., Valtonen, A., Kontunen-Soppela, S., et al., 2017. Susceptibility of silver birch (*Betula pendula*) to herbivorous insects is associated with the size and phenology of birch – implications for climate warming. Scand. J. For. Res. 32, 95–104. https://doi.org/10.1080/02827581.2016.1195867.

Hewitt, H.G., 1974. Conidial germination in *Microsphaera alphitoides*. Trans. Br. Mycol. Soc. 63, 587–628. https://doi.org/10.1016/S0007-1536(74)80107-5.

Horst, R. Kenneth, 2013. Westcott's plant disease handbook. Springer, New York.

Ibáñez, I., Primack, R.B., Miller-Rushing, A.J., et al., 2010. Forecasting phenology under global warming. Phil. Trans. Roy. .Soc B 365, 3247–3260. https://doi.org/10.1098/rstb.2010.0120.

Idoia, G., Nieves, G., Jone, A., 2004. Plant phenology influences the effect of Mycorrhizal Fungi on the development of verticillium-induced wilt in pepper. Eur. J. Plant Pathol. 110, 227–238. https://doi.org/10.1023/B:EJPP.0000019790.45397.90.

Jackson, L.W.R., 1967. Effect of shade on leaf structure of deciduous tree species. Ecology 48, 498–499. https://doi.org/10.2307/1932686.

Jensen, A.M., Götmark, F., Löf, M., 2012. Shrubs protect oak seedlings against ungulate browsing in temperate broadleaved forests of conservation interest: A field experiment. For. Ecol. Manage. 266, 187–193. https://doi.org/10.1016/j.foreco.2011.11.022.

Johnson, M.T.J., Bertrand, J.A., Turcotte, M.M., 2016. Precision and accuracy in quantifying herbivory: Estimating herbivory. Ecol. Entomol. 41, 112–121. https://doi.org/10.1111/een.12280.

Johnson-Green, P.C., Kenkel, N.C., Booth, T., 1995. The distribution and phenology of arbuscular mycorrhizae along an inland salinity gradient. Can. J. Bot. 73, 1318–1327. https://doi.org/10.1139/b95-143.

Kelly, D.L., 2002. The regeneration of *Quercus petraea* (sessile oak) in southwest Ireland: a 25-year experimental study. For. Ecol. Manage. 166, 207–226. https://doi.org/10.1016/S0378-1127(01)00670-3.

Kharouba, H.M., Ehrlén, J., Gelman, A., et al., 2018. Global shifts in the phenological synchrony of species interactions over recent decades. Proc. Natl. Acad. Sci. 115, 5211–5216. https://doi.org/10.1073/pnas.1714511115.

Koricheva, J., Gange, A.C., Jones, T., 2009. Effects of mycorrhizal fungi on insect herbivores: a meta-analysis. Ecology 90, 2088–2097. https://doi.org/10.1890/08-1555.1.

Kremer, A., Le Corre, V., Petit, R., Ducousso, A., 2010. Historical and contemporary dynamics of adaptive differentiation in European oaks. Molecular Approaches in Natural Resource Conservation and Management. Cambridge University Press, Cambridge.

Louda, S.M., Rodman, J.E., 1996. Insect Herbivory as a Major Factor in the Shade Distribution of a Native Crucifer (Cardamine Cordifolia A. Gray, Bittercress). The. J. Ecol. 84 (229) https://doi.org/10.2307/2261358.

Madden, L.V., Hughes, G., van den Bosch, F., 2017. The Study of Plant Disease Epidemics. The American Phytopathological Society.

Marçais, B., Bréda, N., 2006. Role of an opportunistic pathogen in the decline of stressed oak trees. J. Ecol. 94, 1214–1223. https://doi.org/10.1111/j.1365-2745.2006.01173.x.

Marçais, B., Desprez-Loustau, M.-L., 2014. European oak powdery mildew: impact on trees, effects of environmental factors, and potential effects of climate change. Ann. Forest Sci. 71, 633–642. https://doi.org/10.1007/s13595-012-0252-x.

Miller, T.E., Winn, A.A., Schemske, D.W., 1994. The effects of density and spatial distribution on selection for emergence time in *Prunella vulgaris* (Lamiaceae). Am. J. Bot. 81, 1. https://doi.org/10.2307/2445555.

Moreira, X., Castagneyrol, B., Abdala-Roberts, L., et al., 2018. Latitudinal variation in plant chemical defences drives latitudinal patterns of leaf herbivory. Ecography 41, 1124–1134. https://doi.org/10.1111/ecog.03326.

Muth, N.Z., Kluger, E.C., Levy, J.H., et al., 2008. Increased per capita herbivory in the shade: Necessity, feedback, or luxury consumption? Écoscience 15, 182–188. https://doi.org/10.2980/15-2-3095.

Newsham, B.K.K., Oxborough, K., White, R., et al., 2000. UV-B radiation constrains the photosynthesis of *Quercus robur* through impacts on the abundance of *Microsphaera alphitoides*. Forest Pathol. 30, 265–275. https://doi.org/10.1046/j.1439-0329.2000.00213.x.

Nilsson, U., Gemmel, P., Löf, M., Welander, T., 1996. Germination and early growth of sown Quercus robur L. in relation to soil preparation, sowing depths and prevention against predation. New Forest. 12, 69–86. https://doi.org/10.1007/BF00029983.

Norghauer, J.M., Newbery, D.M., 2014. Herbivores differentially limit the seedling growth and sapling recruitment of two dominant rain forest trees. Oecologia 174, 459–469. https://doi.org/10.1007/s00442-013-2769-6.

Parmesan, C., Hanley, M.E., 2015. Plants and climate change: complexities and surprises. Ann. Bot. 116, 849–864. https://doi.org/10.1093/aob/mcv169.

Pearse, I.S., Baty, J.H., Herrmann, D., et al., 2015a. Leaf phenology mediates provenance differences in herbivore populations on valley oaks in a common garden: Oak phenology and herbivory. Ecol. Entomol. 40, 525–531. https://doi.org/10.1111/een.12219.

Pearse, I.S., Funk, K.A., Kraft, T.S., Koenig, W.D., 2015b. Lagged effects of early-season herbivores on valley oak fecundity. Oecologia 178, 361–368. https://doi.org/10.1007/s00442-014-3193-2.

R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ranius, T., Hedin, J., 2001. The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. Oecologia 126, 363–370. https://doi.org/10.1007/s004420000529.

Sala, A., Hopping, K., McIntire, E.J.B., et al., 2012. Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. New Phytol. 196, 189–199. https://doi.org/10.1111/j.1469-8137.2012.04257.x.

Seiwa, K., 1998. Advantages of early germination for growth and survival of seedlings of Acer mono under different overstorey phenologies in deciduous broad-leaved forests. J. Ecol. 86, 219–228. https://doi.org/10.1046/j.1365-2745.1998.00245.x.

Seiwa, K., 2000. Effects of seed size and emergence time on tree seedling establishment: importance of developmental constraints. Oecologia 123, 208–215. https://doi.org/10.1007/s004420051007.

Seiwa, K., 1997. Variable regeneration behaviour of Ulmus davidiana var. Japonica in response to disturbance regime for risk spreading. Seed Sci. Res. 7. https://doi.org/10.1017/S0960258500003536.

Seiwa, K., Kikuzawa, K., 1996. Importance of seed size for the establishment of seedlings of five deciduous broad-leaved tree species. Vegetatio 123, 51–64. https://doi.org/10.1007/BF00044887.

Seiwa, K., Miwa, Y., Sahashi, N., et al., 2008. Pathogen attack and spatial patterns of juvenile mortality and growth in a temperate tree, *Prunus grayana*. Can. J. For. Res. 38, 2445–2454. https://doi.org/10.1139/X08-084.

Shevtsova, A., Graae, B.J., Jochum, T., et al., 2009. Critical periods for impact of climate warming on early seedling establishment in subarctic tundra. Glob. Change Biol. 15, 2662–2680. https://doi.org/10.1111/j.1365-2486.2009.01947.x.

Soininen, E.M., Ravolainen, V.T., Bråthen, K.A., et al., 2013. Arctic Small Rodents Have Diverse Diets and Flexible Food Selection. PLoS ONE 8, e68128. https://doi.org/10.1371/journal.pone.0068128.

Solé, R., Gripenberg, S., Lewis, O.T., et al., 2019. The role of herbivorous insects and pathogens in the regeneration dynamics of *Guazuma ulmifolia* in Panama. NC 32, 81–101. https://doi.org/10.3897/natureconservation.32.30108.

Southwood, T.R.E., 1961. The Number of Species of Insect Associated with Various Trees. J. Animal Ecol. 30, 1–8. https://doi.org/10.2307/2109.

Sunyer, P., Espelta, J.M., Bonal, R., Muñoz, A., 2014. Seeding phenology influences wood mouse seed choices: the overlooked role of timing in the foraging decisions by seed-dispersing rodents. Behav. Ecol. Sociobiol. 68, 1205–1213. https://doi.org/10.1007/s00265-014-1731-x.

Suthaparan, A., Solhaug, K.A., Bjugstad, N., et al., 2016. Suppression of powdery Mildews by UV-B: application frequency and timing, dose, reflectance, and automation. Plant Dis. 100, 1643–1650. https://doi.org/10.1094/PDIS-12-15-1440-RE.

Thackeray, 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature 535, 241–245.

Valladares, F., Martinez-Ferri, E., Balaguer, L., et al., 2000. Low leaf-level response to light and nutrients in Mediterranean evergreen oaks: a conservative resource-use strategy? New Phytol. 148, 79–91. https://doi.org/10.1046/j.1469-8137.2000.00737.x.

Vautard, R., Gobiet, A., Sobolowski, S., et al., 2014. The European climate under a 2 °C global warming. Environ. Res. Lett. 9, 1–11. https://doi.org/10.1088/1748-9326/14/034006.

Vazquez-Yanes, C., Orozco-Segovia, A., Rincon, E., et al., 1990. Light beneath the litter in a tropical forest: effect on seed germination. Ecology 71, 1952–1958. https://doi.org/10.2307/1937603.

Verdú, M., Traveset, A., 2005. Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. Ecology 86, 1385–1394. https://doi.org/10.1890/04-1647.

Welander, N.T., Ottosson, B., 1998. The influence of shading on growth and morphology in seedlings of *Quercus robur* L. and *Fagus sylvatica* L. For. Ecol. Manage. 107, 117–126. https://doi.org/10.1016/S0378-1127(97)00326-5.

Zanetto, A., Roussel, G., Kremer, A., 1994. Geographic variation of inter-specific differentiation between *Quercus robur* L. and *Quercus petraea (MATT.) LIEBL.* For. Genet. 1, 111–123.