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Fagus sylvatica dominance in European forests

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In memory of Peter Brang

I remember your smile

SUMMARY

Gaining an improved understanding of the strategies, traits and conditions that enable tree species to achieve dominance in forest ecosystems is important for predictions of community assembly and for the question how these species will respond to global change. A striking example of a species with strong dominance is *Fagus sylvatica* L. (European beech). In temperate European forests, the adoption of ‘close-to-nature silviculture’ and the cessation of forest management in forest reserves have allowed *Fagus sylvatica* to increase its share and have sparked new interest in the mechanisms of its dominance. An outstanding object to study its dominance is the largest remnant primary *Fagus sylvatica* forest, Uholka-Shyrokyi Luh in the Ukrainian Carpathians. The main objective of this thesis is to investigate the competitive advantages of *Fagus sylvatica* over *Acer platanoides, A. pseudoplatanus* and *Ulmus glabra.* To do so, traits of shade tolerance and associated competitive advantages were studied: i) the influence of species identity, tree age and biomass partitioning to leaves and shoots on leaf area ratio, absolute growth rate of tree biomass and storage pools in stem and root; ii) mortality rates and survival times of *Fagus sylvatica* and *Acer spp.*; and iii) the abundance of understory trees under canopy trees of *Fagus sylvatica*, *Acer* spp. and *U. glabra* as a proxy of replacement probability.

The aim of the first chapter is to investigate how species identity and biomass partitioning to leaves and shoots affect the development of leaf area ratio, the absolute growth rate of tree biomass and the amount of the storage pools with increasing age. Specifically, the impact of the potential trade-off between absolute growth rate and biomass allocation to storage in stem and roots on the survival time of juvenile trees growing in deep shade was studied. This study was carried out in the Uholka part of the reserve, on six rectangular plots where mature and juvenile *Acer platanoides, A. pseudoplatanus, Fagus sylvatica* were present, and which varied from 0.2 to 0.7 ha in size. In total 289 seedlings (0-129 cm height) and saplings (130-500 cm height) of the three species were excavated, and their diameter at the root collar, height increment, leaf area, crown projection, age and concentration of non-structural carbohydrates were measured. With increasing tree age, leaf area ratio and growth rate decreased while storage increased. Juvenile trees experienced a trade-off between absolute growth rate and storage at decreasing leaf area ratio with biomass development. High leaf area ratio but slow absolute growth rate and low storage confer

Fagus sylvatica a marked ability to persist in deep shade more than a decade longer than its competitors awaiting canopy release. In turn, a comparably small leaf area ratio in combination with a high absolute growth rate and high storage, as observed in *Acer* spp., reduces their survival time, thus offering an explanation why beech reaches dominance whereas *Acer* spp. disappear in the understory of primary beech forests.

The second chapter focuses on age-specific mortality rates and survival times of regeneration (inferred only in the first chapter) in deep shade. *Fagus sylvatica* featured a higher leaf area ratio and slower growth while its mortality rate in the age of 40-50 years reached 3.6% over a periode of 3 years. In contrast, a combination of lower leaf area ratio and higher growth rate corresponded with higher age-specific mortality rates of 7-8% at an age of 40-50 years in the two *Acer* species. The mean survival time of *Fagus sylvatica* juveniles was higher, with an estimated value of 72 years vs. 47-48 years for both *Acer* species when adjusted for their low radial growth (20-100 µm yr^{-1}) and for the height class 131-200 cm. The longer survival time of *Fagus sylvatica* before the first release due to a canopy opening enables it to reach the canopy more often and in higher numbers than *Acer* spp.

The third chapter complements the second with respect to the question how many saplings and poles (dbh 6-25 cm) are found under canopy trees, with the potential to replace mature host trees. The study used data from four inventories carried out on a 10-ha permanent plot in Uholka. Due to the lower mortality of *Fagus sylvatica* in the sapling class (see Chapter 2), more poles are available for replacement than in *Acer* spp. and *U. glabra*. Despite an increase of *Acer spp.* and *Ulmus glabra* saplings over time, *Fagus sylvatica* advance regeneration was much more numerous than that of the two minor species, in particular if a host was surrounded by other canopy trees. This indicates a high chance for recruitment of this species into the canopy. *Acer spp.* had a chance to recruit a pole mostly in the vicinity of a dead lying tree or a gap while *Fagus sylvatica* poles were dominating even in gaps, thus further compromising the chances for *Acer* spp. and *Ulmus glabra* to reach the canopy.

Overall, the findings of this thesis reveal that shade tolerance and its underlying traits such as leaf area ratio, growth rate and storage confer crucial advantages to *Fagus sylvatica* over its competitors in the understory. A long survival time and a low mortality rate in deep shade

as well as a high chance to replace the dead canopy trees in the pole phase are the main competitive advantages explaining the dominance of beech in temperate forests.

ZUSAMMENFASSUNG

Ein besseres Verständnis der Strategien, Eigenschaften und Bedingungen, die es Baumarten ermöglichen, in Waldökosystemen Dominanz zu erreichen, ist wichtig für Vorhersagen der Zusammensetzung von Ökosystemen und für die Frage, wie diese Arten auf den globalen Wandel reagieren werden. Ein markantes Beispiel für eine Art mit starker Dominanz ist *Fagus sylvatica* L. (Rotbuche). In den Wäldern der gemäßigten Zonen Europas haben die Einführung von naturnahem Waldbau und die Einstellung der Waldbewirtschaftung in Waldreservaten dazu geführt, dass der Anteil von *Fagus sylvatica* zugenommen hat, was ein neues Interesse an den Mechanismen der Dominanz dieser Art geweckt hat. Ein herausragendes Objekt zur Untersuchung der Dominanz von *Fagus sylvatica* ist der größte verbliebene Urwald von *Fagus sylvatica*, Uholka-Shyrokyi Luh in den ukrainischen Karpaten. Das Hauptziel dieser Arbeit ist es, die Konkurrenzvorteile von *Fagus sylvatica* gegenüber *Acer platanoides, A. pseudoplatanus* und *Ulmus glabra* zu untersuchen. Zu diesem Zweck wurden Merkmale der Schattentoleranz und damit verbundene Konkurrenzvorteile untersucht, im Besonderen i) der Einfluss der Artenidentität, des Baumalters und der Biomasseverteilung auf Blätter und Triebe auf das Blattflächenverhältnis, die absolute Wachstumsrate der Baumbiomasse und die Speicherpools in Stamm und Wurzel; ii) Mortalitätsraten und Überlebenszeiten von *Fagus sylvatica* und *Acer spp.* und iii) baumweise Ersatzraten von *Fagus sylvatica*, *Acer* spp. und *U. glabra*.

Im ersten Kapitel wurde untersucht, wie sich altersabhängig die Artenidentität und die Biomassverteilung auf Blätter und Triebe auf die Entwicklung des Blattflächenverhältnisses, die absolute Wachstumsrate der Baumbiomasse und die Menge der Speicherpools auswirken. Insbesondere wurde untersucht, wie sich der potenzielle Trade-off zwischen der absoluten Wachstumsrate und der Biomasseverteilung auf die Speicher in Stamm und Wurzeln auf die Überlebenszeit junger Bäume auswirkt, die im tiefen Schatten wachsen. Die Studie wurde im Uholka-Teil des Reservats auf sechs rechteckigen Parzellen durchgeführt, auf denen ausgewachsene und junge Bäume von *Acer platanoides, A. pseudoplatanus und Fagus sylvatica* vorkamen und die zwischen 0,2 und 0,7 ha groß waren. Insgesamt wurden 289 Sämlinge (0-129 cm Höhe) und Nachwuchsbäume (130-500 cm Höhe) der drei Arten

ausgegraben und ihr Durchmesser am Wurzelhals, ihr Höhenzuwachs, ihre Blattfläche, ihr Kronenansatz, ihr Alter und ihre Konzentration an nicht-strukturellen Kohlenhydraten gemessen. Mit zunehmendem Alter der Bäume nahmen der Blattflächenanteil und die Wachstumsrate ab, während die Speicherung zunahm. Bei jungen Bäumen kam es mit zunehmender Biomasseentwicklung zu einem Trade-off zwischen absoluter Wachstumsrate und Speicherung bei abnehmendem Blattflächenverhältnis. Beim Abwarten auf eine Lücke im Kronendach verleihen ein hoher Blattflächenanteil, aber eine langsame absolute Wachstumsrate und eine geringe Speicherung *Fagus sylvatica* eine ausgeprägte Fähigkeit, im tiefen Schatten mehr als ein Jahrzehnt länger zu überleben als ihre Konkurrenten. Ein vergleichsweise kleiner Blattflächenanteil in Kombination mit einer hohen absoluten Wachstumsrate und einer hohen Speicherung, wie sie bei *Acer* spp. beobachtet wird, verkürzt wiederum deren Überlebenszeit und bietet somit eine Erklärung dafür, warum die Buche Dominanz erreicht, während *Acer* spp. in der Unterschicht von Buchenurwäldern verschwindet.

Das zweite Kapitel befasst sich mit den altersspezifischen Mortalitätsraten und den Überlebenszeiten der Verjüngung im tiefen Schatten. Das höhere Blattflächenverhältnis und langsamere Wachstum von *Fagus sylvatica* ging einher mit einer altersspezifischen Sterblichkeitsrate im Alter von 40-50 Jahren von 3,6 % für drei Jahre. Im Gegensatz dazu war bei den beiden *Acer*-Arten eine Kombination aus geringerem Blattflächenverhältnis und höherer Wachstumsrate mit höheren altersspezifischen Sterblichkeitsraten von 7-8 % im Alter von 40-50 Jahren verbunden. Die mittlere Überlebenszeit von *Fagus sylvatica*-Jungbäumen war höher, mit einem geschätzten Wert von 72 Jahren gegenüber 47-48 Jahren für beide *Acer*-Arten, geschätzt für geringes radiales Wachstum (20-100 µm pro Jahr) und die Höhenklasse 131-200 cm. Die längere Überlebenszeit von *Fagus sylvatica* entspricht der durchschnittlichen Zeit bis zur ersten Freistellung aufgrund einer Öffnung des Kronendachs, wodurch sie das Kronendach häufiger und in größerer Zahl erreichen kann als *Acer* spp.

Das dritte Kapitel ergänzt das zweite in Bezug auf die Frage, wie viele Bäume in der Verjüngung und im Stangenholz (Durchmesser 6-25 cm) unter dem Kronendach stehen und dieses potenziell erreichen können, um dominante Bäume zu ersetzen. Für diese Studie wurden Daten aus vier Erhebungen verwendet, die auf einer 10 ha großen Dauerfläche in Uholka durchgeführt wurden. Aufgrund der geringeren Mortalität von *Fagus sylvatica* in der Verjüngung (2-5 m Höhe, vgl. Kapitel 2) findet man eine höhere Stammzahl dieser Art unter dem Kronendach als bei *Acer* spp. und *Ulmus. glabra*. Trotz einer zeitlichen Zunahme der Verjüngung von *Acer* spp. und *U. glabra* war die Vorverjüngung von *F. sylvatica* viel zahlreicher als jene der Nebenbaumarten, insbesondere wenn ein dominanter Baum von anderen dominanten Bäumen umgeben war. Dies deutet darauf hin, dass diese Art eine hohe Chance hat, wiederum dominante Bäume zu stellen. *Acer* spp. hatte vor allem in der Nähe eines abgestorbenen Baumes oder einer Lücke eine Chance, ins Stangenholz zu gelangen. Der Jungwuchs von *Fagus sylvatica* dominierte sogar in Lücken, was die Chancen von *Acer* spp. und *U. glabra* neue dominante Bäume hervorzubringen weiter verschlechterte.

Insgesamt zeigen die Ergebnisse dieser Arbeit, dass die Schattentoleranz und die ihr zugrundeliegenden Eigenschaften wie Blattflächenverhältnis, Wachstumsrate und Speicherung *Fagus sylvatica* in der Unterschicht entscheidende Vorteile gegenüber ihren Konkurrenten verschaffen. Eine lange Überlebenszeit im tiefen Schatten und eine niedrige Sterblichkeitsrate in der Sämlings- und Nachwuchsphase und eine grosse Wahrscheinlichkeit, in der Stangenholzphase tote Oberschichtbäume ersetzen zu können, sind die wichtigsten Wettbewerbsvorteile, die die Dominanz der Buche in gemäßigten Wäldern erklären.

GENERAL INTRODUCTION

Monodominant forests, in which a single late-successional tree species comprises > 50% of the canopy trees by stem number (>10 cm dbh) (Connell and Lowman 1989), occur in tropical forests of Asia, Central and South America as well as Africa, and in temperate forests of Europe (Connell and Lowman 1989; Hart 1990; Peters 1992; Torti et al. 2001; Visser et al. 2011). The term 'dominant species' was used by Grime (1998) in the mass ratio hypothesis, which predicts that species that are abundant in communities should, due to their large biomass, also contribute proportionally to resource use and production, thereby strongly affecting the light availability, energy flow, biogeochemical cycling and decomposition of dead biomass. For many decades, monodominance in the tropics has been a topic of intensive research, with controversial findings (Peh et al. 2011). In contrast, in Europe dominance was attributed to one species, *Fagus sylvatica* (Barna 2011; Bolte et al. 2007; Peters 1992), but has never been studied as a phenomenon because primary *Fagus sylvatica* forests remain only in scattered and relatively small areas (Sabatini et al. 2018; Standovár and Kenderes 2003). In these remnants, *Fagus sylvatica* sometimes occurs with strikingly high abundance (Figure 1), as for instance in the largest primary beech forest of Uholka-Shyrokiy Luh (Ukraine). The species has a proportion of 97% of the basal area on an area of 10 383 ha (Commarmot et al. 2013), whereas its competitors *Acer platanoides*, *A. pseudoplatanus* and *Ulmus glabra* (Norway and sycamore maples and elm, respectively) comprise less than 1% each. Moreover, the adoption of 'close-to-nature silviculture' in Europe (Brang et al. 2014), i.e. forest management that emulates or promotes natural processes, and the cessation of forest management in forest reserves allow *Fagus sylvatica* to increase its share in previously managed forests (Figure 1), which has sparked renewed interest in the mechanisms underlying monodominance in temperate forests.

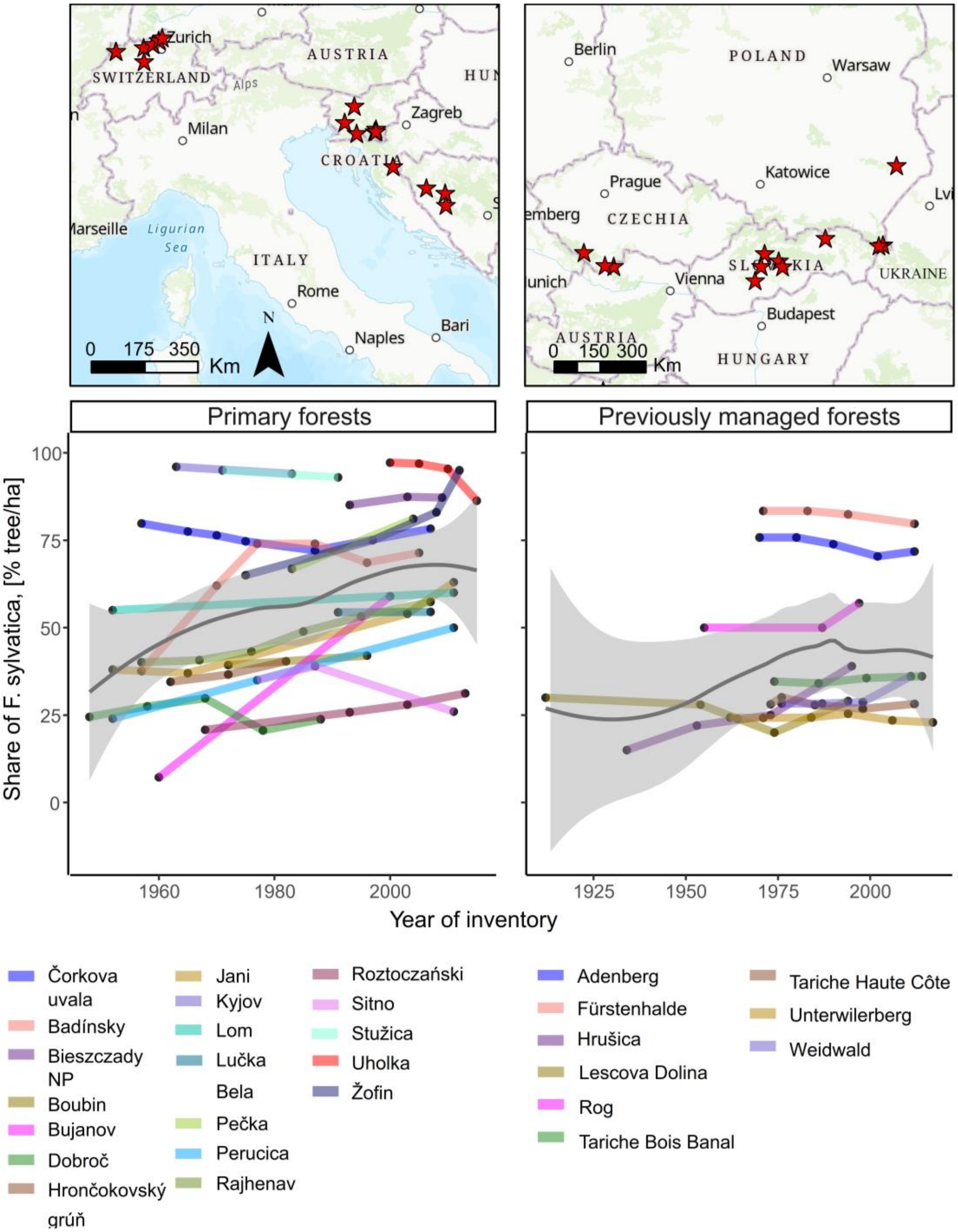

Figure 1. Fagus sylvatica share in tree density (>6 cm dbh) in primary and previously managed forests in Europe including Bosnia and Herzegovina (Perucica, Lom and Jani primary forests), Croatia (Čorkova uvala primary forest), Czech Republic (Boubin and Žofin primary forests), Poland (Bieszczady and Roztoczański primary forests), Slovakia (Badínsky, Sitno, Kyjov, Stužica, Dobroč, Hrončokovský grúň and Bujanov primary), Slovenia (Rajhenav, Pečka, Lučka Bela as primary

forests, and Lescova Dolina, Hrušica, Rog previously as managed forests), Switzerland (Adenberg, Fürstenhalde, Tariche Bois Banal, Tariche Haute Côte, Unterwilerberg, Weidwald, all previously managed forests), Ukraine (Uholka primary forest). Colored lines – inventory per forest, black line – smoothed conditional mean, grey area – uncertainty in data. Sources: Esri topo, F. sylvatica data (Balanda et al. 2013; Boncina et al. 2003; Diaci et al. 2010; Firm et al. 2009; Heiri et al. 2009; Jaloviar et al. 2017; Janík et al. 2016; Keren et al. 2014; Korpel' 1995; Maciejewski and Szwagrzyk 2011; Nagel and Diaci 2006; Radoš 2018; Saniga et al. 2014; Stillhard et al. 2019; Sugiero et al. 2009; Vrška et al. 2001).

Some of the mechanisms identified and proposed for explaining dominance in tropical species (Connell and Lowman 1989) may also be relevant for *Fagus sylvatica* dominance: i) slow canopy turnover, partly resulting from a low frequency of large-scale disturbance events, which favours shade-tolerant species like *Fagus sylvatica* (Kenderes et al. 2008; Feldmann et al. 2020; Jaloviar et al. 2020); ii) high sapling survival under the canopy due to high shade tolerance (Kobe et al. 1995; Petriţan et al. 2007); iii) slow decomposition of leaf litter, hindering the germination of competing species that have small seeds (Asplund et al. 2018; Schmidt et al. 2009); iv) strong root competition (Beyer et al. 2013; Lang et al. 2010); v) mast behaviour leading to predation satiation and, potentially, a high number of offspring (Nilsson and Wästljung 1987); v) escape from herbivory (Kitajima 1994; Ohse et al. 2017) and, finally, vi) several factors affecting *Fagus sylvatica* competitors such as short- and long-term human interventions, e.g. alpine grazing and predator hunting (Vrška et al. 2009) negatively affecting conifers; air pollution leading to conifer decline (Hinrichsen 1987); and pest and pathogen outbreaks which reduce the abundance of broadleaved *(Ulmus glabra*, Martin et al. 2010) as well as conifer species (De Groot and Ogris 2019); the latter may partly be linked to rising temperatures. However, empirical studies in tropical forests (Peh et al. 2011) about monodominant species have shown that these species do not share all of the traits and exogenous factors described above. Most likely, an interplay of some of these traits and positive feedbacks under low forest disturbance or human intervention drive forest ecosystems towards monodominance (Kazmierczak et al. 2016; Peh et al. 2011).

The importance of some of the possible mechanisms for *Fagus sylvatica* dominance reviewed above, e.g. the slow decomposition of its litter or root competition, are unclear. Moreover, there is no recognised conceptual framework for studying tree dominance in general and in temperate forests in particular. Gaining an improved understanding of the mechanisms, traits and conditions that enable species to dominate will aid in predictions of community assembly and how dominant species will respond to global change.

CONCEPTUAL FRAMEWORK EXPLAINING *FAGUS SYLVATICA* DOMINANCE

Tree dominance can be defined in terms of density, basal area or biomass (Figure 2, 1.1), although these metrics do not fully reflect which functional traits – i.e. morphological, physiological or phenological features that reflect a species' ecological strategy (Pérez-Harguindeguy et al. 2013) – grant competitive advantages and promote species dominance (Avolio et al. 2019). Particular traits may confer competitive advantages to a species, leading to competitive exclusion and its dominance in the long term. Such a species possesses traits that strongly reduce the growth of its competitors and so the species has a strong competitive 'effect' (1.2 in Figure 2, Kunstler et al. 2016). For instance, the very dense and plastic crowns of *Fagus sylvatica* trees strongly hamper the growth of the regeneration of less shade-tolerant species. Furthermore, the growth and survival of the monodominant species may be less affected by competition from neighbours due to traits resulting in a better tolerance of competition or a high competitive 'response' (1.3, ibid.) For example, the survival of *Fagus sylvatica* regeneration is only weakly affected by the crowns of competitor species due to its very high shade tolerance.

Traits related to the competitive 'effect' and 'response' of a monodominant species operate at different stages of tree development. Shade tolerance in regeneration is a complex strategy (Valladares and Niinemets 2008) that involves several traits such as leaf, growth, storage and defensive compounds (2.1 in Figure 2), which are leading to a competitive 'response', i.e., long survival time (Piovesan et al. 2005) and low mortality (Kunstler et al. 2009) in shade. It also enables the formation of a higher number of poles to replace a mature tree in the canopy. High reproduction under competition in mature trees (2.2) (i.e., high fecundity per unit plant size per unit time) is linked to high biomass production (2.3) and may confer a species a strong competitive 'effect'. Consequently, competitive 'effect' and 'response' at different levels of tree development ensure higher fitness of the dominant species compared to competitors (Aarssen 2005). Ultimately, high fitness is determined by a higher lifetime output of reproductive offspring in relation to competing species (Aarssen 2005). Based on the literature review presented below, the conclusion arises that the importance of different traits in species dominance is decreasing from shade tolerance to biomass production.

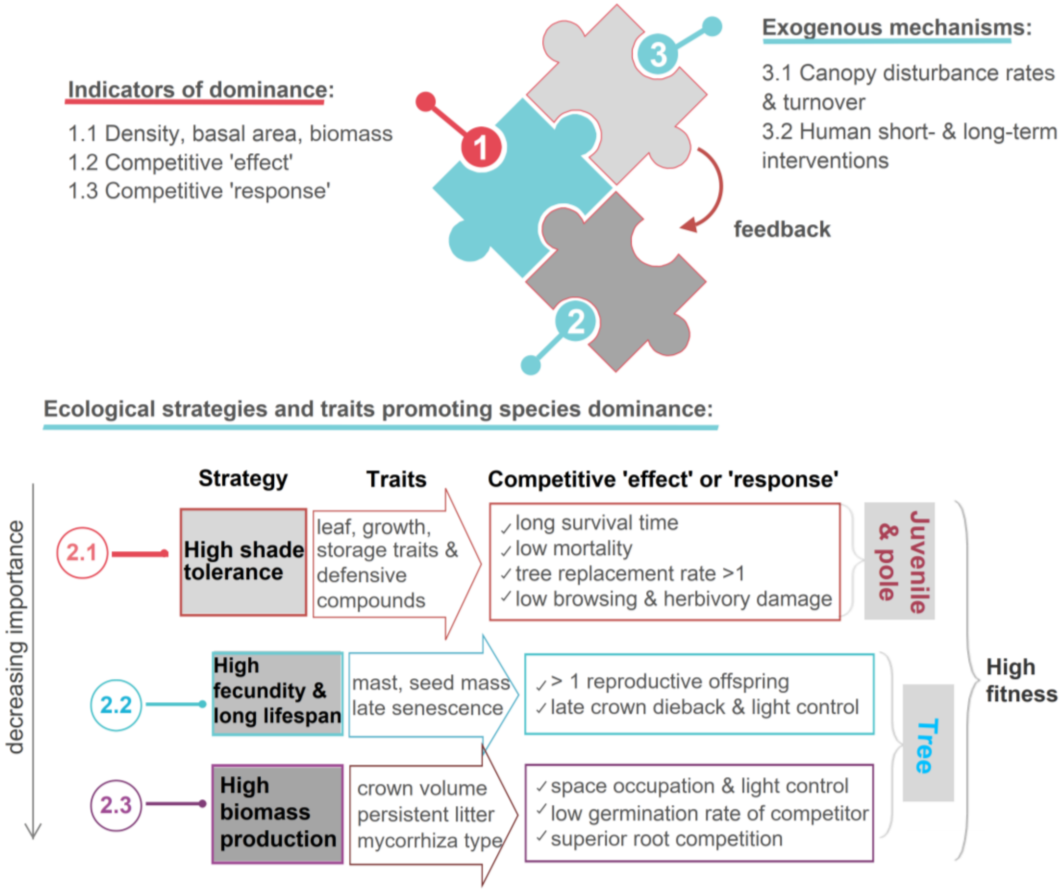

Figure 2. Conceptual framework for Fagus sylvatica dominance in a temperate forest (based on Aarssen 2005; Avolio et al. 2019; Kunstler et al. 2016; Peh et al. 2011; Valladares and Niinemets 2008).

In the following chapters, the definitions of tree size classes indicated in Table 1 will be used.

Table 1. Definitions of tree size classes used in this study.

Germinants – 0–9.9 cm height
Seedlings – 10.0–129.9 cm height
Saplings – ≥130 cm height up to 9.9 cm dbh
Pole – 10.0–25.0 cm dbh
Reproductive tree ≥ 20 cm dbh

HIGH SHADE TOLERANCE

Shade tolerance is associated with plant traits such as leaf (leaf area ratio), growth (absolute growth rate), storage (non-structural carbohydrates) and with defensive metabolites (Figure 2, 2.1, Valladares and Niinemets 2008). In primary forests with disturbance rates <1% yr^{-1} (Hobi et al. 2015) and canopy turnover between 100 and 220 years (Drößler and Von Lüpke 2005; Valverde and Silvertown 1997), saplings typically must survive in the shade for more than 50 years (Piovesan et al. 2005; Trotsiuk et al. 2012). In deep shade (i.e., 1-3% of diffuse radiation), they achieve this by reducing their growth (Lin et al. 2001, 2002), developing an extensive leaf surface per unit of tree mass (LAR, Annighöfer et al. 2017), increasing storage (Kobe 1997; Weber et al. 2018, 2019) and investing carbon in defence mechanisms (Kitajima 1994; Ohse et al. 2017; Stiegel et al. 2017). During the development from seedlings to saplings, LAR diminishes in deciduous young trees (Niinemets 1998), and thus the capacity of the leaf area may be limited in providing photosynthates for both growth and storage. Allocation to storage increases proportionally to plant mass (Plavcová et al. 2016), which in turn may decrease growth under carbon limitation (Wiley and Helliker 2012). Thus, during biomass development young trees are likely to experience a trade-off between growth and storage, potentially leading to carbon starvation and thus a shorter survival time.

Most of the studies on the relationships among traits of shade tolerance in broadleaved species (cf. Gibert et al. 2016) focus on seedlings and do not focus on the development of the combined leaf, growth and storage traits with age, thus leading to patchy evidence (Valladares et al. 2016; Valladares and Niinemets 2008). Moreover, it is unclear how ontogenetic changes in the traits underlying shade tolerance affect the survival time of broadleaved juvenile trees of species such as *Fagus sylvatica, Acer platanoides* and *A. pseudoplatanus*.

The survival of tree regeneration plays an important role in determining plant success at low light levels (Figure 2, 2.1). Shade-tolerant species do not necessarily grow faster than shade-intolerant species at low light levels, but they may have a higher survival rate (Kitajima 1994; Kobe et al. 1995; Kobe and Coates 1997). The trade-off between fast growth at high light levels but low survival in shade and high survival at low light levels but low growth at high light levels could be the key explanation for the shade tolerance of species. Lin et al. (2001, 2002) found that shade-intolerant species had a higher mortality risk at slow growth than shade-tolerant ones. In this sense, high shade tolerance can be characterised by low mortality in spite of slow growth. Due to the scarcity of empirical data on regeneration mortality, previous studies have modelled the mortality rate of regeneration mainly as a function of the radial growth of dead and living juvenile trees (Dekker et al. 2009; Lin et al. 2001; Petriţan et al. 2007). However, the species-specific mortality showed high variation due to insufficient sample size at very low light levels because some of these studies were conducted at wide range of light gradients (5–100% in full sun, Kunstler et al. 2005, or 3–33% indirect light, Petriţan et al. 2007). Furthermore, it remains unclear how other traits underlying shade tolerance, for example LAR, affect tree mortality, specifically in deep shade.

If juvenile shade-tolerant trees are able to survive for long periods, they form numerous young trees under the canopy (so-called "advance regeneration"). When a canopy tree is characterized by a long lifespan and slow senescence, a shade-tolerant pole will typically replace it because competing shade-intolerant poles tend to lag too far behind in size compared to shade-tolerant poles (Fox 1977). Replacement of one species by another one and vice versa (i.e. reciprocal replacement) was observed for *Fagus grandifolia* and *Acer saccharum*, two co-dominant shade-tolerant species in North America (Horn 1975; Poulson and Platt 1996; Woods 1979, 1984). To date, only two studies have reported reciprocal species replacement for conifers and *Fagus sylvatica* in primary forests in Europe (Keren et al. 2014; Nagel et al. 2010), while there is no study on broadleaved species. Previously, replacement was modelled as transition probability based on the proportions of advance regeneration under mature trees, with a focus on replacement either in the canopy (Culver 1981; Fox 1977; Horn 1975; Woods 1984), or in gaps (Lertzman 1992, 1995; Nagel et al. 2010; Runkle 1981). Models of replacement in the canopy (poles under living trees) generally predicted an increase in the importance of shade-tolerant species over time, while models of replacement in gaps (poles near dead trees) featured an increase in the importance of shade-intolerant species (White et al. 1985). Therefore, a balanced approach is needed that includes both canopy and gaps in measuring abundance of advance regeneration for *Fagus sylvatica*, *Acer* spp. and *Ulmus glabra*.

HIGH FECUNDITY, LONG LIFESPAN

A species with high fitness can achieve dominance by producing more than one reproductive offspring per tree (2.2 in Figure 2), enabling self-replacement and the exclusion of individuals of other species (Aarssen 2005). To date, there is no life cycle study on *Fagus sylvatica* that has linked the increased frequency of its masting in Central and Northern Europe over the last two to three decades (Ascoli et al. 2017; Drobyshev et al. 2014; Hilton and Packham 2003; Övergaard et al. 2007) with the number of its reproductive offspring. Researchers either focused on *Fagus sylvatica* seed production (Nilsson and Wästljung 1987; Nussbaumer et al. 2016), biomass allocation to seeds (Genet et al. 2010; Wenk and Falster 2015) or the establishment of germinants/seedlings (Szwagrzyk et al. 2001), without linking seed production of a mother tree to the number of offspring recruited. A preliminary analysis of data from a 10-ha permanent plot in Uholka (not shown) demonstrated that earlier seed production in *Acer* spp. than in *Fagus sylvatica* (Hein et al. 2009; Wesołowski et al. 2015) supports a seedling bank similar to that of the dominant *Fagus sylvatica* trees, despite the lower density of maple mother trees. Nevertheless, only *Fagus sylvatica* saplings and poles dominate in canopy replacement, suggesting that high fecundity (Szwagrzyk et al. 2015) is not a primary contributor to species dominance.

Extreme conditions (e.g., deep shade at juvenile stage, low temperatures) are associated with the occurrence of particularly old and slow-growing trees (Bigler and Veblen 2009; Piovesan et al. 2005), suggesting that low metabolism contributes to their delayed senescence. Slow senescence (Petit and Hampe 2006) in *Fagus sylvatica* leads to gradual crown fragmentation and dieback only after a tree reaches 120 years (Innes 1998), enabling the species to exert a long term control on understory light and thus allowing canopy replacement only for regeneration that is able to survive long periods with little light.

BIOMASS PRODUCTIVITY

There is evidence that species richness declines at the highest productivity levels, suggesting that competitive exclusion is an important mechanism in forest communities (Brun et al. 2019; Grime 1973). *Fagus sylvatica* trees develop higher crown biomass and maintain a higher plasticity at high age than conifers (Pretzsch and Schütze 2005) or *Acer* spp. (Hein et al. 2009; Pretzsch et al. 2015). *Fagus sylvatica* has lower maintenance costs than *Picea abies* on a crown volume basis (Grams et al. 2002), allowing it to occupy twice as much crown space (Pretzsch and Schütze 2005) and cast deep shade at the regeneration of its competitors. Furthermore, lateral growth of crown branches in beech is able to close a 180–470 m^2 canopy gap in just 3–4 years (Madsen and Hahn 2008).

It has long been known that *Fagus sylvatica* leaf litter (2.3, Figure 2) acidifies topsoil due to higher lignin and lower N contents compared with other broadleaved species (except oak), resulting in a lower litter decomposition rate (Augusto et al. 2003; Langenbruch et al. 2012; Leuschner et al. 2006). Although the accumulation of *Fagus sylvatica* litter may enhance the number of germinated beech seeds (Ammer et al. 2002) and physically impair the germination of small seeds, for instance, *Picea abies* (Asplund et al. 2018) or herbs (Schmidt et al. 2009), failure to disentangle the impacts of light from those of litter on the germination success suggests insufficient evidence. Another study reported opposite results, showing an overall lower germination and survival of *Fagus sylvatica* seedlings in leaf litter and a higher germination and survival of other species, especially *Acer pseudoplatanus* (Bianchi et al. 2019). Thus, explaining the role of leaf litter in germination and survival of seedlings of beech in comparison to those of its competitors requires more research.

There is no evidence for the type of mycorrhiza (2.3, Figure 2) having an impact on competitive strength in temperate forests (Kubisch et al. 2015, 2016). *Fagus sylvatica* with ectomycorrhiza showed a similar ratio of belowground to aboveground biomass when compared to *Acer* spp. and *Fraxinus excelsior* with arbuscular mycorrhiza (ibid.). Research on root competition of mature trees led to contradictory results. On the one hand, *Fagus sylvatica* is an inferior belowground competitor compared to *Fraxinus excelsior* in terms of fine root biomass (Jacob et al. 2013). On the other hand, *Fagus sylvatica* was found to be a superior belowground competitor in stands of *Fagus sylvatica* and *Quercus petraea* (Leuschner et al. 2001; Rewald and Leuschner 2009) as well as in stands of *Fagus sylvatica* and *Picea abies* (Bolte and Villanueva 2006; Grams et al. 2002). According to Leuschner et al. (2001), *Fagus sylvatica* produces a five-fold higher fine root biomass than *Quercus petraea* under similar stem density and leaf area. However, it is unclear how belowground biomass production affects aboveground biomass and overall species competitiveness. Moreover, the comparison of root biomass of deciduous *Fagus sylvatica* and conifers is not entirely valid as, in general, broadleaved species have a higher root biomass than conifers (Finér et al. 2007). It seems that root competition depends on species mixture, tree age and the environment, and therefore the same species may be a superior or inferior competitor in contrasting neighbourhoods.

In summary, the conceptual framework proposed in Figure 2 embraces traditional and novel indicators for measuring tree competitiveness. It also ranks the importance of major ecological strategies and traits leading to beech dominance and highlights the role of some of the relevant exogenous factors. Taking into account the limited state of knowledge about the role of particular traits and the multi-faceted challenges in studying dominance, the overarching aim of this thesis is to investigate traits of shade tolerance, in particular juvenile survival time, juvenile mortality and abundance of advance regeneration as potential successors of canopy trees.

STUDY AREA AND DATA SOURCES

The Uholka-Shyrokyi Luh reserve (circa 10,383 ha) in Ukraine is a *Fagus sylvatica*-dominated primary forest, listed as a UNESCO World Heritage site (Figure 3). The Uholka part covers 4,729 ha, ranging between 400 and 1300 m a.s.l. in elevation. The mean annual temperature is about 8 °C at 430 m a.s.l (−3 °C in January and 18 °C in July), and the mean annual precipitation sum amounts to 1134 mm (Commarmot et al. 2013). The Uholka forest contains small shares of minority species such as *Acer platanoides* (0.1% of basal area), *A. pseudoplatanus* (1.4%), *Fraxinus excelsior* (0.1%) and *Ulmus glabra* (0.8%), and was therefore selected for this thesis. In the Shyrokyi Luh part (Commarmot et al. 2013), these minority species are much less abundant. Both parts of the reserve are subject to a small-scale disturbance regime, resulting in a mosaic of mainly small canopy gaps (98% under 200 m^2); only a few large stand-replacing events were detected in a previous study that used high-resolution satellite imagery (Hobi et al. 2015).

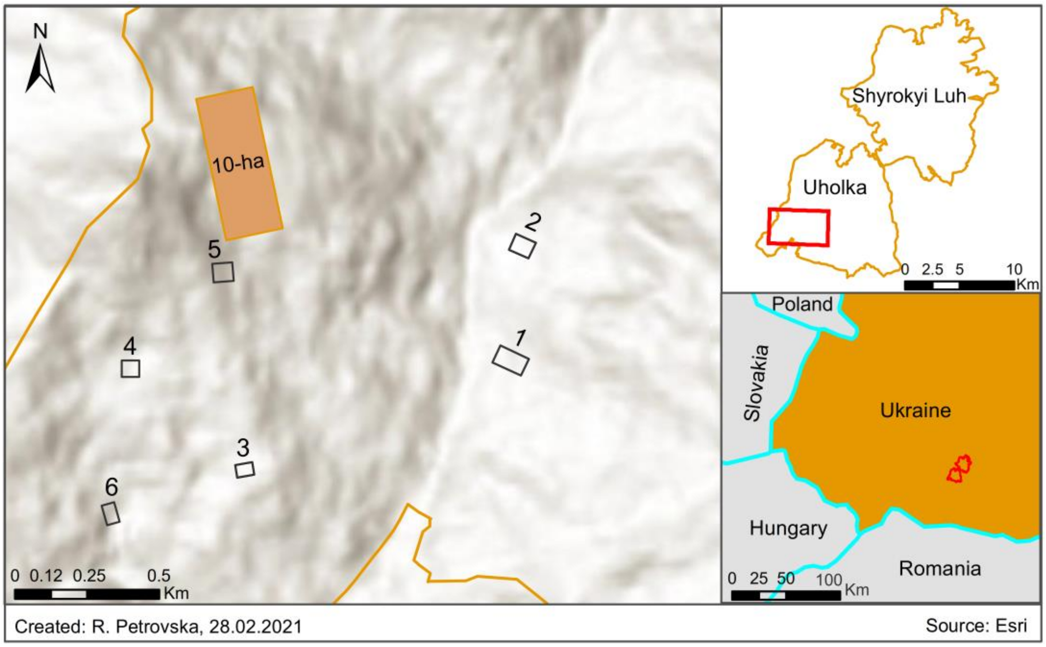

Figure 3. Map showing the six experimental plots, the 10-ha permanent plot (left) and zoom-outs on the Uholka-Shyrokyi Luh forest reserve (top right) and the western Ukraine (bottom right).

A permanent inventory plot of 200 × 500 m was established in Uholka in 2000 and has since been re-measured in 2005, 2010 and 2015 (Stillhard et al. 2019). It is located in an old-growth stand and is situated at 48.2695°N, 23.6207°E at an elevation of 700-800 m a.s.l. (Figure 3). The plot faces mainly south-east with a slope between 20 and 40%. Soils mainly consist of dystric cambisols (Commarmot et al. 2005). Since plot establishment, two medium-sized wind and heavy snowfall disturbance events occurred in 2007 and 2009, resulting in several gaps (Stillhard et al. 2019).

This thesis is based on two datasets collected in the Uholka part of reserve. The first dataset was collected by me and includes measurements of biomass allocation to leaves, branches, stem and roots in living seedlings and saplings collected on six plots (total area 1.44 ha; Figure 3). In total, 289 living seedlings and saplings of *Fagus sylvatica*, *Acer platanoides* and *A. pseudoplatanus* were excavated and measured. In addition, 179 juvenile trees of the same species assumed to be dead for the last 3 years were collected on the six plots. The second dataset was collected by inventory teams in the context of a Swiss-Ukrainian cooperation project; it contains measurements from four inventories on the 10-ha permanent plot in the same forest (Figure 3). It includes 8,127 living young trees (>4.6 and up to 20 cm dbh) and 4,896 living mature trees (>20 cm dbh).

STRUCTURE OF THE THESIS

Primary beech forests are characterised by low light availability (<3% of diffuse light, Emborg 1998; Wagner et al. 2010). It is therefore important to study leaf, growth and storage traits associated with shade tolerance, the survival time and mortality of juvenile trees in low-light environments. I set up the thesis to consist of three parts, as follows:

In Chapter 1, I evaluated the effects of the ontogenetic development of leaf, growth and storage traits on the survival time of juvenile trees of the three species *Acer platanoides*, *A. pseudoplatanus* and *Fagus sylvatica* (dataset 1). As a result, the identified trade-off between growth and storage allows for drawing inferences about the survival times of the three species.

In Chapter 2, I addressed the need to include not only growth but also other traits underlying shade tolerance into the estimation of mortality for the above-mentioned species (dataset 1). To this end, the impact of leaf and growth traits on species-specific mortality rates and survival times was statistically modelled.

In Chapter 3, I assessed the abundance of advance regeneration under canopy trees for four species (*Acer platanoides*, *A. pseudoplatanus*, *Fagus sylvatica* and *Ulmus glabra*) based on the four inventories of the 10-ha plot (dataset 2). For this purpose, the amount of advance regeneration was modelled with respect to pole size and dbh class, pole species identity and canopy tree location.

CHAPTER 1

Earlier studies on relationships among traits of shade tolerance in broadleaved species often focused on seedlings, while the development of leaf, growth and storage traits with age was neglected, thus leading to patchy evidence. Further, no clear link between shade tolerance and survival time has been established yet. To fill this gap, I developed a MANCOVA model that estimates leaf, growth and storage traits with respect to biomass development of three species (*Fagus sylvatica, Acer platanoides, A. pseudoplatanus*) and allows for inference on the survival time of juvenile trees. In particular, I addressed the following questions: i) Which traits regarding leaf, growth and storage can discriminate between low- and high-vitality regeneration? ii) Is there a species-specific trade-off between growth and storage traits among individuals of low and high vitality? iii) How are these traits affecting the survival time of juvenile trees?

CHAPTER 2

Previous studies have mainly used radial stem growth to explain mortality rates in juvenile trees, whereas leaf area ratio (LAR), a key component of shade tolerance, has been neglected so far. To address this gap, I expanded existing mortality models by including LAR as a covariate. The resulting survival model was used to evaluate the age- and species-specific death rates and survival times of three species (*Fagus sylvatica, Acer platanoides, A. pseudoplatanus*). Specifically, I focused on two research questions i) How do LAR, radial stem growth and tree height affect the species-specific survival time of juvenile trees? ii) What are the age-specific death rates and survival times for these species?

CHAPTER 3

Tree replacement patterns provide insight into mechanisms of species dominance. In mixed forests subject to a small-scale disturbance regime, dead canopy trees are often replaced by advance regeneration. Here, I studied the abundance of saplings (6.0-10.0 cm dbh) and poles (10.1-25.0 cm dbh) under canopy trees based on four inventories on the 10-ha permanent plot in the Uholka primary forest. Saplings and poles of *Fagus sylvatica*, *Acer platanoides*, *A. pseudoplatanus* and *Ulmus glabra* were spatially linked to canopy trees ('hosts', dbh > 25 cm) based on the hosts' crown radius, and the hosts' neighbourhood was classified according to the presence of a lying or standing dead tree. The number of saplings and poles under hosts was modelled with a Bayesian hurdle Poisson model. Specifically, I investigated the following questions: i) How many saplings and poles of *Fagus sylvatica, Acer platanoides, A. pseudoplatanus* and *Ulmus glabra* grow under mature canopy trees in this primary forest? ii) Which factors drive species presence and abundance?

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Chapter

1

Grow Slowly, Persist, Dominate – Explaining Beech Dominance in a Primeval Forest

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ABSTRACT

Being able to persist in deep shade is an important characteristic of juvenile trees, often leading to a strong dominance of shade-tolerant species in forests with low canopy turnover and a low disturbance rate. While leaf, growth and storage traits are known to be key components of shade tolerance, their interplay during regeneration development and their influence on juveniles' survival time remains unclear. We assessed the ontogenetic effects of these three traits on the survival time of beech (*Fagus sylvatica*), Norway and sycamore maples (*Acer pseudoplatanus*, *Acer platanoides*) in a primeval beech forest. Biomass allocation, age and content of non-structural carbohydrates (NSC) were measured in the stems and roots of 289 seedlings and saplings in high- and low-vitality classes. Saplings experienced a trade-off between absolute growth rate (AGR), and storage (NSC) as the leaf area ratio (LAR) decreases with biomass development. High LAR but low AGR and low NSC corresponded to beech with a marked ability to persist in deep shade while awaiting canopy release. In turn, a comparably small LAR in combination with a high AGR and higher storage (NSC), as observed in Norway maple and sycamore maple, reduced sapling survival time, thus offering an explanation for beech dominance and maple disappearance in the undergrowth of old-growth beech forests.

Keywords: *Acer*, AGR, dominance, *Fagus*, LAR, functional trait, NSC, regeneration, shade tolerance

1 INTRODUCTION

In primeval monodominant *Fagus sylvatica* L. forests, seedlings (0–130 cm tall) and saplings (131–500 cm tall) often grow in deep shade for extended periods, due to low canopy turnover (Hobi et al. 2015; Runkle 1985; Valverde and Silvertown 1997). If canopy turnover is low (i.e. the mean time between recurring gap formation at any point in the forest), saplings that are able to persist for decades in shade are more likely to experience a canopy opening (i.e. a release event) enabling the subsequent promotion to canopy (Canham 1985, 1990). Hence, high juvenile shade tolerance is pivotal in determining the survival time of *Fagus sylvatica* and may be compromised in co-occurring species, explaining the low tree species diversity and *Fagus sylvatica* dominance frequently observed during succession (Korpel' 1995; Rey et al. 2019).

Shade tolerance can be assessed via functional traits, i.e. morphological, physiological and phenological features that reflect a species' ecological strategy (Pérez-Harguindeguy et al. 2013). One of the concepts used to explain shade tolerance, the 'carbon gain' hypothesis, postulates that saplings can enhance carbon gain in the shade, either by minimising CO_2 losses via respiration or by investing in the light-harvesting capacity (greater leaf area and crown volume, Givnish 1988) while maintaining a higher growth rate (Popma and Bongers 1988; Walters and Reich 1996). Another concept, the 'defence and storage' hypothesis, relates shade tolerance to the resistance to herbivory, pathogens and mechanical damage (Kitajima 1994) and to storage (Kobe 1997). Accordingly, shade-tolerant species do not maximise growth in low light but invest a larger fraction of non-structural carbohydrates (NSC) in storage to buffer against stress during a prolonged period of shade (Kobe 1997). The two concepts, 'carbon gain' and 'defence & storage', are not mutually exclusive, but rather present different mechanisms of the complex phenomenon of shade tolerance.

The traits of shade tolerance change during ontogeny, i.e. the development from seedlings to saplings. Maintenance and construction costs increase with tree height because the proportion of non-photosynthetic support tissue increases continually (Delagrange et al. 2004). At the same time the ratio of leaf area to total tree biomass (LAR) diminishes as young deciduous trees grow (Niinemets 1998), and thus the leaf area capacity may be limited in terms of providing photosynthates for both growth and storage. NSC dynamics in juvenile regeneration during ontogenetic development are not well understood (Hartmann et al. 2018). Although the NSC concentration is expected to decrease with tree height (Machado and Reich 2006), the growing volume of support tissue suggests that allocation to storage increases in proportion to plant mass (Plavcová et al. 2016), which in turn may decrease growth under carbon limitation (Wiley and Helliker 2012). Thus, during ontogenetic development young trees may experience a trade-off between growth and storage, leading to a shorter survival time.

Studies on the relationships among the traits of shade tolerance in broadleaved species have mostly been focused on seedlings in garden experiments (Gibert et al. 2016) and have not involved investigations of how leaf, growth and storage traits development with age, thus leading to patchy evidence (Valladares et al. 2016; Valladares and Niinemets 2008). Moreover, we are not aware of any existing study on deciduous trees addressing how ontogenetic changes in traits of shade tolerance may affect the survival time of juvenile trees. We define ‘regeneration survival time’ as the potential time that seedlings and saplings can survive in the unfavourable environment of deep shade, which corresponds to the time until the first canopy release. In the present study, we aimed to combine leaf, growth and storage traits as proxies of shade tolerance to infer the survival time of juvenile beech and co-occurring species.

Due to low tree diversity in monodominant *Fagus sylvatica* forests, we studied its seedlings and saplings (0–5 m height) and the most abundant competitor species, such as *Acer pseudoplatanus* and *Acer platanoides*, in two vitality classes. Comparisons of traits between trees with high and low vitality (i.e. the capacity to grow, resist stress and acclimate to environmental conditions; adapted from Brang 1998, Dobbertin 2005) made it possible to relate trait performance to survival time. In particular, we investigated the following research questions: (i) Which traits relating to leaf, growth and storage can discriminate between low- and high-vitality regeneration? (ii) Is there a trade-off between growth and storage traits among species of low and high vitality? (iii) How do these traits affect regeneration survival time?

2 MATERIALS AND METHODS

2.1 STUDY AREA and PLOT SELECTION

The Uholka-Shyrokyi Luh reserve in Ukraine belongs to one of the most investigated *Fagus sylvatica*-dominated primeval forests of Europe and is listed as a UNESCO World Heritage site (Stillhard et al. 2019; Trotsiuk et al. 2012; Zenner et al. 2020). In this study we focused on the Uholka part of the forest (coordinates: 48° 16′ N, 23° 40′ E), which was selected because it has a greater share of *Acer* spp. than in the Shyrokyi Luh part of the reserve. The Uholka part covers 4,729 ha, ranging from 400 to 1300 m a.s.l., with a mean annual temperature of about 8°C (−3°C in January and 18°C in July at 430 m latitude) and a mean annual precipitation of 1134 mm (Commarmot et al. 2013). *Fagus sylvatica* is abundant in the regeneration, constituting 83–97% in density for the height classes 10–129 cm and ≥130 cm up to 5.9 cm DBH (diameter at breast height, i.e. 1.3 m; Commarmot et al. 2013). The share of *Acer pseudoplatanus* shrinks from 15% in the 10–39.9 cm height class to 3% in the 3–3.9 cm DBH class, while the share of *A. platanoides* is almost zero for trees with a DBH >2 cm (inventory 2010, analysis not shown). The forest is dominated by a small-scale disturbance regime with a mosaic of mainly small canopy gaps (98% are <200 m^2); only a few large, stand-replacing events were detected in a study using high-resolution satellite imagery (Hobi et al. 2015).

We randomly selected six plots (total area 2.53 ha) varying from 0.2 to 0.7 ha in size, in which mixed regeneration of the three species was present in sub-plots. Within the six plots, nine sub-plots from 140 to 520 m^2 (total 0.26 ha) were delineated to contain as many seedlings/saplings of the target species/sizes/vitality classes as possible. Among this regeneration, 289 target seedlings and saplings were randomly selected and marked according to the following criteria: three species (*Fagus sylvatica, Acer pseudoplatanus, A. platanoides*), two vitality classes (low and high) and eight height classes: 0–10, 11–20, 21–35, 36–60, 61–90 and 91–130 cm as seedlings, 131–200 and 201–500 cm as saplings, one seedling/sapling per plot in each height and vitality class (see Supplementary Material, Table S1). Browsing was apparent on all plots, with many recovered *Acer* spp. trees having scars while *Fagus sylvatica* regeneration was almost untouched.

2.2 CLASSIFICATION INTO VITALITY CLASSES

We developed criteria for juvenile trees based on the vitality assessment used for adult trees, in which tree crowns are assessed visually (Eichhorn et al. 2016; Roloff 1991) and growth is measured in the field (Dobbertin 2005). Crown transparency has been shown to correlate well with relative growth rate (Lorenz et al. 2004; Solberg 1999) and also with subsequent tree mortality and survival (Dobbertin and Brang 2001; Schmid-Haas 1993). Hence, we classified seedlings and saplings (Table 1), taking into account crown transparency (leaf loss and/or dieback) and the increment of the apical shoot for several years, but we used the branching pattern and stem condition as additional discriminators to differentiate between high- and low-vitality trees (Collet et al. 2011; Roloff et al. 2016). To avoid an inconsistent crown transparency assessment (Dobbertin 2005), only one evaluator assessed all seedlings and saplings, using site-specific reference trees. A reference tree is a tree with full foliage (defoliation 0%) that grows at a particular site, considering altitude/latitude, site conditions, and social status (Eichhorn et al. 2016). Trees browsed during the current season were not considered.

Table 1. Criteria used to classify juvenile trees into high- and low-vitality classes based on (i) crown transparency, (ii) apical shoot increment, (iii) branching pattern and (iv) stem damage.

Parameter	**High vitality**	**Low vitality**
Crown transparency (leaf loss, crown dieback)	• Leaf loss <20% • No dead branches and no crown dieback	• Leaf loss >20% • Dead branches or crown dieback
Apical shoot increment for several years	• Large apical increments for 3–5 years • Browsed in the past but recovered	• Small apical increments for 3–5 years • Browsed in the past and not recovered
Branching pattern	• Vigorous branching	• Degenerative branching
Stem damage	• Intact stem, no diseases	• Scars, bacterial/fungi diseases

2.3 MEASUREMENTS AND CALCULATIONS

2.3.1 FIELD MEASUREMENTS

The following measurements were taken before tree excavation: diameter at root collar (DRC), tree height and height of the crown base (height of the lowest foliage, excluding epicormic shoots). We measured crown area projection by two perpendicular crown diameters using a pendulum suspended from the outermost branches to the ground. Stem height increment was measured for the most recent 5–10 years (until the last visible bud scale scar) to the nearest millimetre. Leaf area index and indirect site factor (ISF), i.e. the proportion of diffuse solar radiation at a given location relative to that in the open, were assessed with hemispherical photos (*Coolpix 4500, Nikon, Japan*) with a 183° fish-eye lens (*Nikon FC-E8*) mounted on a tripod (Thimonier et al. 2010). Photos were taken just above the uppermost leaves of every tree, bending saplings taller than 1.5 m to allow photo shooting of canopy. We then excavated trees manually and cleaned roots with water to avoid damage to the fine roots.

2.3.2 POST-HARVEST PROCESSING (MID-MAY TO MID-JULY)

The sampled trees were separated at the root collar into aboveground biomass (foliage, stem, branches) and belowground biomass (roots). Pieces of 5 cm length from the stem at the level of the root collar and from the coarse roots (diameter >2 mm) were cut for NSC analysis and placed in a microwave at 900 W twice for 15 s immediately after the harvest (Popp et al. 1996). In the case of seedlings without coarse roots, we used the taproot. All fresh leaves per tree were scanned with a smartphone (*Petiole, version 2.0.1, Petiole Ltd. 2019*) after calibration of the camera. Foliage, stems, branches and roots were dried at 65°C for three days until a constant weight was reached and then weighed to the nearest 0.01 g.

2.3.3 CALCULATIONS

Crown area projection was calculated based on the quadratic mean radius (Pretzsch et al. 2015). We multiplied crown area projection by the difference between tree height and the height of the crown base to obtain crown volume (assuming it is a cylinder). Hemispherical photos were analysed with the program Hemisfer (*version 2.2, ©Patrick Schleppi, WSL*). ISF was estimated using the method introduced by Thimonier et al. (2010). We calculated the trait variables according to the formulae in Table 2 and present the final results in Table S 1.

Table 2. Variables calculated for leaf and growth traits.

Traits	Variable	Formula	Units
Leaf	Leaf area ratio, *LAR*	$\mathbf{LAR} = \frac{\mathbf{LA}}{\mathbf{m_{total}}}$ (1) where $\mathbf{LA}$ is the leaf area per tree and $\mathbf{m_{total}}$ is the total dry mass per tree	cm^2/g
	Specific leaf area, *SLA*	$\mathbf{SLA} = \frac{\mathbf{LA}}{\mathbf{m_{leaf}}}$ (2) where $\mathbf{LA}$ is the leaf area per tree and $\mathbf{m_{leaf}}$ is the total leaf dry mass per tree	cm^2/g
	Leaf mass fraction, *LMF*	$\mathbf{LMF} = \frac{\mathbf{m_{leaf}}}{\mathbf{m_{total}}}$ (3) where $\mathbf{m_{leaf}}$ is the total leaf dry mass per tree and $\mathbf{m_{total}}$ is the total dry mass per tree	
	Crown area	$\boldsymbol{p} = \overline{\boldsymbol{r^2}}\boldsymbol{\pi}$ (4) where $\bar{\boldsymbol{r}} = \sqrt{\frac{r_1^2+r_2^2+r_3^2+r_4^2)}{4}}$ and r$_1$..r$_4$ are radii in four cardinal directions	m^2
Growth	Absolute growth rate, *AGR*	$\mathbf{AGR} = \frac{\mathbf{m_{total}}}{\mathbf{t}}$ (5) where $\mathbf{m_{total}}$ is the total dry mass per tree and t is tree age	g/year
	Shoot mass growth rate (leaves + branches)	$\mathbf{r_{shoot}} = \frac{\mathbf{m_{shoot}}}{\mathbf{t}}$ (6) where $\mathbf{m_{shoot}}$ is the total dry shoot mass per tree and t is tree age	g/year

2.4 NSC ANALYSIS

Non-structural carbohydrates (NSC) represent the storage trait in the 'defence and storage' concept of our study; they are sugars of low molecular weight (glucose, fructose and sucrose) and starch. NSCs were analysed according to the Wong (1990) protocol modified by Hoch et al. (2003). The harvested (mid-May to mid-July) coarse root sections of larger saplings (2–4 cm DRC) were limited to 5 to 10 mm diameter and the harvested stem sections to 10 mm of wood directly under the bark. The milled stem sections (without bark) and the

root (without bark if possible) of each sapling (10–12 mg) were boiled in 2 ml of distilled water for 30 min. After centrifugation, we added invertase and isomerase (baker's yeast; *Sigma-Aldrich, St Louis, MO, USA*) to an aliquot of 200 µl to degrade sucrose and convert fructose into glucose. After enzymatic conversion to gluconate-6-phosphate with the hexokinase reaction (hexokinase produced by *Sigma Diagnostics, St Louis, MO, USA*), the total amount of glucose (sugars) was determined photometrically at 340 nm in a 96-well microplate photometer (*HR 7000; Hamilton, Reno, NE, USA*). We took 500 µl of the extract (including sugars and starch) and incubated it with a fungal amyloglucosidase from *Aspergillus niger* (*Sigma-Aldrich*) for 15 h at 49°C to break starch into glucose. Total glucose (corresponding to NSC) was determined photometrically as described above. The concentration of starch was calculated as NSC concentration minus the free sugar concentration determined in the first step. Standards of pure starch and glucose, fructose and sucrose solutions were used as controls, and standard plant powder (orchard leaves; *Leco, St Joseph, MI, USA*) was included to test the reproducibility of the extraction. NSC concentrations were expressed on a gram per dry matter basis and scaled to the whole stem and root dry biomass to obtain the absolute value of total NSCs pool per tree. We assumed no large vertical or horizontal NSC gradient within the wood (which is all sapwood); therefore, upscaling to the whole stem and dry root mass should give realistic absolute values for the NSC content per tree. We ran the analysis in the same laboratory with no change in protocol (Quentin et al. 2015).

2.5 DENDROCHRONOLOGICAL ANALYSIS

From each harvested tree, a stem disc was cut at the level of the root collar using a microtome to determine age and radial growth. The stained discs were photographed (Canon EOS 700D) and analysed with WinDENDRO™ (Regent Instruments Inc., Quebec, Canada) under a microscope. The number and width of the rings were measured in 2–4 perpendicular directions because of the eccentric tree piths, and then arithmetically averaged.

2.6 STATISTICAL ANALYSIS

2.6.1 VARIABLE SELECTION & DISCRIMINATION BETWEEN VITALITY CLASSES

Principal Component Analysis (PCA) was used to select variables among leaf and growth traits with the highest contribution to principal components (Figure S 1). The comparison of means among vitality classes (Table S3) was made with Yuen's trimmed t-test (Yuen 1974) with the Benjamini-Hochberg p-value adjustment, with the significance level set to 0.05 (Benjamini and Hochberg 1995); and among species with a heteroscedastic two-way factorial ANOVA (Figure S 2) based on trimmed means (20% trimming level). This procedure downplays outliers, heavy-tailed distributions and unequal sample sizes and is robust against violations of homogeneity. We waived the violation of normality because our sample size exceeded 50 observations.

2.6.2 EFFECT OF BIOMASS PARTITIONING ON TRAITS OF SHADE TOLERANCE

We modelled the influence of biomass partitioning to leaves and shoots on traits of shade tolerance such as LAR, AGR and NSC with multivariate analysis of covariance MANCOVA (R package *car*), the Pillai-Bartlett trace test and ANOVA type III for unbalanced designs (details in S1). The multivariate linear regression is able to capture linear growth observed in young trees within selected height classes and to model the simultaneous influence of explanatory variables such as species, tree age, LMF and shoot growth rate on the response variables LAR, AGR and NSC (Eq. 1). The pairwise comparison of species' means (R package *emmeans)* was made with a post-hoc Tukey Honest Significant Difference or Tukey HSD test (Tukey 1949).

$$\left\{\begin{matrix} \ln(\mathrm{LAR}) \\ \ln\,(\mathrm{AGR}) \\ \ln\,(\mathrm{NSC}) \end{matrix}\right. = \beta_0 + \beta_1 species + \beta_2 \ln(LMF) + \beta_3 \ln(shoot\ growth) * age + \beta_4 \ln(shoot\ growth) + \beta_5\, age + \varepsilon \quad (1)$$

where ε is the error term that follows a standard normal distribution (Figure S 3). All continuous variables were log-transformed, except for tree age, and centred. The assumption of homogeneity of covariance (Box's M test at alpha <0.001)) was not violated (p=0.03). Correlation between the covariates was moderate: r=0.50 between shoot growth

rate and tree age, low correlation r=-0.11 between shoot growth rate and LMF, and r=-0.36 between LMF and age. Multicollinearity was tested with variance inflation factor VIF (R package *olsrr*) and did not exceed 3, indicating low to moderate multicollinearity. The analyses and visualisation were run in R, version 3.6.1 (R Core Team 2020).

3 RESULTS

3.1 BIOMASS ALLOCATION

In deep shade (mean ISF 1.95–3.34% on the six plots, Table S1), *Fagus sylvatica* invested more heavily in leaf area development and crown volume starting from the height class >36 cm in both high- and low-vitality trees than its competitor species, while its mean leaf area and crown volume were smaller than those of the competitors for smaller seedlings <36 cm height (Figure 1). Mean biomass allocation to leaves increased with tree height for all species, with *Fagus sylvatica* investing more in leaves than *Acer* spp. above a tree height of 60 cm (Figure 1). Patterns in branch biomass allocation were similar to those for leaf biomass, but maples seedlings <60 cm tall generally did not grow branches if not browsed. Allocation to the stem was more similar in the three species than allocation to leaves and branches. Mean biomass partitioning to roots was higher in *Acer* spp. up to a height of 90 cm. In short, *Acer* spp. focused on conservative investments in the stem and roots, while *Fagus sylvatica* pursued light harvesting and space occupation strategies by allocating biomass to leaves and branches.

As expected, species identity significantly affected leaf traits such as leaf area (p=0.018) and crown volume (p=0.025) in the heteroscedastic two-way factorial ANOVA where the two vitality classes and two height classes were pooled together (Figure S 2). The species effect was also significant for the growth trait shoot biomass (leaf and branch mass, p=0.004), but not for total dry mass (p=0.335). The total mean biomass of *Acer* spp. trees (39 ± 6.7 g for *A. pseudoplatanus* and 44 ± 8.4 g for *A. platanoides*) was smaller, although not significantly so, than that of *Fagus sylvatica* (86 ± 17 g, mean ± SE).

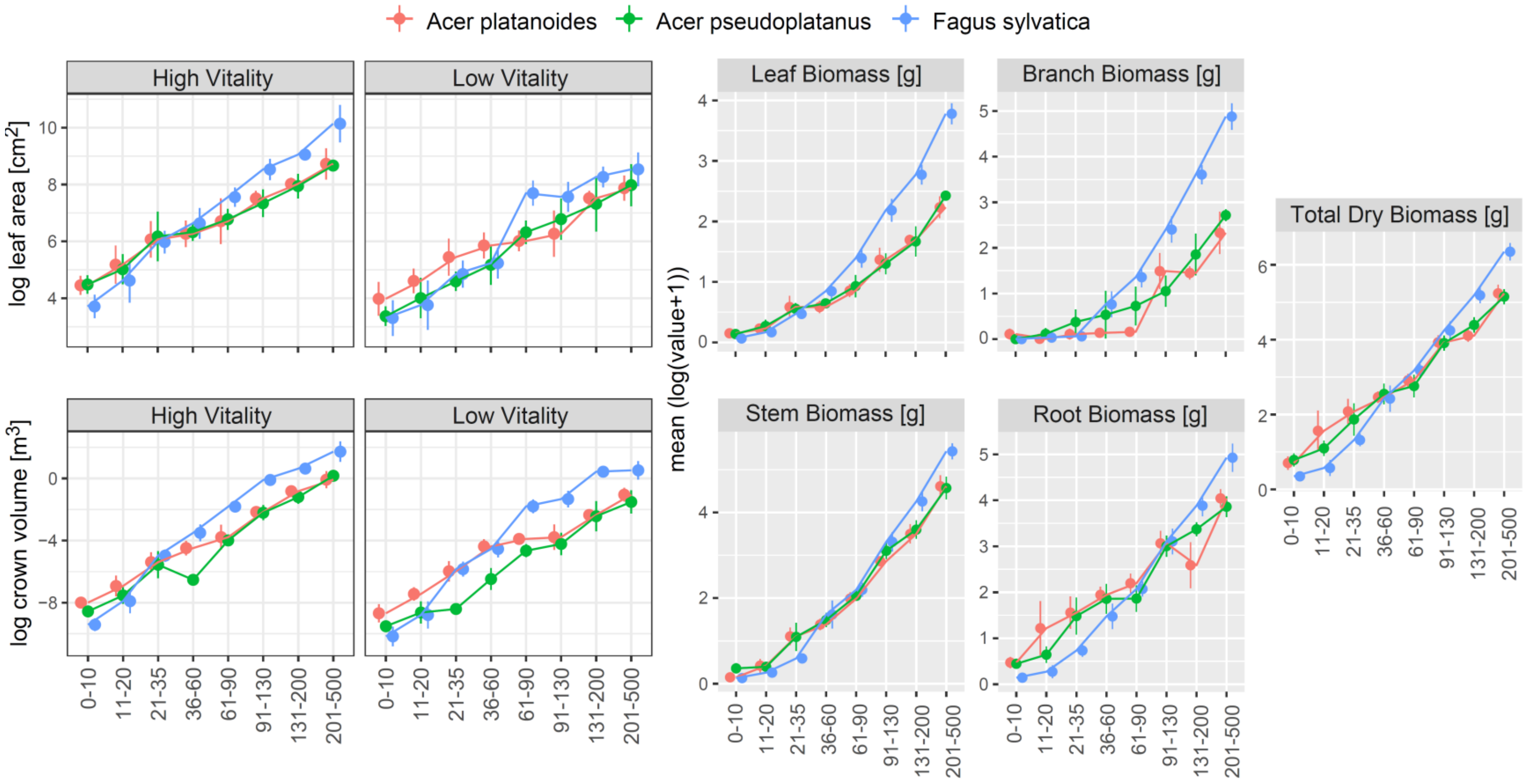

Figure 1. Panel A: mean leaf area, panel B: mean crown volume according to species and height class for trees of high and low-vitality. Panel C: mean leaf, branch, stem, root and total dry biomass of the high-vitality trees in height classes: dots represent means and whiskers represent standard errors.

The three species allocated biomass differently: *Fagus sylvatica* had a significantly larger leaf area (3320 ± 39 cm^2) than *Acer pseudoplatanus* (1170 ± 179 cm^2, p=0.046) and *A. platanoides* (1516 ± 267 cm^2, p=0.07), a larger crown volume (1.0 ± 0.3 m^3, p=0.029) than both *Acer* spp. (0.1 ± 0.0 m^3 for *A. pseudoplatanus* and 0.2 ± 0.1 m^3 for *A. platanoides*), and a much greater shoot (leaf+branch) biomass (21 ± 5 g, p=0.006) than the two competitors (4.6 ± 0.7 g for *A. platanoides* and 4.9 ± 0.9 g for *A. pseudoplatanus*).

3.2 Discrimination between Vitality Classes

Leaf traits (LAR, leaf area, crown projection area, crown volume), together with growth traits (AGR, root collar diameter, mean height increment; growth rates of leaf, stem, roots and shoots biomass per year) and storage (NSC) contributed 56.6% to the first axis in the PCA, while LAR, LMF, SLA and tree ring width contributed 13.6% to the second axis, summing to 70.1% of the total variance in the tree traits (Figure S 1). The major contributors to the two principal components were AGR (11.0%), NSC pool (7.6%), LAR (32.6%) and LMF (33.0%)

High-vitality trees differed from low-vitality individuals in that they had a significantly higher LAR (t(205.71)=4.92, p<0.001), LMF (t(219.37)=5.88, p<0.001) and NSC (t(178.60)=2.47, p=0.015) (Yuen’s t-test for trimmed means, Table S 3). Unlike leaf and storage traits, growth (AGR) did not differ between high- and low-vitality trees (p=0.181). Also, the mean annual height increment was similar for both vitality classes and varied between 5.2 and 6.5 cm for high-vitality trees and between 4.4 and 5.7 cm for low-vitality individuals (Figure S 4).

3.3 Influence of LAR, AGR and NSC Pool on Species’ Juvenile Survival Time

Effects of tree age, shoot growth (leaf+branch mass per year), species identity, LMF and the interaction between tree age and shoot growth were significant for the response variables LAR, AGR and NSC in the MANCOVA model, based on a Pillai test (Figure S4). For every 1% increase in tree age, LAR decreased by 1.33% and AGR by 0.74%, while NSC increased by 9.37% (Table 3). For every 1% increase in shoot growth rate, LAR significantly decreased by 0.04% while AGR and NSC were enhanced by 0.83% and 0.82%, respectively.

Compared with *Acer platanoides*, *A. pseudoplatanus* had a lower leaf area ratio and growth rate but a higher storage demand (although not to a significant degree). Compared with *Acer platanoides*, *Fagus sylvatica* was associated with a higher LAR (not significant), significantly slower growth and lower NSC storage if all other predictors were held constant. A 1% change in LMF significantly affected all response variables, positively influencing LAR by 0.83% and negatively affecting AGR and NSC, by 0.89% and 0.49%, respectively. The model featured a low standard deviation of the residuals (prediction errors or RMSE) except for NSC, and a high goodness-of-fit (R^2=0.83–0.98).

Table 3. MANCOVA summary: effect of explanatory variables tree age, shoot growth rate, species identity, leaf mass fraction (LMF) and interaction between tree age and shoot growth rate on leaf area ratio (LAR), absolute growth rate (AGR) and content of non-structural carbohydrates (NSC). CI –0.95 confidence intervals, SE – standard error, RMSE – root mean square error or prediction errors, R^2 – the variance of the response variable explained by the explanatory variables.

Response	Predictors	P-value	T-stat	Coef	CI	SE	RMSE	R^2
Ln(LAR)	(Intercept)	**<0.001**	125.66	3.92	3.87 – 3.99	0.03	*0.26*	*0.88*
	Tree age	<0.001	-3.84	-0.01	(-0.02) – (-0.01)	0.00		
	Ln(shoot growth rate)	0.002	-2.99	-0.04	(-0.07) – (-0.01)	0.01		
	A. platanoides			reference				
	A. pseudoplatanus	0.024	-2.27	-0.10	(-0.18) – (-0.01)	0.04		
	F. sylvatica	0.385	0.87	0.04	(-0.05) – (-0.13)	0.04		
	Ln(LMF)	<0.001	32.86	0.83	0.78 – 0.88	0.02		
	Tree age x ln(shoot growth rate)	0.001	3.33	0.00	0.00 – 0.01	0.00		
					F(6, 241) = 268.6, p-value: < 2.2e-16			
Ln(AGR)	(Intercept)	0.849	-0.19	-0.00	3.87 – 3.99	0.02	*0.41*	*0.98*
	Tree age	0.006	-2.75	-0.01	(-0.02) – (-0.00)	0.02		
	Ln(shoot growth rate)	<0.001	76.24	0.83	(-0.07) – (-0.01)	0.01		
	A. platanoides	reference						
	A. pseudoplatanus	0.126	-1.53	-0.05	(-0.18) – (-0.01)	0.03		
	F. sylvatica	<0.001	-5.48	-0.19	(-0.05) – (-0.13)	0.03		
	Ln(LMF)	<0.001	-45.49	-0.89	0.78 – 0.88	0.01		
	Tree age x ln(shoot growth rate)	<0.001	-5.78	-0.00	0.00 – 0.00	0.00		
					F*(6, 241) = 2270, p-value: < 2.2e-16*			

Response	Predictors	P-value	T-stat	Coef	CI	SE	RMSE	R^2
Ln(NSC)	(Intercept)	<0.001	-27.09	-2.65	3.87 – 3.99	0.09	*0.85*	*0.83*
	Tree age	<0.001	8.15	0.09	(-0.02) – (-0.01)	0.01		
	Ln(shoot growth rate)	<0.001	18.41	0.81	(-0.07) – (-0.01)	0.04		
	A. platanoides	reference						
	A. pseudoplatanus	0.146	1.46	0.19	(-0.18) – (-0.01)	0.13		
	F. sylvatica	<0.001	-3.41	-0.48	(-0.05) – (-0.13)	0.14		
	Ln(LMF)	<0.001	-6.14	-0.49	0.78 – 0.88	0.08		
	Tree age x ln(shoot growth rate)	<0.001	-6.62	-0.03	0.00 – 0.01	0.00		

F(6, 241) = 224.4, p-value: < 2.2e-16

The predictions of the MANCOVA model for LAR, AGR and NSC over tree age suggest that juvenile trees of the three species are facing similar trade-offs between investment to leaves (LAR), growth (AGR) and storage (NSC) (Figure 2). The decline in LAR over time is due to an increasing tree biomass, while the increase in AGR means that tree biomass is increasing at ever higher rates, in particular given the log scale of the vertical axis (Figure 2). In line with the increasing AGR, the absolute value of the NSC pool is also increasing, due to the growing parenchyma tissue. The relevant pattern in Figure 2 is, therefore, the difference in slope between LAR on the one hand, and AGR and NSC on the other hand. Unfortunately, we lack data for trees in the height class >5 m (and thus of older age) and can only hypothesise that the trajectory of AGR and NSC would have continued to develop in a linear (on a log scale) manner or would have taken another trajectory. Another trajectory assumes a slowing of growth and/or storage, when both may reach a plateau. Still, the pattern emerging from Figure 2 is that, in high-vitality trees of the same age, the two *Acer* spp. have a smaller LAR at their disposal (smaller LAR intercept values) than *Fagus sylvatica*, due to faster growth (higher AGR intercept value) than in *Fagus sylvatica*, and also need more storage than *Fagus sylvatica* (visible from the higher NSC intercept value in Figure 2.

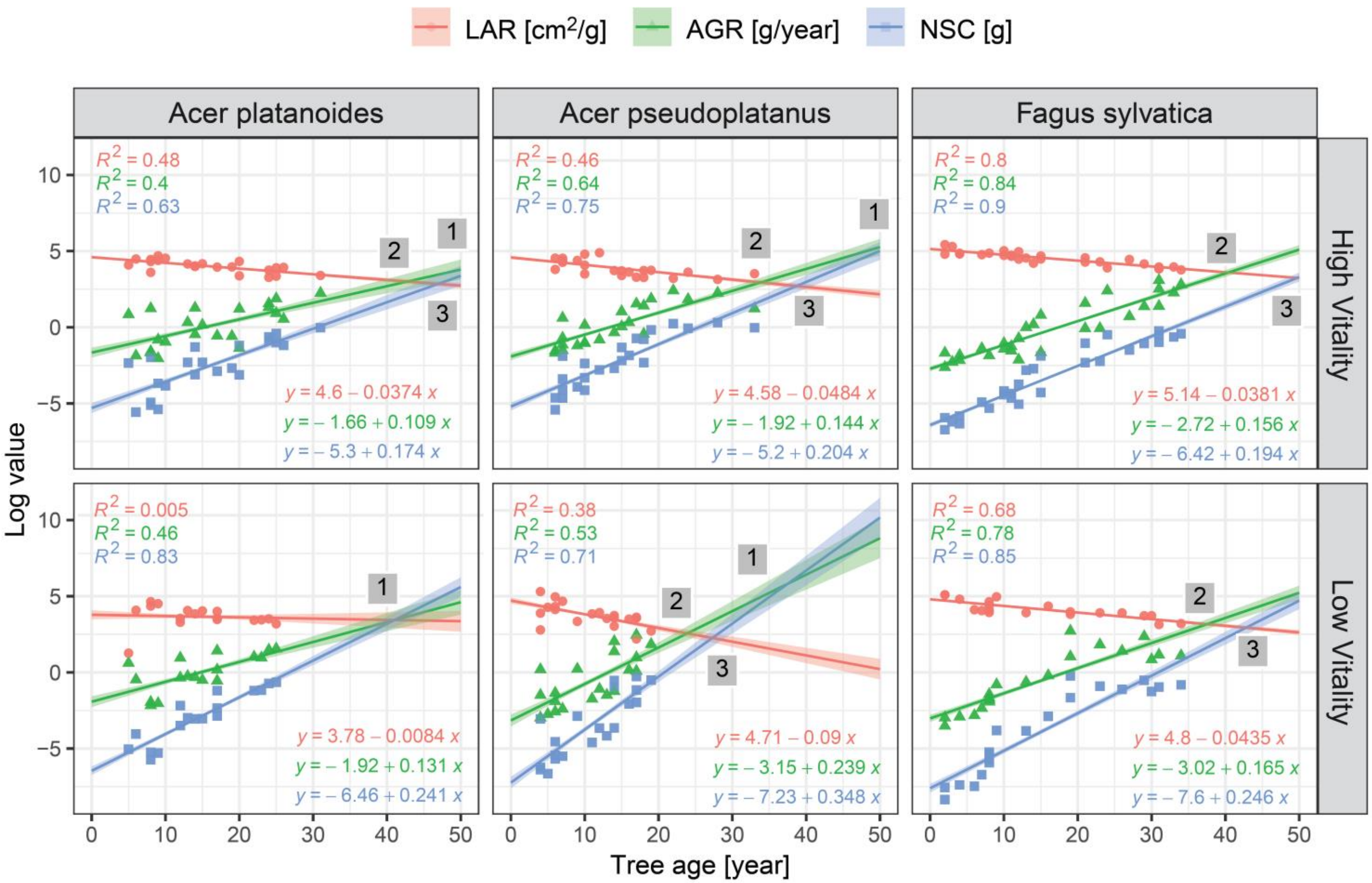

Figure 2. Linear regression predicting the development of LAR, AGR and NSC with tree age: dots represent observed values, bands represent 0.95 confidence intervals (CI), point 1 indicates carbon limitation as a result of a trade-off between AGR (growth) and NSC pool (storage), point 2 indicates a limiting LAR capacity to support growth, and point 3 indicates a limiting LAR capacity to support storage.

This relationship is more evident in low-vitality *Acer* spp. trees where LAR is lower or decreasing faster (steeper slope) than in high-vitality regeneration while AGR and NSC increase faster. Low-vitality *Fagus sylvatica* trees differ from high-vitality trees in that they have a lower LAR and exhibit faster growth of AGR and NSC values, as indicated by the comparably steeper lines. The different rates of change in LAR, AGR and NSC lead to a trade-off point between AGR and NSC due to carbon limitation, which is reached earlier in low-vitality trees than in high-vitality trees (point 1, Figure 2). Carbon limitation occurs as a result of the ever-shrinking capacity of LAR to support both growth (point 2) and storage (point 3), assuming no improvement of light availability during this development.

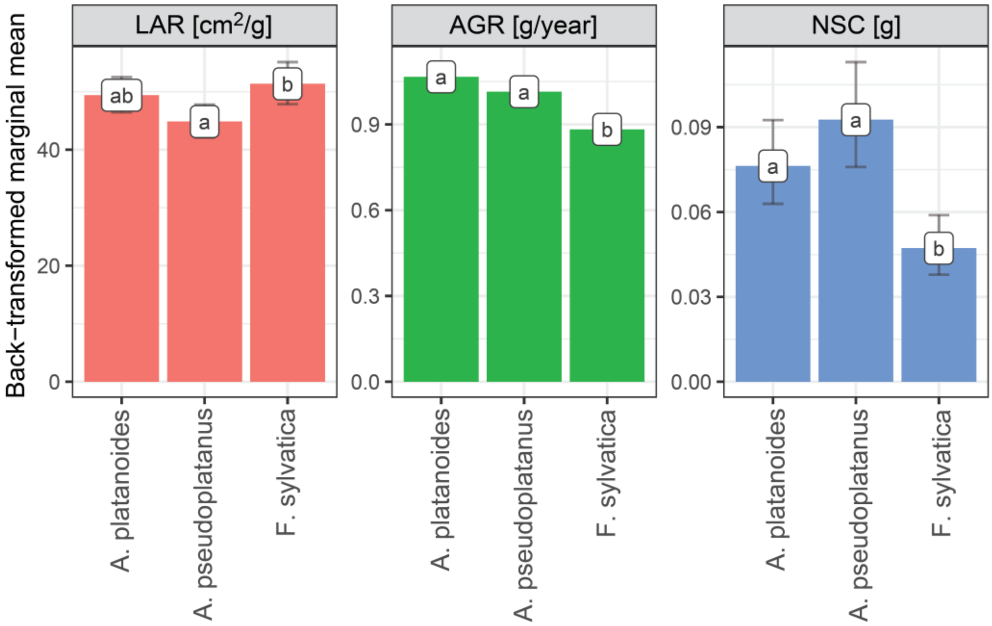

Figure 3. Pairwise comparison among species with the post-hoc Tukey HSD test: different letters indicate significance differences, whiskers represent 0.95 CI, and marginal mean assumes tree age =14.3, shoot growth = 0.4 g/year and LMF = 0.1.

The three species have different allocation strategies, as confirmed by the predicted marginal mean of the MANCOVA model (assuming tree age =14.1, shoot growth=0.4 g and LMF= 0.1). Compared with *Acer platanoides* (Figure.3), *A. pseudoplatanus* had the lowest and *Fagus sylvatica* the highest marginal mean of LAR, although the difference was not significant. However, a significant difference was observed between the mean LAR of *Acer pseudoplatanus* (44.85 cm^2/g), and that of *Fagus sylvatica* (51.36 cm^2/g, p-value=0.007).

The high AGR of *Acer platanoides* (1.07 g/year) did not differ from the moderate growth rate of *A. pseudoplatanus* (1.01 g/year), although the growth rate of both of these species was significantly higher than that of *Fagus sylvatica* (0.88 g/year, p-value<0.001). Compared with *Acer platanoides* (0.08 g), mean NSC allocation was higher in *A. pseudoplatanus* (0.09 g) and lower in *Fagus sylvatica* (0.05 g, p<0.001). In short, *Acer platanoides* put growth at stake and maintained a moderate leaf area ratio and storage allocation, while *A. pseudoplatanus* invested in storage at the expense of allocation to leaves. At the same time, *Fagus sylvatica* sacrificed growth and storage to increase LAR.

4 DISCUSSION

4.1 TRAITS OF SHADE TOLERANCE AND THEIR IMPACT ON SURVIVAL TIME

The aggregation of traits, rather than each trait alone, and their shift during ontogeny determine the performance and the persistence strategy of species occurring in the shade (Ameztegui et al. 2017; Gibert et al. 2016). Although LAR, AGR and NSC pool are traits associated with shade tolerance (Valladares and Niinemets 2008), they have not previously been combined to infer their impact on regeneration survival time. The potential trade-off between growth and storage traits in juvenile trees growing in deep shade has not been shown so far (Palacio et al. 2014). In our study, the trade-off between growth (AGR) and storage (NSC) at decreasing capacity of LAR can lead to a reduction in survival time under carbon limitation (point 1, Figure 2). Thus, our model can partly explain the long survival time of *Fagus sylvatica* in old-growth deciduous forests.

The 'carbon gain' concept is based on the assumption that shade-tolerant species have a higher LAR, and therefore improved light interception, than shade-intolerant species and thus a larger fraction of biomass is allocated to foliage (Bazzaz 1979; Givnish 1988). Indeed, in our study the marginal mean LAR of *Fagus sylvatica* was higher and declined more slowly during ontogeny compared with its competitors (Figure 2), confirming findings by other authors (Annighöfer et al. 2017; Niinemets 1998). Such phenotypic plasticity can be explained by two factors: (i) low annual growth allows *Fagus sylvatica* to balance leaf area per unit mass and (ii) the energy (glucose) required for building a unit of leaf area is lower

in juvenile *Fagus sylvatica* than in *Acer pseudoplatanus* (Petriţan et al. 2010). A failure to balance leaf area with growth leads to consistently higher mortality in seedlings of species with a higher relative growth rate than in seedlings with a lower relative growth rate in deep shade (Walters and Reich 1996). Hence, *Fagus sylvatica* maintains a higher LAR for more efficient capture of diffuse light at a relatively 'cheap' leaf construction cost.

According to several studies (Popma and Bongers 1988; Walters and Reich 1996), the growth rate of young trees in low light should be higher for shade-tolerant species and lower for shade-intolerant species. Our findings imply the opposite, however, as *Fagus sylvatica* grew slowly at a young age and focused biomass allocation to branches and leaves (horizontal growth), supporting the findings of Petriţan et al. (2010) and Collet et al. (2011). The negative relationship between growth and survival time in *Fagus sylvatica* for the first 70 years of its life was observed in studies by Di Filippo et al. (2012, 2015). Similar relationships have been observed between the growth rate of conifers and lifespan in the first 50 years of life, i.e. fast early growth was associated with decreased lifespan (Bigler 2016).

Following the 'defence and storage' concept, shade-tolerant species partition a major fraction of photosynthates to internal stores at the expense of rapid growth (Kitajima 1994; Kobe 1997). In our study, *Fagus sylvatica* trees had a lower NSC content during slow growth compared with the less shade-tolerant *Acer* spp., thus contradicting the 'defence and storage' concept. Similar results as in our study were found for *Acer saccharum* (Kobe 1997) and for evergreen shade-tolerant species (Lusk and Piper 2007; Piper et al. 2009); however, no difference has been reported for other deciduous species – *Castanea crenata* and *Quercus mongolica* (Imaji and Seiwa 2010). On the one hand, early spring leaf-out of *Acer pseudoplatanus* compared with juvenile *Fagus sylvatica* produces more photosynthates before canopy closure (Vitasse 2013). A high concentration of NSCs in *Acer* spp. may also reflect high levels of browsing and defoliation, as starch and sugars are used to survive periods of a negative net carbon balance after defoliation (Myers and Kitajima 2007) or stem loss (Latt et al. 2000). On the other hand, faster-growing juvenile trees increase total storage (Canham et al. 1999; Niinemets 1998). In our study, both *Acer* spp. had higher AGR values than *Fagus sylvatica* and also maintained higher NSC content, while *Fagus sylvatica* showed the opposite (Figure 2).

Assuming that light had not improved and LAR reached its carrying capacity in carbon supply to growth (point 2) and storage (point 3, Figure 2), a tree can have two strategies: (i) slow down growth to save storage while keeping LAR high; or (ii) deplete storage to maintain growth while decreasing LAR. Many empirical studies have shown that storage is prioritised over growth under carbon limitation (Weber et al. 2018; Wiley et al. 2013). A replenishment of a certain level of NSCs before growth leads to allocation of carbon first to storage and then to growth (Imaji and Seiwa 2010; Weber et al. 2018). However, larger saplings require more storage to support the increasing operational costs of tissue maintenance and defence (Wiley and Helliker 2012). This is why allocation to storage may increase disproportionately compared with allocation to growth (point 1, Figure 2), leading to a trade-off between growth and storage.

Under environmental conditions leading to carbon limitation (long-term deep shade or sustained severe defoliation), a trade-off between storage and growth is possible (Palacio et al. 2014), causing carbon starvation and tree death (to the right of point 1, Figure 2) (Weber et al. 2018). Presently, it is unclear whether saplings deplete their NSC reserves before growth reduction or death in the shade. In an experiment by Weber et al. (2019), mortality of shaded *Fagus sylvatica* seedlings (0–60 cm tall) occurred after NSC concentrations in the stem dropped to approx. 3% (dry mass basis) after insect herbivore attack. In our study, the mean NSC concentration in the stem of low-vitality *Fagus sylvatica* seedlings was 7.8% of dry mass for the same height class (comparison is valid if the method is the same). The mortality of *Acer pseudoplatanus* happened at less than 1% (dry mass basis) NSC concentration in the study by Weber et al. (2018), while our low-vitality *A. pseudoplatanus* seedlings maintained mean NSC levels of 9.7% (dry mass basis) for the same height classes. In our study, we did not observe growth reduction, as LAR was still able to support both growth and storage, hence lethal carbon starvation could not be assumed. However, unlike trees in the canopy, young trees do not have the opportunity to replenish NSC reserves in autumn (Hoch et al. 2003) because leaf senescence of trees and regeneration occurs at same time (Varsamis et al. 2019; Vitasse et al. 2009). Therefore, the NSC reserves of young trees may decrease for decades, eventually leading to tree death. We therefore conclude that the earlier crossing point of the AGR and NSC regression lines

for the two *Acer* spp. indicates that carbon starvation occurs at a younger age compared with *Fagus sylvatica*.

With a slow AGR, species can have a longer survival time because the trade-off between growth and storage is postponed in time. In our study, slower growth – indicated by low AGR values and low storage demand (indicated by low NSC values) – postponed this trade-off, thus extending the survival time of *Fagus sylvatica* in both vitality classes compared with that of the two *Acer* spp., under the assumption of a linear development of AGR and NSC on a log scale. *Fagus sylvatica* of both vitality classes most likely do not experience the trade-off (point 1, Figure 2) before the age of 50, while both *Acer* spp. in the two vitality classes are likely to approach this point at an age of 40–45 years. Taking into account that the average period of the first release to nearby canopy gaps is at 65 years for beech in Uholka (Trotsiuk et al. 2012), we suggest that *Fagus sylvatica* is able to balance LAR, NSC and AGR trajectories and extend its survival time by at least two decades compared with the two *Acer* spp. Thus, this model can explain the overall dominance of *Fagus sylvatica* juveniles, the drop in the share of *Acer* spp. trees from 15% to 3% in DBH class 3–3.9 cm, and the absence of *Acer platanoides* regeneration starting from 2 cm DBH in Uholka (Figure S5). *Acer* spp. of high vitality would have reached up to 5 cm diameter at root collar (corresponding to 3 cm DBH, based on a regression between DRC and DBH) and died if there was no change in light availability following a canopy opening, while beech would have grown up to 7 cm diameter at root collar (up to 5 cm DBH) and would have had a higher chance of survival until the first release into the canopy.

4.2 SPECIES BIOMASS ALLOCATION AND TREE VITALITY

Biomass allocation of trees with low and high vitality differed significantly in our study, reflecting different performance in shade. Biomass allocation patterns to leaves (LMF, leaf area, LAR) and storage pool (NSC) define vitality, whereas AGR and height increment do not and do not differ between low- and high-vitality regeneration (Table S3). In addition, similar height increments for all species do not indicate shade avoidance (Henry and Aarssen 2001). In previous studies, *Fagus sylvatica* saplings in the height class 201–500 cm featured greater leaf areas compared with *Acer* spp., while greater biomass allocation to branches in *Fagus sylvatica* led to larger crowns compared with the more slender form of *Acer* spp.

(Annighöfer et al. 2017; Petriţan et al. 2009). Both *Acer* spp. studied here, even in the larger height classes, tend to grow long petioles over branches (Beaudet and Messier 1998). Such kind of leaf display may be an adaptation to browsing (Modrý et al. 2004), enabling minimisation of biomass loss by allocating less biomass to branches and leaves and concentrating it on the top to avoid self-shading. In our study, *Fagus sylvatica* and *Acer* spp. of low vitality had a smaller leaf area and crown volume than high-vitality trees. As a result of crown decline and reduced leaf area, the level of NSCs was reduced in trees with low vitality (Table S3), in agreement with previous research (Hartmann and Trumbore 2016; Schönbeck et al. 2018).

4.3 LIMITATIONS

Although our model offers a plausible explanation for the regeneration growth processes, it is, nevertheless, linear and can thus be applied only to the period of intensive growth when response and explanatory variables are developing mostly linearly. Furthermore, it assumes equal annual AGR and shoot growth, which may be theoretically possible but in reality varies with tree age and size (Gibert et al. 2016). The model does not take into account NSC pool of branches and the seasonal variation, an aspect that might be needed for a better understanding of the annual storage balance. Moreover, NSC concentrations were scaled to the whole stem and root. This is justified for relatively small saplings with wood consisting almost entirely of sapwood but seems problematic for saplings with larger vertical and horizontal NSC gradients within the stem.

5 CONCLUSION

The proposed integrated model of shade tolerance explains the longer survival time of *Fagus sylvatica* juveniles compared with *Acer* spp. species in deep shade. It combines traits from the 'carbon gain' (LAR and AGR) and the 'defence and storage' (NSC) hypotheses. Despite mechanistic approaches for the explanation of trait development, the model leads to inferences about the survival time of young trees without its direct measurement. Due to shifts in the above three traits with increasing tree height and age, juvenile trees may increasingly face a trade-off because a diminishing LAR becomes insufficient to produce the

photosynthates needed to support both growth and storage. In this case, a tree can either reduce growth to retain storage, or deplete storage to achieve growth. The ability of a species to balance LAR, AGR and NSC to postpone or avoid this trade-off defines its shade tolerance and thus its regeneration survival time. *Fagus sylvatica* is able to minimise both AGR and NSC, maintaining a high LAR, while the two *Acer* spp. cannot reduce storage and/or growth. The increased storage in *Acer* spp. may be explained by early leaf-out in spring and a focus on defence, sacrificing investment into leaf and branch biomass.

Our findings only partly confirm the 'carbon gain' concept: beech optimises carbon gain with an extensive leaf display, large crown volume and slowly decreasing LAR, but it grows slowly in the shade. However, with only storage in focus, our results also cannot fully support the 'defence and storage' concept, as shade-tolerant *Fagus sylvatica* stores less NSCs than its competitors.

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ELECTRONIC SUPPLEMENTARY MATERIALS

Table S 1. Mean and standard deviation () of variables for high- and low-vitality trees (H: height class; Sp: species; N: number of trees; a_pla: A. platanoides; a_pse: A. pseudoplatanus; f_syl: F. sylvatica; LMF: leaf mass fraction; LAR: leaf area ratio; AGR: absolute growth rate; NSC: non-structural carbohydrates; ISF: indirect site factor).

		High vitality										**Low vitality**									
				Leaf traits				Growth		Storage	ISF			Leaf traits				Growth		Storage	ISF
H	Sp	N	Age	Leaf area [cm^2]	Crown volume [m^3]	LMF	LAR [cm^2/g]	AGR [g/yr]	Shoot gr. rate [g/yr]	NSC [g]	%	N	Age	Leaf area [cm^2]	Crown volume [m^3]	LMF	LAR [cm^2/g]	AGR [g/yr]	Shoot gr. rate [g/yr]	NSC [g]	%
0–10 cm	a_pla	7	6.43 (1.90)	113.8 (98.55)	0.00 (0.00)	0.17 (0.08)	107.83 (54.53)	0.18 (0.17)	0.05 (0.08)	0.01 (0.01)	3.25 (0.01)	6	6.50 (1.87)	57.82 (25.08)	0.00 (0.00)	0.08 (0.05)	59.89 (46.8)	0.54 (0.83)	0.01 (0.01)	0.01 (0.01)	2.91 (0.01)
	a_pse	7	7.00 (1.10)	113.57 (80.78)	0.00 (0.00)	0.14 (0.08)	113.23 (86.97)	0.22 (0.09)	0.02 (0.01)	0.01 (0.01)	3.37 (0.01)	7	5.33 (1.21)	30.87 (11.98)	0.00 (0.00)	0.13 (0.1)	92.22 (66.16)	0.09 (0.07)	0.03 (0.05)	0.00 (0.00)	2.82 (0.01)
	f_syl	5	3.20 (1.1)	46.64 (26.14)	0.00 (0.00)	0.17 (0.10)	118.36 (50.76)	0.14 (0.07)	0.02 (0.01)	0.00 (0.00)	3.34 (0.02)	6	4.50 (2.81)	29.85 (15.78)	0.00 (0.00)	0.09 (0.06)	134.07 (125.99)	0.09 (0.06)	0.01 (0)	0.00 (0.01)	3.48 (0.02)
11–20 cm	a_pla	5	9.00 (2.58)	214.96 (157.41)	0.00 (0.00)	0.14 (0.08)	91.34 (86.11)	0.24 (0.11)	0.03 (0.02)	0.06 (0.08)	2.13 (0.01)	4	7.50 (1.91)	110.72 (47.24)	0.00 (0.00)	0.11 (0.07)	76.42 (49.96)	0.41 (0.56)	0.02 (0.01)	0.02 (0.03)	2.68 (0.01)
	a_pse	5	9.6 (2.61)	195.9 (181.29)	0.00 (0.00)	0.16 (0.09)	102.79 (62.71)	0.22 (0.10)	0.05 (0.05)	0.01 (0.01)	3.13 (0.01)	7	8.00 (3.46)	75.51 (66.98)	0.00 (0.00)	0.08 (0.07)	52.92 (40.82)	0.21 (0.16)	0.01 (0.00)	0.01 (0.01)	2.78 (0.01)
	f_syl	6	5.17 (5.23)	131.08 (100.64)	0.00 (0.00)	0.25 (0.08)	185.68 (71.41)	0.17 (0.05)	0.04 (0.01)	0.00 (0.00)	2.29 (0.01)	6	5.33 (2.34)	51.67 (33.19)	0.00 (0.00)	0.08 (0.03)	91 (48.97)	0.13 (0.08)	0.02 (0.01)	0.00 (0.00)	2.40 (0.01)
21–35 cm	a_pla	6	11.00 (4.86)	702.9 (708.17)	0.01 (0.01)	0.10 (0.05)	77.55 (44.67)	0.94 (0.97)	0.10 (0.10)	0.06 (0.05)	2.82 (0.01)	6	11.17 (2.99)	260.5 (151.91)	0.00 (0.01)	0.07 (0.03)	53.22 (23.27)	0.49 (0.22)	0.03 (0.02)	0.05 (0.05)	3.04 (0.01)
	a_pse	8	11.43 (3.95)	597.27 (478.04)	0.08 (0.21)	0.14 (0.08)	89.76 (59.90)	1.49 (2.69)	0.14 (0.15)	0.12 (0.17)	3.05 (0.01)	5	10.00 (3.39)	104.98 (39.49)	0.00 (0.00)	0.08 (0.05)	52.34 (33.10)	0.26 (0.12)	0.02 (0.01)	0.02 (0.02)	2.23 (0.00)
	f_syl	7	8.57 (3.15)	434.4 (209.95)	0.01 (0.01)	0.22 (0.04)	154.46 (43.02)	0.40 (0.28)	0.10 (0.09)	0.02 (0.02)	3.9 (0.01)	9	10.78 (3.63)	143.59 (52.52)	0.01 (0.01)	0.09 (0.06)	65.91 (47.46)	0.33 (0.31)	0.03 (0.05)	0.02 (0.02)	3.09 (0.02)
36–60 cm	a_pla	6	12.00 (4.77)	565.78 (205.09)	0.02 (0.02)	0.07 (0.03)	49.69 (7.37)	1.12 (0.69)	0.11 (0.10)	0.07 (0.04)	3.27 (0.01)	6	14.83 (5.23)	459.37 (289.89)	0.02 (0.03)	0.04 (0.03)	32.56 (15.82)	1 (0.35)	0.08 (0.07)	0.05 (0.04)	2.85 (0.01)
	a_pse	5	14.00 (5.70)	583.24 (200.23)	0.00 (0.01)	0.08 (0.04)	54.61 (34.40)	0.95 (0.36)	0.17 (0.19)	0.09 (0.07)	2.35 (0.00)	6	9.50 (4.55)	233.15 (211.24)	0.00 (0.00)	0.06 (0.05)	48.58 (48.84)	1 (0.95)	0.04 (0.04)	0.04 (0.03)	2.03 (0.01)
	f_syl	8	15.25 (5.70)	890.84 (523.19)	0.06 (0.05)	0.14 (0.06)	91.87 (53.49)	0.85 (0.65)	0.18 (0.13)	0.08 (0.07)	2.76 (0.01)	7	15.00 (3.7)	301.49 (213.16)	0.02 (0.02)	0.09 (0.09)	53.09 (49.84)	0.56 (0.22)	0.06 (0.05)	0.03 (0.02)	2.72 (0.01)
61–90 cm	a_pla	6	12.00 (3.85)	869.92 (316.08)	0.04 (0.03)	0.08 (0.02)	49.64 (15.77)	1.80 (1.18)	0.15 (0.07)	0.14 (0.05)	3.34 (0.01)	6	14.00 (3.52)	431.25 (134.92)	0.03 (0.02)	0.04 (0.02)	28.03 (10.26)	1.3 (0.73)	0.09 (0.05)	0.04 (0.04)	2.21 (0.01)
	a_pse	6	13.17 (5.04)	1005.35 (646.07)	0.02 (0.02)	0.1 (0.03)	63.85 (24.95)	1.46 (0.88)	0.28 (0.23)	0.20 (0.15)	3.01 (0.01)	7	14.00 (4.62)	606.84 (267.41)	0.01 (0.01)	0.06 (0.04)	29.46 (12.27)	1.63 (0.56)	0.12 (0.10)	0.18 (0.13)	2.59 (0.02)
	f_syl	7	15.57 (2.82)	2137.21 (1050.28)	0.22 (0.17)	0.13 (0.04)	87.04 (25.23)	1.63 (0.78)	0.44 (0.26)	0.15 (0.06)	2.32 (0.01)	4	23.25 (6.6)	2571.28 (1677.05)	0.17 (0.12)	0.11 (0.04)	71.2 (28.60)	1.62 (0.82)	0.45 (0.36)	0.20 (0.04)	2.27 (0.00)
91–130 cm	a_pla	7	18.57 (6.35)	2187.04 (1362.52)	0.13 (0.07)	0.06 (0.03)	41.45 (19.11)	3.03 (1.07)	0.47 (0.40)	0.30 (0.2)	3.68 (0.01)	6	12.83 (5.04)	672.9 (402.56)	0.05 (0.06)	0.04 (0.03)	29.79 (25.22)	2.89 (1.87)	0.34 (0.38)	0.10 (0.11)	2.42 (0.01)
	a_pse	7	22.29 (6.60)	1672.26 (773.25)	0.20 (0.27)	0.05 (0.01)	33.2 (11.80)	2.41 (0.87)	0.24 (0.13)	0.25 (0.18)	3.02 (0.01)	5	15 (5.66)	1349.3 (1527.17)	0.04 (0.07)	0.05 (0.03)	31.85 (16.22)	2.81 (1.63)	0.26 (0.21)	0.29 (0.18)	2.25 (0.01)
	f_syl	5	23.20 (3.77)	5521.82 (2445.22)	1.15 (0.62)	0.11 (0.04)	77.41 (28.50)	3.33 (1.84)	0.81 (0.51)	0.31 (0.18)	3.35 (0.02)	5	22.2 (3.42)	2260.35 (1416.53)	0.39 (0.36)	0.05 (0.02)	47.14 (26.40)	2.62 (1.11)	0.54 (0.29)	0.20 (0.17)	1.78 (0.01)
	a_pla	5	18.50 (7.72)	3310.88 (1655.16)	0.46 (0.14)	0.08 (0.02)	58.79 (35.55)	3.37 (1.21)	0.45 (0.23)	0.31 (0.11)	2.42 (0.01)	5	16.4 (5.08)	1900.4 (532.16)	0.11 (0.05)	0.12 (0.16)	35.23 (14.64)	3.7 (1.27)	0.43 (0.46)	0.25 (0.13)	3.31 (0.01)

		High vitality										**Low vitality**									
				Leaf traits				Growth		Storage	ISF			Leaf traits				Growth		Storage	ISF
H	Sp	N	Age	Leaf area [cm^2]	Crown volume [m^3]	LMF	LAR [cm^2/g]	AGR [g/yr]	Shoot gr. rate [g/yr]	NSC [g]	%	N	Age	Leaf area [cm^2]	Crown volume [m^3]	LMF	LAR [cm^2/g]	AGR [g/yr]	Shoot gr. rate [g/yr]	NSC [g]	%
131–200 cm	a_pse	4	19.75 (3.20)	2936.3 (933.39)	0.38 (0.34)	0.06 (0.03)	35.9 (6.73)	4.18 (1.20)	0.58 (0.37)	0.64 (0.42)	2.4 (0.01)	5	16.8 (2.28)	1592.15 (510.09)	0.22 (0.2)	0.05 (0.02)	32.64 (18.91)	3.5 (1.20)	0.24 (0.12)	0.37 (0.16)	2.23 (0.00)
	f_syl	8	26.57 (7.55)	9400.06 (4678.56)	2.08 (1.01)	0.08 (0.03)	49.54 (12.78)	8.21 (4.11)	2.32 (1.57)	0.81 (0.44)	2.47 (0.00)	7	25 (3.2	4576.51 (2707.01)	2.05 (1.51)	0.06 (0.03)	32.92 (19.86	6.28 (3.04)	1.27 (0.65)	0.45 (0.41)	2.12 (0.01)
201–500 cm	a_pla	8	23.62 (6.44)	7418.56 (5260.26)	2.02 (2.48)	0.06 (0.03)	34.69 (10.24)	9.1 (4.99)	0.99 (0.57)	1.14 (1.35)	2.33 (0.01)	6	22.17	3080.32 (1585.94)	0.42 (0.43)	0.04 (0.02)	29.21 (15.18	5.64 (1.96)	0.34 (0.24)	0.46 (0.42)	3.24 (0.01)
	a_pse	5	22.8 (3.83)	5919.78 (1323.89)	1.25 (0.49)	0.06 (0.02)	35.29 (10.39)	7.84 (2.43)	1.1 (0.14)	0.93 (0.51)	2.1 (0.01)	5	20.6 (7.7	3736.18 (2882.62)	0.43 (0.46)	0.03 (0.02)	23.05 (17.59	10.01 (5.91)	0.97 (0.98)	1.75 (1.49)	2.53 (0.02)
	f_syl	5	30.6 (3.91)	25982.97 (6692.77)	9.25 (8.07)	0.08 (0.01)	42.38 (10.02)	19.97 (7.89)	6.19 (2.87)	1.92 (1.23)	2.28 (0.01)	5	29 (5.8	6804.82 (4783.76)	3.15 (4.3)	0.05 (0.02)	23.61 (11.06	10.88 (7.54)	1.77 (1.73)	1.25 (1.4)	2.81 (0.01)

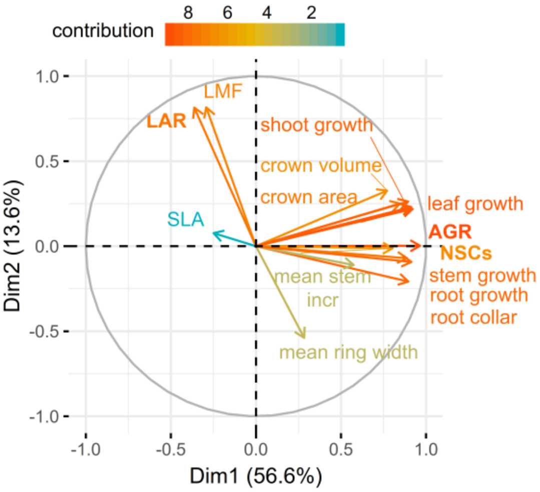

Figure S 1. Leaf, growth and storage traits' contributions to principal components. Variables in blue contribute the least and those in red the most to the two principal components.

Table S 2. Variables' contributions to the two principal components.

Trait	Variable	PC1,%	PC2,%
Growth	AGR [g/year]	10.96	0.00
Leaf	Leaf area [cm^2]	10.00	2.35
Growth	Root growth rate [g/year]	9.85	0.42
Growth	Leaf growth rate [g/year]	9.83	2.60
Growth	Diameter at root collar [cm] [cm]	9.46	2.13
Growth	Shoot growth rate [g/year]	9.43	3.39
Growth	Stem growth rate [g/year]	9.30	0.25
Leaf	Crown area [m^2]	8.46	3.09
Storage	NSC [g]	7.59	0.01
Leaf	Crown volume [m^3]	7.01	5.24
Growth	Mean H incr. [cm/y]	3.89	0.60
Leaf	LAR [cm^2/g]	1.55	32.61
Leaf	LMF	1.01	32.74
Growth	Mean ring [μm]	0.95	14.27
Leaf	SLA [cm^2/g]	0.73	0.29

Table S 3. Results of Yuen's t-test for trimmed means between the trees of low and high vitality.

Traits	Variable	Yuen's t-test	p-value
Leaf	LAR	t (205.71) = 4.92	<0.001
	LMF	t (219.37) = 5.88	<0.001
Storage	NSC	t (178.60) = 2.47	0.015
Growth	AGR	t (221.21) = 1.34	0.181

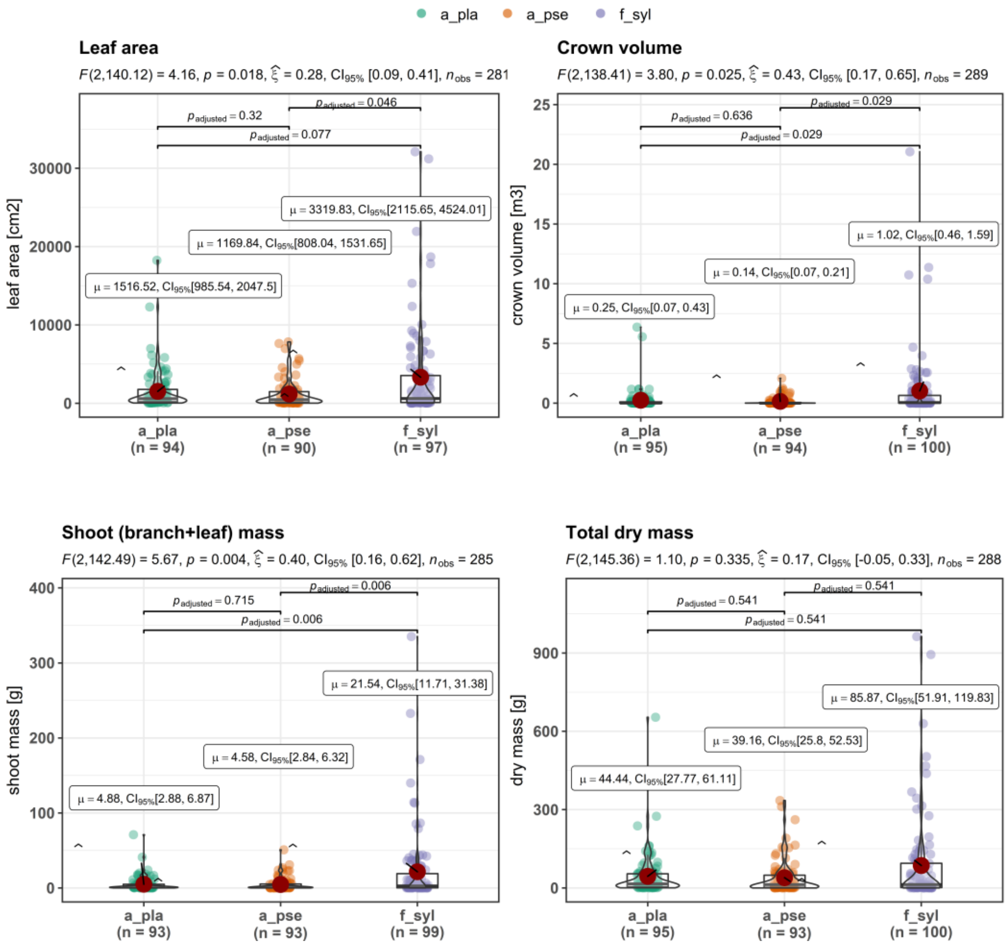

Figure S 2. Results of the heteroscedastic two-way ANOVA for all trees: leaf area, crown volume, shoots and total dry mass for Acer platanoides (a_pla), A. pseudoplatanus (a_pse) and Fagus sylvatica (f_syl). Red dots represent mean values.

S1. MANOVA AND 50 × 50 MANOVA

Result of the Pillai Test are presented in Table S 4 (upper part). The significance of explanatory variables was additionally checked with a 50 × 50 MANOVA with rotation testing (R package *ffmanova*, Langsrud and Mevik 2019), a variant of classical MANOVA modified to handle highly correlated responses using a Monte Carlo simulation (10,000 iterations) enabling exact significance testing under multivariate normality (Table S 4, lower part). The unbalanced design was handled by using a variant of Type II sums of squares (Langsrud 2003), which is insensitive to the ordering of the model terms and to scale changes.

Table S 4. Results of the classical MANCOVA showing the Pillai test for ANOVA type III and 50 × 50 MANOVA with bootstrapping with ANOVA type II. Vitality and height classes are pooled.

MANCOVA, Pillai test	Df	Pillai	Approx F	num Df	den Df	p-value (>F)
Tree age	1	0.96766	2383.77	3	239	< 2.2e-16
Ln(shoot growth)	1	0.94576	1389.09	3	239	< 2.2e-16
Species	2	0.73665	46.65	6	480	< 2.2e-16
Ln(LMF)	1	0.93178	1088.12	3	239	< 2.2e-16
Tree age × ln(shoot growth)	1	0.20909	21.06	3	239	3.848e-12

50 × 50, Hotelling-Lawley test	Df	exVarSS	nPC	nBU	exVarPC	exVarBU	p-value
Tree age	1	0.00897	3	0	1.00	1	7.56e-07***
Ln(shoot growth)	1	0.25897	3	1	0.94	1	< 2e-16***
Species	2	0.01321	3	0	1.00	1	3.12e-08***
Ln(LMF)	1	0.25086	2	1	0.95	1	< 2e-16***
Tree age × ln(shoot growth)	1	0.01554	3	0	1.00	1	1.04e-08***

exVarSS: explained variances calculated from sums of squares summed over all responses, nPC: number of principal components used for testing, nBU: number of principal components used as buffer components, exVarPC: variance explained by nPC components, exVarBU: variance explained by (nPC+nBU) components.

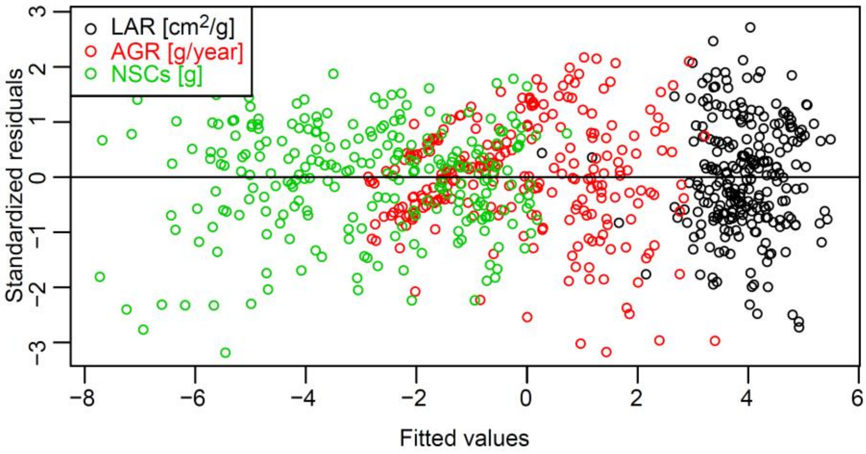

Figure S 3. Standardised residuals of the MANCOVA model for three response variables: LAR (leaf area ratio), AGR (absolute growth rate) and NSC (non-structural carbohydrates).

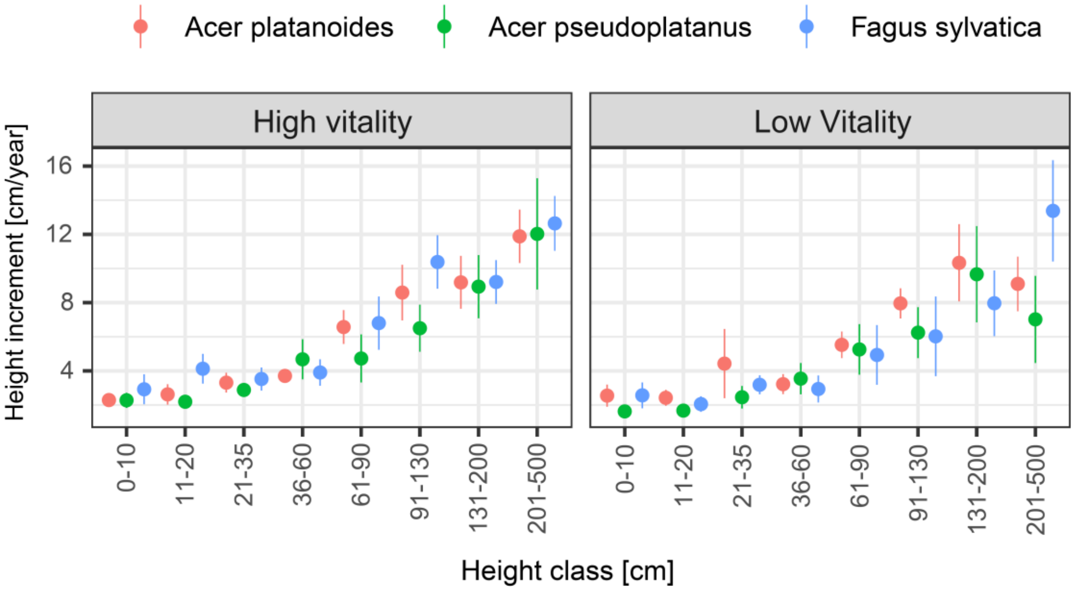

Figure S 4. Mean (dot) and standard error (whiskers) of tree height increment according to species and height class for trees of high and low vitality.

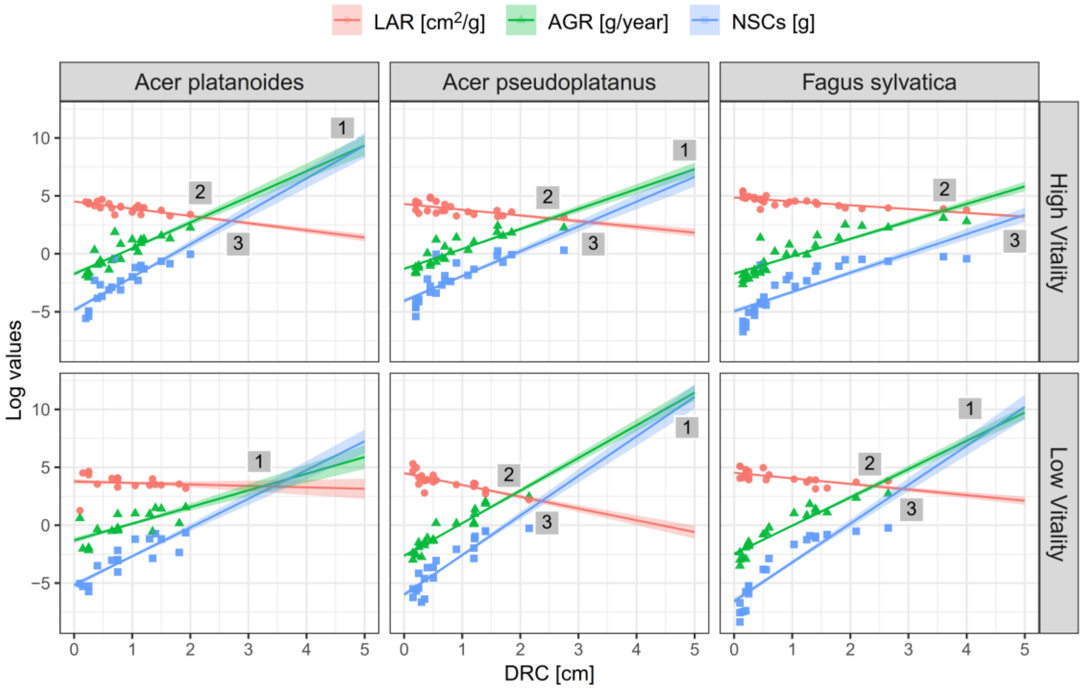

Figure S 5. LAR (leaf area area), AGR (absolute growth rate) and NSC (non-structural carbohydrates) development with diameter at root collar (DRC). Dots: fitted values, shaded bands: 0.95 confidence intervals.

CHAPTER

2

SURVIVAL TIME AND MORTALITY RATE OF REGENERATION IN THE SHADE OF A PRIMEVAL BEECH FOREST

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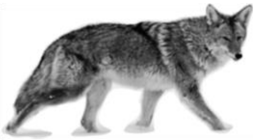
ABSTRACT

Low mortality rates and slow growth differentiate shade-tolerant from shade-intolerant species and define the survival strategy of juvenile trees growing in deep shade. While radial stem growth has been widely used to explain mortality in juvenile trees, leaf area ratio (LAR), known to be a key component of shade tolerance, has been neglected so far. We assessed the effects of LAR, radial stem growth and tree height on survival time and the age-specific mortality rate of juvenile *Fagus sylvatica* L. (European beech), *Acer pseudoplatanus* L. (sycamore maple) and *Acer platanoides* L. (Norway maple) in a primeval beech forest (Ukraine). Above- and belowground biomass and radial stem growth were analysed in 289 living and 179 dead seedlings and saplings. Compared to the other species, *F. sylvatica* featured higher LAR, slower growth and a lower mortality rate. The average survival time of *F. sylvatica* regeneration (72 years) matches the time this species needs to survive until the first release to canopy, thus allowing it to reach the canopy more often than its competitors. In contrast, a combination of lower LAR, higher growth rate and higher age-specific mortality rate of the two *Acer* species resulted in their shorter survival times and thus renders their presence in the canopy a rare event. Overall, this study suggests that shade tolerance commonly defined as a relationship between sapling mortality and growth can alternatively be formulated as a relationship between survival time and the interplay of growth and LAR.

Keywords: *Acer*, *Fagus*, dominance, LAR, mortality rate regeneration, shade tolerance, survival time



1 INTRODUCTION

The success of forest regeneration in reaching the canopy is related to species-specific patterns of radial and height growth, with shade-tolerant species growing better in the shade than shade-intolerant ones and vice versa (Givnish 1988; Popma and Bongers 1988). The better performance of shade-tolerant species under low light conditions has been attributed to a more efficient use of light due to higher leaf area per plant mass (leaf area ratio = LAR), a larger and deeper crown as well as faster growth (Bazzaz 1979; Givnish 1988). The trade-off between high-light growth and low-light growth, i.e. that shade-tolerant species grow faster than shade-intolerant species in low light and vice versa, has been widely viewed as the general explanation of shade tolerance (Spurr and Barnes 1980; Thomas and Bazzaz 1999).

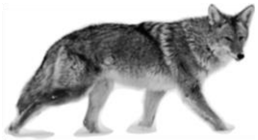
More recently, survival was argued to be more important than growth in determining regeneration success at low light levels (Canham et al. 1999; Kitajima 1994; Kobe et al. 1995; Veneklaas and Poorter 1998). Shade-tolerant species do not necessarily grow faster than shade-intolerant species at low light levels, but they may have a higher survival rate (Kitajima 1994; Kobe et al. 1995; Kobe and Coates 1997). For a long time, the high survivorship of shade-tolerant species under low light conditions has been attributed to efficient carbon allocation and storage, acting as a buffer against stress (Canham et al. 1999; Kobe 1997; Reich et al. 1998). Thus, the survival of regeneration may play a more important role than growth in determining plant success at low light levels, and the trade-off between growth at high light levels and survival (rather than growth) at low light levels would be the key explanation for the shade tolerance of species. The two trade-offs were considered to be mutually exclusive until Lin et al. (2001, 2002) found that shade-intolerant species had a higher mortality risk at slow growth than shade-tolerant ones. In this sense, high shade tolerance can be characterised by low mortality despite of slow growth.

In studies on regeneration mortality, at most one or two tree traits were used to characterize shade tolerance, because the collected dead juvenile trees (0-5 m tall) offered limited information. Mortality was modelled as a function of radial stem growth of dead and living juveniles, assuming that the collected samples provide a reliable estimate of the death rate at a given point in time in heterogeneous light environments (Dekker et al. 2009; Kobe et al. 1995; Kunstler et al. 2005; Petriţan et al. 2007) or on permanent plots (Kobe and Coates

1997; Pacala et al. 1996; Wyckoff and Clark 2000). Others applied Survival Analysis with radial stem increment and stem radius as explanatory variables, based on census data collected over more than 15 years (Lin et al. 2001, 2002). Collet and Le Moguedec (2007) used three variables, namely, tree height, a competition index and radial growth, whereas Kneeshaw et al. (2006) included only tree height and radial stem growth. So far, the potential influence of other traits of shade tolerance (Valladares and Niinemets 2008), such as leaf (Valladares and Niinemets 2008) or storage (Piper and Fajardo 2016) traits on survival time have to our knowledge not been studied.

We define 'regeneration survival time' as the average number of years a young tree can grow in deep shade. A young tree is likely to die before the first canopy release if the latter occurs only rarely, e.g. every 100-200 years in forests with a low disturbance rate, such as less than 1% (Hobi, Ginzler, et al. 2015; Valverde and Silvertown 1997)). In a companion study (Petrovska et al. 2021), the combination of high LAR with low absolute growth rate and low storage in seedlings (0-130 cm tall) and saplings (131-500 cm tall) of shade-tolerant *Fagus sylvatica L.* (European beech) was found to affect the survival time of beech and *Acer* spp. (Norway maple *Acer platanoides L.* and sycamore maple *Acer pseudoplatanus L.*). However, it remains unclear whether LAR influences mortality and what mean survival time of young trees is, mainly because dead trees do not retain leaves and partly lose biomass such that LAR and biomass variables cannot be assessed in hindsight. Moreover, there is no study assessing mean survival time for juvenile *Acer* spp. while estimation of *F. sylvatica* survival time by mean of dendrochronological analysis is highly variable (Trotsiuk et al. 2012).

With the present study, we complement existing mortality models with LAR as a new variable based on the performance of low-vitality trees in deep shade (Petrovska et al. 2020 in review). We assume that low-vitality juvenile trees are likely to die shortly, and thus use their allometry to model leaf area and total biomass for dead trees. With this, we can overcome the problem of limited information about dead saplings. According to Cleavitt et al. (2008), the number of leaves per seedling and, therefore, leaf area is significantly lower in dying than in vigorous seedlings. Another study reported that dry biomass was almost two times lower in dead than in living young trees (Piper and Fajardo 2016; Zhang et al.



2018). Hence, in this study we would like to answer the following questions for the three most abundant species in an old-growth beech-dominated forest, i.e. *F. sylvatica, A. platanoides* and *A. pseudoplatanus*: i) How do LAR, tree-ring growth and tree height affect the species-specific survival time of juvenile trees? ii) What is the age-specific death rate and survival time for these species?

2 MATERIALS AND METHODS

2.1 STUDY AREA AND SAMPLING DESIGN

The Uholka-Shyrokyi Luh reserve (Ukraine) belongs to the beech-dominated primeval forests of Europe and is since 1992 listed as a UNESCO World Heritage site (Stillhard et al. 2019; Zenner et al. 2020). We focused on the Uholka part of the reserve (centre coordinates: 48° 16′ N, 23° 40′ E) because of the higher share of *Acer* species than in the Shyrokyi Luh part (Commarmot et al. 2013). The Uholka part covers 4,729 ha, ranging between 400 and 1300 m a.s.l. in elevation. Mean annual temperature is about 8 °C (−3 °C in January and 18 °C in July), and mean annual precipitation is 1134 mm (*ibid)*. The almost pure beech forest (97% by basal area) was studied using a non-stratified systematic cluster sampling inventory in 2010 (314 plots) (Hobi, Commarmot, et al. 2015) and 2019 (238 plots). A small-scale disturbance regime dominates the forest with a mosaic of mainly small canopy gaps (98% of gaps <200 m^2). Only a few large stand-replacing events were detected using high-resolution satellite images (Hobi, Ginzler, et al. 2015).

We randomly selected six plots where seed trees of *F. sylvatica, A. platanoides* and *A. pseudoplatanus* were present and their regeneration up to 5 m in height was growing under low light levels. The plots varied in size from 0.2 to 0.7 ha and covered a total area of 2.53 ha. Five plots were in the core zone of the reserve, where natural processes occur without human intervention, and one in the buffer zone, where limited close-to-nature management is allowed (forest management that emulates or promotes natural processes resulting in natural stand structures, Brang et al. 2014). The distance between plots ranged from 400 m to 1000 m. Nine sub-plots with areas ranging from 140 m^2 to 520 m^2 (total 0.26 ha) were established in the six plots. They were delineated to contain a large variety of seedlings (0-130 cm tall) and saplings (131-500 cm tall) of the target species in different size and vitality classes. One individual per species, vitality class (low and high) and height class (8 classes in cm; 0-10, 11-20, 21-35, 36-60, 61-90, 91-130, 131-200, 201-500) was randomly selected and harvested at 6 plots. This resulted in a sample of 82, 80, 89 living individuals of *A. platanoides, A. pseudoplatanus* and *F. sylvatica*, respectively. Also, we randomly harvested stems of dead *Acer* spp*.* trees which had died within the last three years (2015-2018) and dead *F. sylvatica* trees following the method by Kobe et al. (1995), matching wherever possible, the height classes of the harvested living trees. Time since death was estimated based on the dead trees' visual appearance, taking into account i) bud condition (presence, intactness), ii) bark (intactness), iii) stem suppleness, no brittleness and iv) crown integrity and intactness (fraction of branches remaining), as previously determined from characteristics of trees that were known to have been dead in garden experiments at the WSL institute for 1 and 2 years. In total, 179 dead young trees (60 *A. platanoides*, 72 *A. pseudoplatanus* and 47 *F. sylvatica*) were collected. Browsing was evident in all plots, but we excluded only severely browsed dead saplings.

2.2 CLASSIFICATION INTO VITALITY CLASSES

We developed the criteria for juvenile trees based on the vitality assessment of adult trees, in which, tree crowns are assessed visually (Eichhorn et al. 2016; Roloff 1991) whereas growth is measured (Dobbertin 2005). Crown transparency has been shown to correlate well with relative growth rate (Lorenz et al. 2004; Solberg 1999) and also with subsequent tree mortality and survival (Dobbertin and Brang 2001; Schmid-Haas 1993). Hence, we classified seedlings and saplings taking into account crown transparency (leaf loss and/or dieback) and the increment of the apical shoot for several years but also used the branching pattern and stem condition as additional discriminators to differentiate between high- and low-vitality trees (Collet et al. 2011; Roloff et al. 2016) (Table 1). To avoid an inconsistent crown transparency assessment (Dobbertin 2005), only one evaluator assessed all seedlings and saplings using site-specific reference trees. A reference tree is a tree with full foliage (defoliation 0%) that grows at a particular site, taking into account factors such as altitude/latitude, tree age, site conditions, and social status (Eichhorn et al. 2016). Trees browsed during the current season were not considered.

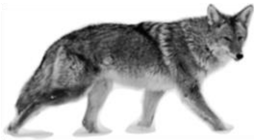


Table 1. Criteria used to classify juvenile trees into high- and low-vitality classes based on i) crown transparency, ii) apical shoot increment, iii) branching pattern and iv) stem damage.

Parameter	High-vitality	Low-vitality
Crown transparency (leaf loss, crown dieback)	• Leaf loss <20% • No dead branches and no crown dieback	• Leaf loss >20% • Dead branches or crown dieback
Apical shoot increment for several years	• Long apical increments for 3-5 years • Browsed in the past but recovered	• Short apical increments for 3-5 years • Browsed in the past and not recovered
Branching pattern	• Vigorous branching	• Degenerative branching
Stem damage	• Intact stem, no diseases	• Scars, bacterial/fungi diseases

2.3 MEASUREMENTS AND CALCULATIONS

2.3.1 FIELD MEASUREMENTS (MAY TO MID-JULY)

The following measurements were made before excavation of the living trees: diameter at root collar (DRC) and tree height (h). The correct assignment of the dead trees to the height classes was sometimes difficult as their tops were often damaged (fall of twigs and entire trees is frequent in a primary forest). Therefore, we modelled the height of such trees based on the allometry of low-vitality living trees. We dug up the trees manually and cleaned their roots with water to avoid damage to the fine roots. The dead trees were cut at the level of the root collar and were not excavated due to the high likelihood of only partial sampling of their root system. Field measurements are summarised in Table S 1 and Table S 2.

The proportion of diffuse solar radiation at a given location relative to that in the open (‘indirect site factor’ ISF) were assessed with hemispherical photos (*Coolpix 4500, Nikon, Japan*) with a 183° fish-eye lens (*Nikon FC-E8*) mounted on a tripod (Thimonier et al. 2010). Photos were taken just above the uppermost leaves of every sampled living tree (trees > 1.3 m being bent). The hemispherical photographs were first transformed into binary black and white pictures by applying the algorithm of Nobis and Hunziker (2005) using Hemisfer 2.2 (© Patrick Schleppi, WSL). Five concentric rings were superimposed on the hemispherical photographs to partition them into zenithal sectors. In each of the five rings, the proportion of visible sky (gap fraction) was determined and ISF was calculated for every young tree on every plot.

2.3.2 LAB WORK

The sampled living trees were separated at the root collar into aboveground biomass (foliage, stem, branches) and belowground biomass (root). All fresh leaves were scanned for leaf area with a smartphone (*application Petiole, version 2.0.1, by Petiole Ltd. 2019*) after calibration of the camera. Tree foliage, stems, branches, and roots were dried at +65 °C for three days until a constant weight was reached and then weighed to the nearest ±0.01 g. Biomass of the dead trees was not assessed as part of it was already lost (no leaves, partly lost branches or broken apical part of a stem). For each living tree, we calculated LAR according to the formula:

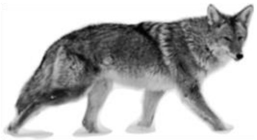
$$\mathrm{LAR} = \frac{\mathrm{LA}}{\mathrm{m_{total}}} \qquad \text{(Eq.1)},$$

where LA denotes leaf area and $\mathrm{m_{total}}$ is the total dry mass of the tree.

2.4 DENDROCHRONOLOGICAL ANALYSIS

To determine age and radial growth from each harvested living and dead tree, a stem disc at the level of the root collar was cut with a microtome. The stained discs were photographed (Canon EOS 700D) and analysed with WinDENDRO™ (Regent Instrument Canada Inc.) under a microscope. The number and width of the rings were recorded in two to four orthogonal directions, because of the acentric tree piths. Radial growth of every year was averaged across all orthogonal directions, and then the last five rings of tree life were arithmetically averaged, excluding the last ring because it was not known if death had occurred at the beginning of the current or at the end of the previous growing season.

The cross-sectional increment of basal area (BAI) should consistently increase at least over the early life of a tree, and is a more accurate indicator of tree growth than radial increment alone (Johnson and Abrams 2009). Therefore, ring width series were converted to BAI series based on the distance between the innermost measured ring and the pith of the tree (R,



package *dplR,* Bunn et al. 2021). This method assumes a circular cross-section (Biondi 1999). Because BAI at year *t* is equivalent to the difference between the cross-sectional area at the end of year *t* and that at the beginning *t-1* (Biondi and Qeadan 2008), it follows:

$$BAI_t = \pi({R_t}^2 - {R_{t-1}}^2), \qquad \text{(Eq. 2)}$$

where R_t is the stem radius at the end of the annual increment and R_{t-1} is the stem radius at the beginning of the annual increment. Then, the series of BAI for the last 5 years of tree life were arithmetically averaged, excluding the last year.

2.5 STATISTICAL ANALYSIS

Missing data (3-5% of the dataset) were imputed using the Multiple Imputation by Chained Equations (MICE) technique with a Random Forest-based approach (R, *mice* package, also see Van Buuren and Groothuis-Oudshoorn, 2011).

2.5.1 MODELLING MISSING HEIGHT, LEAF AREA AND DRY MASS VALUES FOR DEAD TREES

In some cases, the apical parts of the stems of the dead trees were missing, and assignment to height classes was problematic. We solved this problem by modelling the heights (H_{dead}) of the dead trees based on the heights of the low-vitality trees (indicated by the suffix $_{low}$), assuming biomass allocation to be similar in dead and low-vitality trees. Our assumption was based on several studies where dead or low-vitality juvenile trees had on average a lower height growth in the shade compared to living ones (Cleavitt et al. 2008; Collet and Le Moguedec 2007; Piper et al. 2009). Leaf area (LA_{dead}) and dry mass (m_{dead}) were also modelled using similar assumptions (Petrovska et al. 2020, Figure S 1) and variables of the low vitality trees. In all cases, generalised linear models for the gamma distribution with logarithmic link functions (R, package *rms*, Harrell 2019) were applied:

$$\ln\mathrm{E}(H_{dead}) = \beta_0 + \beta_1 \ln(DRC_{low}) + \beta_2 mean\ ring_{low} + \beta_{3.1} species_1 + \beta_{3.2} species_2 + \beta_4 age_{low} \quad \text{(Eq. 3)},$$

$$\ln\mathrm{E}\ (LA_{dead}) = \beta_0 + \beta_1 \ln(DRC_{low}) + \beta_2 mean\ ring_{low} + \beta_{3.1} species_1 + \beta_{3.2} species_2 + \beta_4 age_{low} \quad \text{(Eq. 4)},$$

$$\ln\mathrm{E}\,(m_{dead}) = \beta_0 + \beta_1 \ln(DRC_{low}) + \beta_{2.1} species_1 + \beta_{2.2} species_2 + \beta_3 age_{low} \quad \text{(Eq. 5)}$$

where E denotes expectation, β_0 = intercept, β_i = coefficients of the covariates, DRC_{low} = root collar diameter of low-vitality trees, $mean\ ring_{low}$ = mean ring width, age_{low} = age of low-vitality trees and $species_1$ and $species_2$ are two indicator (dummy) variables for the three tree species. These models assume a linear relationship between the predictors and the link function. Statistical significance of the model coefficients was tested with the Wald Chi-squared test ($p<0.01$) and additionally checked by means of bootstrapping (1000 iterations). The models satisfied the assumptions of linearity between the predictors and the link function and showed no multicollinearity (variance inflation factor VIF cut-off set at 5).

2.5.2 SURVIVAL MODEL

The goal of this analysis was to assess the survival time and age-specific death rate (instantaneous hazard rate) for young trees with the covariates mentioned below. Since there is no general consensus about which time scale is most appropriate in Survival Analysis (Hurley 2015; Korn et al. 1997) – time-of-study or age – we used chronological age as the time scale. This approach has already been applied in many studies (Ingram et al. 1997; Lamarca et al. 1998; Thiébaut and Bénichou 2004), directly taking into account the age effect on the probability of survival. In our case, trees enter the study at random because they are born at a random point in time and exit at their death/censoring age (random, type I censoring), thus the time scale is the age of a tree (in years), and the event of interest is its death. We thus defined three variables: T_i (age at death), c_i (random censoring time) and δ_i (an indicator variable), which equals one if T_i is observed and zero if T_i is censored. The response variable is $min(T_i, c_i)$, i.e. the age of the tree at death if it had died before sampling (in 2018) or its age at the time when the study was completed and the tree was still alive.

The parametric accelerated failure time model (AFT) with a lognormal distribution (R, package *rms,* Harrell 2019) is an alternative to the semi-parametric Cox Proportional Hazard (PH) model if the assumptions of the latter are violated, as in our case (cf. Supplementary Material S1.1). AFT is widely used in medicine and failure tests of industrial products (Wei

1992). In our case, this model was used to explore the direct effect of the explanatory variables LAR, mean ring width, species and height class on the acceleration/deceleration of survival time with the method of full maximum likelihood (Eq. 6):

$$\log(T) = \beta_0 + \beta_1 \log(LAR) + \beta_2 \log(ring) + \beta_{3.1} species_1 + \beta_{3.2} species_2 + \beta_4 height\ class + \sigma\varepsilon \quad \text{(Eq. 6)},$$

where T = age at sampling, β_o = intercept, β_i = coefficients of the covariates, σ = scale parameter, and ε = random error term assumed to follow a standard normal distribution (

Figure S 7). The model with the ring width covariate (Eq. 6) was compared to a model with BAI as a covariate, based on the Akaike Information Criterion (AIC). The model with ring width had the lower AIC and was thus selected for further analysis.

The survival function is the probability S(*t*) that the tree survives beyond time *t*, so that if F denotes the distribution function for age T, then S(*t*) = P(T ≥ *t*) = 1-F(*t*). The first derivative of F(*t*) denoted by f(*t*) is the event density, and the instantaneous hazard rate is defined as h(*t*) = f(*t*)/S(*t*), which is the instantaneous intensity of tree death at time *t* provided that it has survived until time *t.* Let X denote the vector whose elements are unity and the values of the covariates log(LAR), log(ring width), $species_1$, $species_2$ and height class, whereas let $\beta = (\beta_0, \beta_1, \beta_2, \beta_{3.1}, \beta_{3.2}, \beta_4)$ denote the corresponding vector of regression coefficients. Then the survival probability at time *t* for the covariate level X is equal to:

$$\Phi^{-1}[S(t|X)] = \mu_0 + \mu_1 \log(LAR) + \mu_2 \log(ring) + \mu_{3.1} species_1 + \mu_{3.2} species_2 + \mu_4 h.class - \alpha \log(t), \quad \text{(Eq. 7)}$$

where $S(t|X)$ is the survival function at time t and covariate X, Φ denotes the cumulative distribution function of the standard normal distribution, $\alpha = 1/\sigma$ and $\mu_j = \beta_j/\sigma$ for j = 0, 1, ... (Zhang 2005). Let h$(t|X)$ be the hazard function at time *t* and covariate X. Then the log-hazard function can be expressed as:

$$\log h(t|X) = \log h_0\left(t \cdot e^{-X^T\beta}\right) - X^T\beta, \qquad \text{(Eq. 8)}$$

where $\log h_0(t|X)$ is the hazard function given the covariates X when $\beta = 0\ (i.e. \beta_i = 0,\ i = 0,1,..)$ (Zhang 2005).

The regression coefficients were bootstrapped (5000 iterations) and their significance tested with the Wald Chi-square statistics (p<0.001) (package rms). Species differences in survival were evaluated with the Mantel–Haenszel log-rank test (p < 0.001, Table S 4). Overall, the model demonstrated high concordance (predictive discrimination in survival models, Therneau 2020). Finally, multicollinearity of covariates was checked with the variance inflation factor VIF (cut-off set at 5). Due to the absence of dead seedlings of sycamore maple in the height class 0-10 cm, we excluded this class from the analysis. All statistical analyses and visualizations (package *ggplot*, Wickham et al. 2020) were performed using R (version 4.0.3, R Core Team 2019).

3 RESULTS

3.1 AGES AND RADIAL GROWTH ESTIMATIONS

The mean age of dead trees was substantially higher for *F. sylvatica* in the height classes 36-500 cm compared to *Acer spp.*, i.e. *F. sylvatica* survived for a longer time period (Figure 1). Low-vitality *Fagus* trees in the height classes 61-500 cm were considerably older than those of the *Acer* species. High-vitality trees of the three species were on average similar in age up to the height class 91-130 cm, but older in beech than in the two *Acer* species in taller trees. As expected, mean ISF values (i.e., relative diffuse light) were low, varying from 1.9% to 3.3% (Table S 1). Browsing was apparent on all plots, with many *Acer spp.* trees showing scars but having recovered, while most juvenile *Fagus* trees were unaffected.

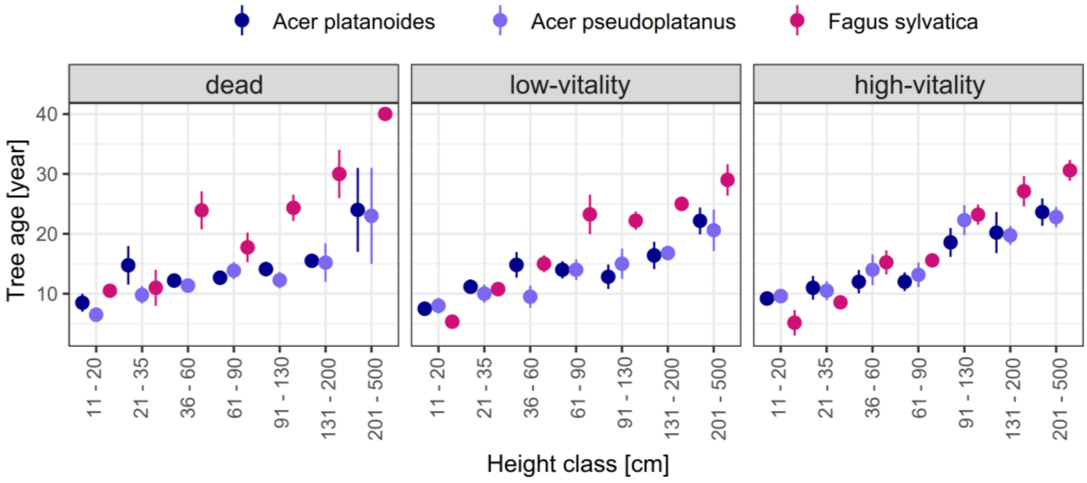


Figure 1. Mean age of dead and living trees of the two vitality classes by height class: dots - mean, whiskers - standard error.

Surprisingly, we observed higher mean radial growth in dead than in living trees (Figure 2, A). Mean ring width was similar in dead beech trees and the two *Acer* species (275 μm vs. 269 μm and 291 μm), whereas the living *F.sylvatica* trees had the lowest mean radial growth (220 μm and 210 μm in low- and high-vitality trees, respectively) compared to living *Acer* competitors (247, 263 μm in low-vitality and 267, 242 μm in high-vitality trees, respectively). Mean ring growth of the high- and low-vitality trees was quite similar on all six plots, while the mean growth of the dead trees was higher except in plots 1 and 5 (Figure 2, B). The ring growth for the dead trees had decreased for the last 5 years in plots 5 and 6 only.

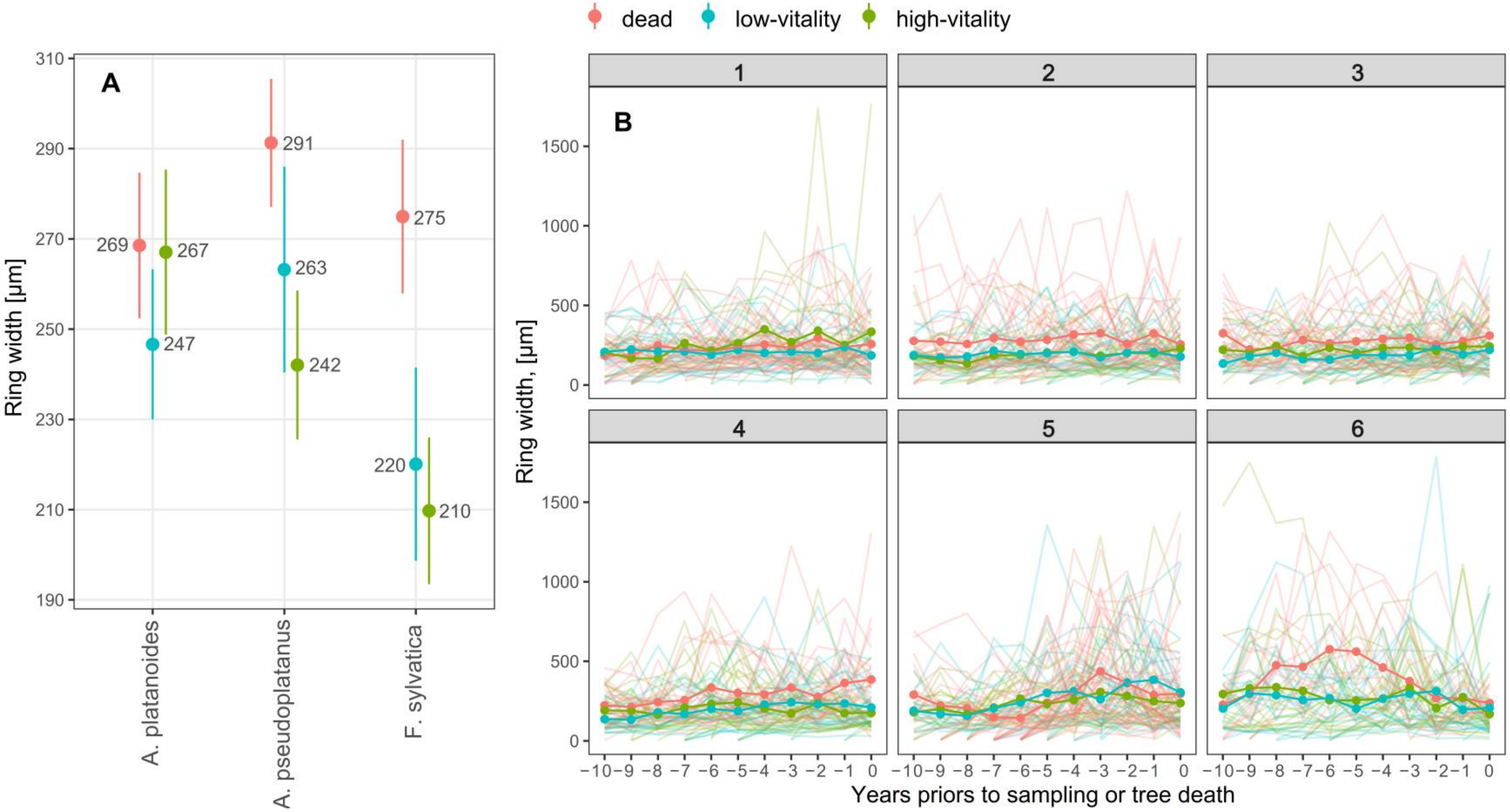


Figure 2. Mean width of tree rings in dead, low- and high-vitality trees of the three species (A). An average ring width, indicating ring growth 10 years prior to sampling or death in the plots 1-6(B). Dots and thick lines – mean width of ring growth, whiskers – standard error, thin lines – ring width data.

3.2 MODELLING OF MISSING VARIABLES FOR DEAD TREES

The explanatory variables DRC, tree age and mean ring width were significant predictors for tree height, leaf area and dry mass, while species identity was significant for leaf area only (Table 2). A one-percent increase in DRC corresponded to increased height growth by 1%, leaf area by 1%, and dry mass by 2%. Although age was significant, its increase affected tree height only by 2%, leaf area by 8% and dry mass by 7%. *A. pseudoplatanus* allocated more biomass to height (not significant) and was associated with significantly lower leaf area compared to *A. platanoides* and *F. sylvatica*.

Table 2. Summaries of generalised linear models for tree height, leaf area and dry mass. SE stands for standard error.

	Tree height			**Leaf area**			**Dry mass**		
Predictors	Exp (Coef)	SE	p	Exp (Coef)	SE	p	Exp (Coef)	SE	p
(Intercept)	53.38	0.14	<0.001	115.21	0.21	<0.001	11.58	0.24	<0.001
Ln DRC (not exponentiated)	1.01	0.06	<0.001	1.06	0.09	<0.001	2.00	0.11	<0.001
Tree age	1.02	0.01	0.006	1.08	0.01	<0.001	1.07	0.01	<0.001
A. platanoides	reference								
A. pseudoplatanus	1.07	0.07	0.352	0.80	0.11	0.048	0.89	0.14	0.432
F. sylvatica	0.99	0.08	0.873	1.09	0.12	0.444	0.77	0.15	0.082
Mean ring width	1.00	0.00	0.001	1.00	0.00	<0.001			
Observations (low-vitality trees)	137			115			135		

In general, modelled height, leaf area and dry mass for dead trees matched the variation observed in low-vitality trees or remained within its lower range. For both *Acer spp.*, modelled tree heights were lower in dead than in low-vitality trees as a consequence of smaller DRC values of the dead trees. Modelled mean leaf area and dry mass of dead trees were similar to those of the low-vitality trees except for *A. pseudoplatanus* (Figure 3). As a result, the calculated LAR values based on the modelled leaf area and dry mass were close to the LAR values observed in low-vitality trees. Details on the modelled results are shown in Table S 2.

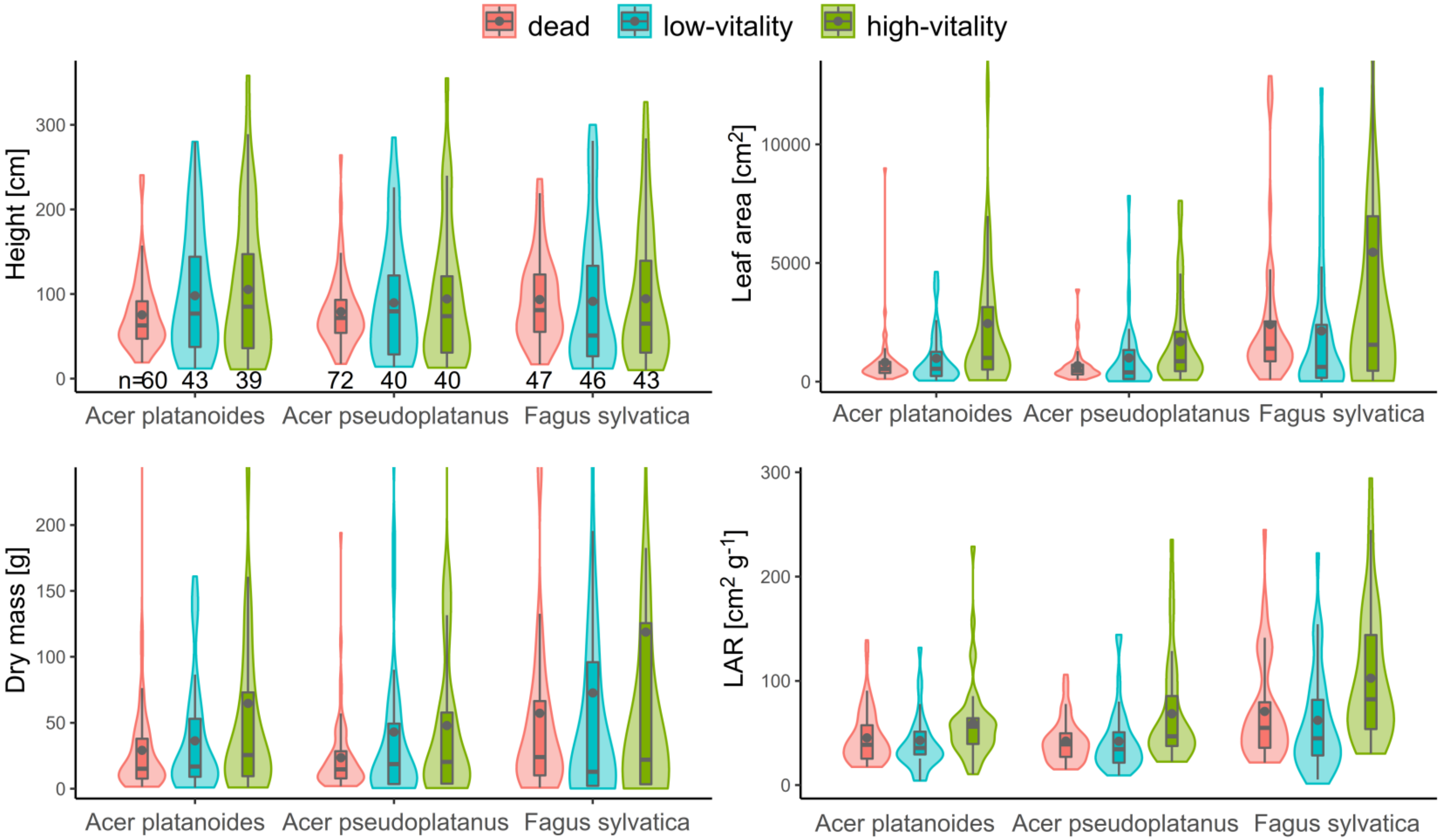


Figure 3. Violin plots of modelled tree height, leaf area, dry mass and calculated LAR. Dot – mean, horizontal line – median, whiskers – 95% confidence intervals, n - sample size per species and vitality classes (shown in top left panel only). The form of violins shows the data probability density and its distribution.

3.3 SURVIVAL MODEL

Species identity, LAR, ring width and height class significantly affected survival time (Table 3). A one-percent increase in LAR prolonged survival time by 0.14%. In comparison to *A. platanoides,* survival time was 3% shorter in *A. pseudoplatanus* and 41% longer in *F. sylvatica*. Compared to the height class 11-20 cm, tree height prolonged survival time by 2% (in height class 21-35 cm) and up to 211% (in height class 201-500 cm). Finally, the model estimated that a one-percent increase in allocation to ring width reduces survival time by 0.38%.

Table 3. Summary statistics of the accelerated failure time (AFT) model, S.E. denotes the standard error.

Survival model	**Coef**	**exp(Coef)**	**S.E.**	**Pr(>|Z|)**
(Intercept)	4.189	66.009	0.388	< 0.0001
Ln (LAR)	0.144	0.144	0.062	0.0211
Species				<0.0001
Acer platanoides	reference			
Acer pseudoplatanus	-0.032	0.969	0.063	0.6153
Fagus sylvatica	0.342	1.407	0.074	<0.0001
Height class				<0.0001
H: 11-20 cm	reference			
H: 21-35 cm	0.021	1.021	0.198	0.9152
H: 36-60 cm	0.025	1.025	0.170	0.8832
H: 61-90 cm	0.097	1.101	0.169	0.5681
H: 91-130 cm	0.366	1.442	0.175	0.0371
H: 131-200 cm	0.729	2.074	0.186	<0.0001
H: 201-500 cm	1.136	3.116	0.213	<0.0001
Ln (ring width)	-0.381	-0.381	0.075	<0.0001
Likelihood ratio	X^2 (10) =173.79, p<0.0001			
Observations	430			
Concordance	0.8			

According to the model, the predicted mean survival time of F. sylvatica was higher with an estimated value of 72 years vs 47-48 years for both Acer spp. adjusted for slow growth (20-100 µm) and height class 131-200 cm. The selected height class (131-200 cm) represented higher number of dead trees than the height class 201-500 cm (Table S 2) and growth (20-100 µm) highlighted the extreme range of observed growth values. Log-rank tests proved significant difference in survival time between F. sylvatica and Acer spp. ($p < 0.001$, in Table S 4) and no difference between *A. platanoides* and *A. pseudoplatanus*. Mortality probability over 3 years increased with radial growth in all species but was significantly lower in *F. sylvatica* (10.6%) at age 25 years (mean age in height class 131-200 cm) and a ring width growth of 210 µm, which is typical for high-vitality *F. sylvatica* in this study, than in *Acer spp*. (32.0%-35.8%) (Figure 4, A). In *F. sylvatica*, the age-specific mortality rate over 3 years increased slowly, reaching 0.036 events (i.e., the conditional probability of death is 3.6%) provided that the trees survived until 40-50 years, (Figure 4, B). In contrast, the age-specific mortality rate over three years for *Acer* spp. increased rapidly, reaching 0.07-0.08 events at age 40-50 years.

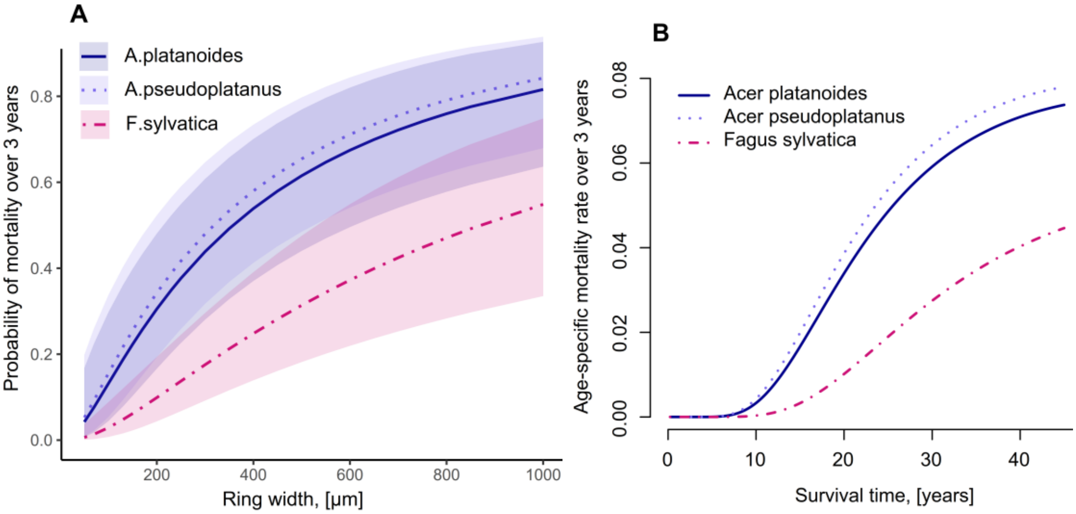
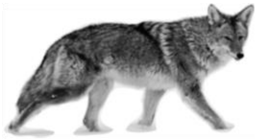


Figure 4. Probability of mortality over 3 years (A) and age-specific mortality rate over 3 years (B) adjusted to LAR = 40 cm^2 g^{-1}, ring width = 210 µm, age=25 years and 131-200 cm height class. Shaded bands – 95% confidence intervals. Note: age-specific mortality (instantaneous hazard rate) is the intensity of tree death events at time t provided that the tree has survived until time t.

An increase in LAR (from 10 to 40 cm^2 g^{-1}) slowed down the age-specific mortality rate in *F. sylvatica* from 0.03 to 0.02 events over 3 years, in *A. platanoides* from 0.07 to 0.05 and in *A. pseudoplatanus* from 0.08 to 0.05 events, given the same values of the other predictor variables as above. A reduction in ring growth (from 410 to 210 µm) decreased the mortality rate by a factor of two, i.e. in beech from 0.04 to 0.02 and in *Acer* spp. from 0.09 to 0.05,



given an age of 25 years, a LAR of 40 cm^2 g^{-1} and the height class 131-200 cm. A change in height class from 61-90 cm to 201-500 cm significantly reduced age-specific mortality rate of beech from 0.1 to 0.003 and for *Acer* spp*.* from 0.14 to 0.02, keeping the same values of the predictor variables as above.

The model coefficients (Table 3) indicated that a reduction in growth enhances the expected survival time to a higher degree than an increase in LAR (Figure 5). Also, higher LAR and lower growth increased the survival time for *F. sylvatica* more strongly (i.e., steeper curves) than for *Acer* spp*.* An increase in LAR from 10 cm^2 g^{-1} to 40 cm^2 g^{-1} (observed min and mean LAR values in height class 131-200 cm) would improve the survival time for beech from 35 to 43 years and for *Acer spp.* from 24 to 31 years*,* given a ring width of 210 µm and a height class of 131-200 cm. At the same time, a reduction of ring growth from 410 µm to 210 µm enhances the estimated survival time for *F. sylvatica* from 33 to 43 years and for the maple species from 23 to 31 years, assuming LAR 40 cm^2 g^{-1}, and height class 131-200 cm. Also, changes in the height class from 61-90 cm to 201-500 cm extended the survival time of *F. sylvatica* from 23 to 64 years and that of *Acer spp.* from 15 to 46 years (Figure 5).

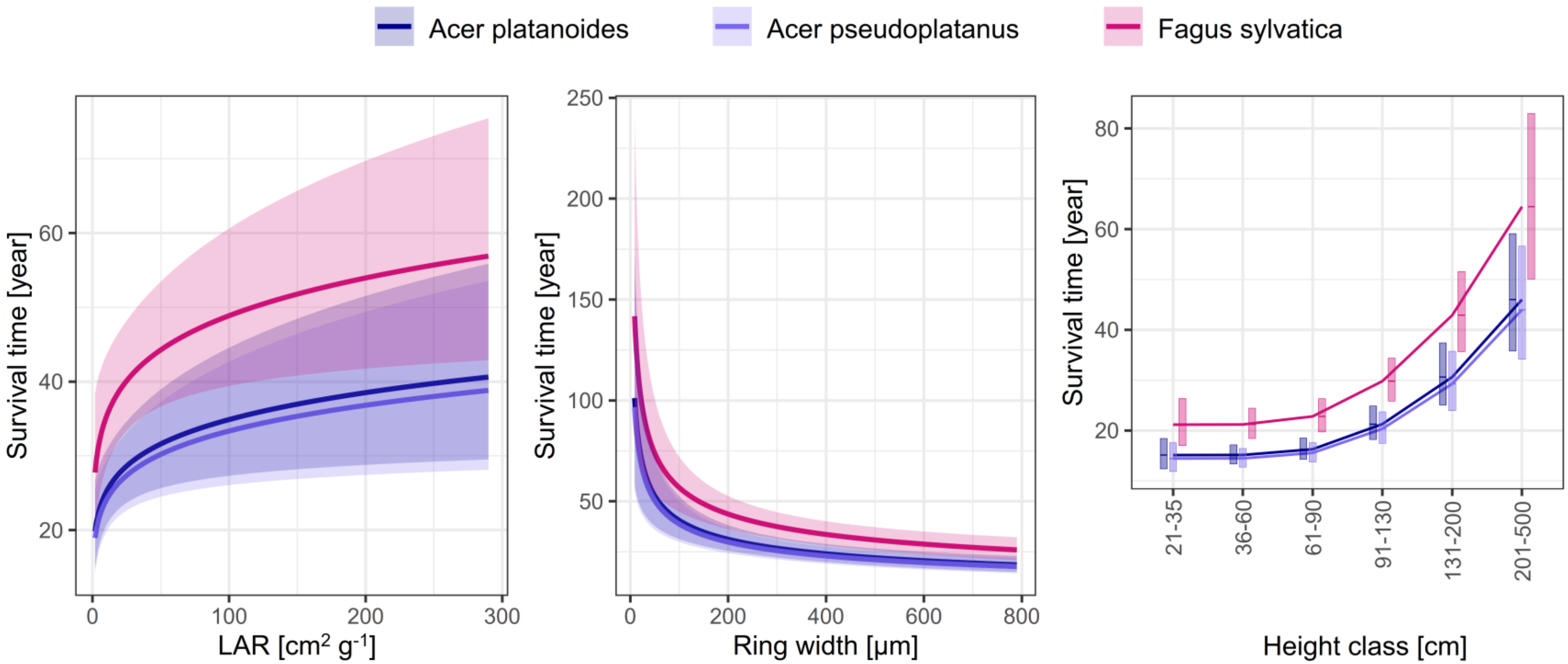


Figure 5. Effect of LAR, mean ring width and height class on survival time. Shaded bands and error bars – confidence intervals .95, adjusted to LAR = 40 cm² g⁻¹, ring growth = 210 μm and height class 131-200 cm.

4 DISCUSSION

4.1 EFFECTS OF LAR, RADIAL STEM GROWTH AND HEIGHT ON SURVIVAL TIME

For the first time, we estimate survival time and age-specific mortality rate for juvenile beech and maple species based on traits of shade tolerance (i.e., growth rate, leaf area ratio). We applied a new methodological approach to model LAR for dead trees based on the difference in performance between high- and low-vitality trees and enrich existing mortality models with the new variable. In contrast to other research, our study focuses on low light conditions, thus enabling the elucidation of different growth pattern.

Trees growing up in deep shade have been shown to maximize light capture through an increase in leaf area and its proper arrangement in space (Canham 1988; Givnish 1988; Poorter 1999). Survival increases with LAR in shade-tolerant species since a larger leaf area per unit of plant biomass supports the production of more photosynthates (Sanford et al. 2003; Valladares et al. 2003). However, LAR is diminishing in ontogeny and can undermine species performance and persistence in the shade (Delagrange et al. 2004; Lusk 2004). Our results confirm that juvenile beech trees with higher LAR survive on average longer than *Acer* spp., while the age-specific mortality rate of beech is half of that of its competitors. Beech saplings in the height class 131-500 cm featured higher leaf area compared to sycamore and Norway maple in two vitality classes (Table S 1). In contrast, both maple species minimise leaf and branch biomass by retaining petioles even in taller height classes (Beaudet and Messier, 1998) as an adaptation to frequent browsing (Modrý et al. 2004). Thus, these species clearly differ in LAR and, therefore, survival time and mortality rates.

The relation between juvenile tree growth and mortality seems contradictory. Current mortality models for tree regeneration are often based on the finding that mortality increases with reduced radial growth under conditions of more than 5% diffuse or direct light (Dekker et al. 2009; Kneeshaw et al. 2006; Kunstler et al. 2005; Petriţan et al. 2007). For instance, Kunstler et al. (2005) demonstrated a 1.5-fold difference between mean ring growth of living (332 µm) vs. dead beech saplings (208 µm) under 5-100% relative irradiance, and Petriţan et al. (2007) measured declining ring growth in dead beech and sycamore maple trees for the last 5 years along a diffuse light gradient of 6.3-9%.

However, the growth patterns of juvenile trees in deep shade (mean range 2-3% of diffuse light) that we investigated may not follow the classical point of view. Dekker et al. (2009) showed that average growth prior to death spanned a large range; for *Pseudotsuga menziesii*, *Pinus sylvestris* and *Larix kaempferi* it even encompassed the full range in growth of live individuals living under conditions of no direct light. In our study, juvenile tree growth patterns in deep shade followed a similar pattern. Mean radial growth of dead trees was similar as or slightly higher than in surviving individuals (Figure 2) and did not show a decreasing trend in the previous 5 years, except for two plots. A physiological explanation for reduced growth in small trees surviving at very low light levels is that constant carbon stress forces both dying and living trees to prioritise carbon allocation to respiration, maintenance and active storage instead of growth (Wiley et al. 2017; Wiley and Helliker 2012). However, we cannot rule out that some dead trees had previously been growing in small gaps, i.e. with higher growth rates than in the deep shade measured now. If such gaps had existed, they were already closed and difficult to recognise at the time of our study.

At low light levels, a young tree tries to minimize CO_2 losses by slowing down growth and respiration rate, an ability that makes shade-tolerant species perform better and survive longer than shade-intolerant species (Walters and Reich 2000). In our study, due to long growth suppression, beech was able to increase its survival time and achieve a low mortality rate. The estimated mean survival time of beech (72 years) is close to the average age (65 years) when trees experienced the first release in Uholka (Trotsiuk et al. 2012). Moreover, juvenile beech in Uholka can survive over >100 years (varying from 21 to 177 years) due to long suppression periods until the first release (ibid). In contrast, higher allocation of biomass to growth occurs at the cost of higher respiration (Walters and Reich 2000) and leads to a shorter survival time of the two maple species.

In other studies, comparing beech with other species, the relation between growth rate and mortality of shade-tolerant and intolerant juvenile trees was different. At a light level of 3%, both beech and sycamore maple showed low radial and height growth but had a high mortality probability over 3 years (ca. 50% and 70%, respectively) (Petriţan et al. 2007). At that same light level, beech relative growth was similar to that of shade-intolerant downy

oak (*Quercus pubescens*), but annual mortality rates were around 2% for beech and 20% for oak (Kunstler et al. 2005). The difference in beech mortality estimation at low growth is likely mainly due to low sample size at a light level 3%, as samples were collected, in both studies, at a wide range of light levels (3-33% indirect light, Petriţan et al. 2007; 5-100% in full sun, Kunstler et al. 2005), in contrast to our study. Moreover, several studies (Kunstler et al. 2005; Lin et al. 2002) conclude that European beech and American beech (*Fagus grandiflora*) are more tolerant to slow growth and thus have a lower mortality rate, while less shade-tolerant species suffered high mortality when growing slowly. Our results suggest that such conclusions do not apply to growth and mortality at mean light levels 2-3% due to the methodological limitations mentioned above. In deep shade, slow growth is advantageous in the long-term due to low maintenance and respiration costs. Shade-tolerant species are able to decrease growth (and respiration) more efficiently than shade-intolerant ones (Rodríguez-Calcerrada et al. 2019; Valladares and Niinemets 2008). Hence, the conventional belief that shade-tolerant species can survive in spite of suppressed growth should be revised because slow growth is a resource-saving strategy which enables survival.

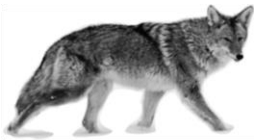
As a consequence of slow growth in deep shade, beech has higher LAR that decreases more slowly with increasing height (Petrovska et al. 2020 in publication) than in other species, which contributes to beech's low mortality rate. In contrast, the LAR of Norway and sycamore maple is lower and decreases faster with height (ibid.), which increases maple's mortality rate and decreases survival time (Figure 4, Figure 5). This difference in strategy is likely to be even larger than shown here since our survival model was built on average LAR values taking into account both low- and high-vitality trees, whereas LAR for low- and high-vitality trees differs significantly (Petrovska et al. 2020 in publication). Therefore, the effect of LAR on survival probability and survival time would be even higher if high-vitality vs. dead trees were studied.

Our findings highlight that tree height is more important for extending survival time than LAR and radial growth; however, the absolute number of years of acceleration resulting from our models should be interpreted with caution, as we evaluated the effect of height by keeping the other covariates fixed. Biomass allocation to tree height greatly improved survival in the shade, probably since light conditions improve with size (Collet and Le Moguedec 2007; Eerikäinen et al. 2014). In contrast, survival in North American hard- and softwood species did not differ significantly between small and large saplings at radial growth of < 200 μm across light gradients between gap and non-gap environments (Kneeshaw et al. 2006). Moreover, mortality increased with height in shade-tolerant species at a radial growth of 500 μm (ibid.). In our case, growth at 500 μm seems excessive (Figure 2), and the probability of survival diminished (Figure 5) with height due to increased maintenance cost and reduced LAR. However, at a radial growth of 200 μm, typical for our data set, height growth was positively related to survival probability and extended survival time.

4.2 EVALUATION OF ANNUAL MORTALITY

Data on the annual mortality of juvenile trees, although being scarce in Europe, are important for comparison with the model results presented here. Annual mortality in young beech (3.3%) and sycamore maple (7.3%) was observed on long-term plots in the UK (Kerr and Mackintosh 2012). Similar results for beech saplings (4.2%-4.9%) were reported by Collet and Le Moguedec (2007) along a light gradient from closed canopy to large gaps in France. Kunstler et al. (2005) observed an annual mortality of 2% in beech saplings in a transect featuring a 5-100% light gradient in a sub-Mediterranean forest in France. In Austria, mean annual mortality of juvenile beech reached 2.6% in the dbh class 2.6-7.5 cm (Platter 2008). Our results on age-specific mortality rate (although estimated over 3 years) in beech (3.6% conditional probability) and in sycamore maple (7-8% conditional probability) are close to the observed ones. It seems that the annual mortality of juvenile beech usually varies between 2%-3.3%, with the highest value being reported (4.9%) after windthrow (Collet and Le Moguedec 2007). Such a low variation of the observed annual mortality in beech across Europe suggests that its survival strategy varies only slightly within the temperate zone. Wang et al. (2020) have recently confirmed that beech seedlings of different geographic provenances show similar trait response in shade, drought or combined stress conditions. Given the low variability in observed annual mortality of beech across Europe, we hypothesize that beech responses to shade (i.e. ontogenetic changes in LAR and growth) are likely similar across the temperate zone.

In contrast to the observed annual mortality rate, the modelled probability of mortality varies strongly depending on (1) light conditions, (2) other variables included in the mortality



models (cf. *Introduction*), and (3) regional differences that cannot be explained by the environment. In our study, the probability of beech mortality (10.6%) over 3 years was much lower compared to the study by Petriţan et al. (2007) - circa 19% over 3 years at a radial growth of 210 µm. In our study, the probability of mortality of sycamore maple over 3 years (35.8%) was much lower than that reported as almost 50% over 3 years at a radial growth of 210 µm by Petriţan et al. (2007). Finally, Kobe et al. (1995) suggested that there was little variation in modelled mortality for the same species sampled in different forests and climate zones in the USA, but our comparison of the variability in modelled probability of mortality for European forests demonstrates the contrary.

5 CONCLUSIONS

A species' survival time and mortality can be explained better by a combination of different traits (leaf, growth and, storage) than with just one or two variables capturing growth traits. Ideally, one method, one model and a fixed set of variables from the traits mentioned above would be used for studying mortality of juvenile species validated across low, moderate and high light levels and different regions of the temperate zone. Standardization of survival/mortality models allows to minimise variability and achieve comparable results. Our approach extends the variables used in mortality models while focusing on low light levels.

In our model, the interplay of variables such as species identity, LAR, ring width and tree height played an important role in determining survival time and mortality of the three species living in deep shade. High LAR, slow growth and height extended survival time and decreased mortality, while low LAR in combination with higher growth shortened survival time and increased mortality. Juvenile beech featured higher LAR and grew more slowly, which enabled the species to extend its survival time at a low mortality rate. Beech's ability to sustain low mortality over extended periods makes it more independent of long canopy turnover time and likely to reach the canopy once a gap is formed. In contrast, a combination of lower LAR and higher growth rate of the two maple species leads to shorter survival time and a higher age-specific mortality rate compared to beech. The lower survival time of Norway and sycamore maple renders their presence in the canopy a rare event. Thus, our study shows that shade tolerance commonly defined as a relationship between sapling mortality and growth can alternatively be formulated as a relationship between survival time and the interplay of growth and LAR, leading to a more general explanation of the survival of shade-tolerant trees in deep shade.

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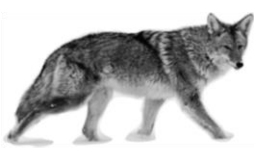

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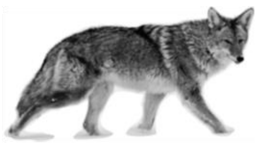

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ELECTRONIC SUPPLEMENTARY MATERIALS

Table S 1. Mean and standard deviation (in brackets) of collected and calculated data for trees with high and low vitality (a_pla - A. platanoides; a_pse - A. pseudoplatanus; f_syl - F. sylvatica, LA – leaf area, LAR- leaf area ratio, AGR – absolute growth rate, ISF – indirect site factor.

		High-vitality										**Low-vitality**									
Sp	H class [cm]	N	Tree age	DRC [cm]	Height [cm]	LA [cm^2]	LAR [cm^2/g]	AGR [g/year]	Dry mass [g]	Ring width [μm]	ISF	N	Tree age	DRC [cm]	Height [cm]	LA [cm^2]	LAR [cm^2/g]	AGR [g/year]	Dry mass [g]	Ring width [μm]	ISF
a_pla	0 - 10	7	6.43	0.23	8.71	113.8	107.8	0.18	1.22	112	3.25	6	6.5	0.2	9.67	57.8	59.9	0.54	2.76	98.1	2.91
			(1.9)	(0.04)	(2.04)	(98.5)	(54.53)	(0.17)	(1.21)	(56.6)	(0.01)		(1.87)	(0.07)	(1.44)	(25.1)	(46.8)	(0.83)	(4.05)	(18.8)	(0.01)
a_pla	11 - 20	5	9	0.27	16.5	215	91.3	0.24	7.45	154	2.13	4	7.5	0.49	14.62	110.7	76.4 (50)	0.41	2.62	136.9	2.68
			(2.58	(0.09)	(6.6)	(157.4)	(86.11)	(0.11)	(11.69)	(69.3)	(0.01)		(1.91)	(0.26)	(2.14)	(47.2)		(0.56)	(3.26)	(25)	(0.01)
a_pla	21 - 35	6	11	0.53	29.42	702.9	77.5	0.94	9.35	219	2.82	6	11.17	0.57	29.42	260.5	53.2	0.49	5.4	246.6	3.04
			(4.86	(0.15)	(3.11)	(708.2)	(44.67)	(0.97)	(8.89)	(96.5)	(0.01)		(2.99)	(0.16)	(5.2)	(151.9)	(23.3)	(0.22)	(3.1)	(148.6)	(0.01)
a_pla	36 - 60	6	12	0.67	46.33	565.8	49.7	1.12	11.3	243	3.27	6	14.83	0.82	51.25	459.4	32.6	1 (0.35)	14.72	224.4	2.85
			(4.77	(0.14)	(7.31)	(205.1)	(7.37)	(0.69)	(4.04)	(71.2)	(0.01)		(5.23)	(0.17)	(8.07)	(289.9)	(15.8)		(8.23)	(51.8)	(0.01)
a_pla	61- 90	6	12	0.85	72.58	869.9	49.6	1.8	18.6	341	3.34	6	14	1.03	76.58	431.2	28 (10.3)	1.3	16.23	211.1	2.21
			(3.85	(0.17)	(10.66)	(316.1)	(15.77)	(1.18)	(7.64)	(158.7)	(0.01)		(3.52)	(0.44)	(9.72)	(134.9)		(0.73)	(5.4)	(140.7)	(0.01)
a_pla	91 -130	7	18.5	0.97	115.21	2187	41.5	3.03	54.39	338 (134)	3.68	6	12.83	1.06	112.42	672.9	29.8	2.89	30.12	399.1	2.42
			7	(0.28)	(11.12)	(1362.5)	(19.11)	(1.07)	(23.83)		(0.01)		(5.04)	(0.28)	(15.29)	(402.6)	(25.2)	(1.87)	(16.76)	(172.6)	(0.01)
a_pla	131-200	5	18.5	1.3	155.3	3310.9	58.8	3.37	62.26	292	2.42	5	16.4	1.22	157.6	1900.4	35.2	3.7	56.36	283.9	3.31
			(7.72	(0.23)	(20.97)	(1655.2)	(35.55)	(1.21)	(20.75)	(167.9)	(0.01)		(5.08)	(0.21)	(18.38)	(532.2)	(14.6)	(1.27)	(11.39)	(60.3)	(0.01)
a_pla	201 - 500	8	23.6	1.88	247.19	7418.6	34.7	9.1	227.03	310	2.33	6	22.17	1.6	224.9	3080.3	29.2	5.64	120.81	372.6	3.24
			2	(0.48)	(51.69)	(5260.3)	(10.24)	(4.99)	(182.7)	(181.6)	(0.01)		(5.49)	(0.18)	(35.63)	(1585.9	(15.2)	(1.96)	(35.44)	(209.1)	(0.01)
a_pse	0 - 10	7	7	0.19	9	113.6	113.2	0.22	1.36	141	3.37	7	5.33	0.22	10.57	30.9	92.2	0.09	0.43	113.7	2.82
			(1.1)	(0.03)	(2.27)	(80.8)	(86.97)	(0.09)	(0.94)	(39.7)	(0.01)		(1.21)	(0.08)	(1.9)	(12)	(66.2)	(0.07)	(0.26)	(14.9)	(0.01)
a_pse	11 - 20	5	9.6	0.33	15.6	195.9	102.8	0.22	2.19	164	3.13	7	8	0.4	17.43	75.5	52.9	0.21	1.83	187.8	2.78
			(2.61	(0.08)	(3.21)	(181.3)	(62.71)	(0.1)	(1.23)	(23.8)	(0.01)		(3.46)	(0.21)	(2.42)	(67)	(40.8)	(0.16)	(1.97)	(103.2)	(0.01)
a_pse	21 - 35	8	11.4	0.48	28.62	597.3	89.8	1.49	10.99	178 (81)	3.05	5	10	0.4	27.2	105	52.3	0.26	2.69	158.3	2.23
			3	(0.11)	(4.15)	(478)	(59.9)	(2.69)	(15.52)		(0.01)		(3.39)	(0.09)	(3.55)	(39.5)	(33.1)	(0.12)	(1.79)	(42.5)	(0.0)
a_pse	36 - 60	5	14	0.72	50.4	583.2	54.6	0.95	13.1	189	2.35	6	9.5	0.58	52.17	233.2	48.6	1 (0.95)	10.92	254.7	2.03
			(5.7)	(0.14)	(18.19)	(200.2)	(34.4)	(0.36)	(5.54)	(59.1)	(0.0)		(4.55)	(0.13)	(4.54)	(211.2)	(48.8)		(15.94)	(125.6)	(0.01)
a_pse	61- 90	6	13.1	0.82	74.25	1005.4	63.9	1.46	18.21	279	3.01	7	14	0.91	81.71	606.8	29.5	1.63	20.7	327.1	2.59
			7	(0.17)	(10.31)	(646.1)	(24.95)	(0.88)	(13.97)	(127.3)	(0.01)		(4.62)	(0.16)	(5.65)	(267.4)	(12.3)	(0.56)	(3.82)	(154.9)	(0.02)
a_pse	91 -130	7	22.2	1.04	113.36	1672.3	33.2	2.41	54.92	232	3.02	5	15	1.22	107.2	1349.3	31.9	2.81	44.67	305.1	2.25
			9	(0.31)	(10.77)	(773.2)	(11.8)	(0.87)	(32.86)	(24.2)	(0.01)		(5.66)	(0.36)	(9.83)	(1527.2	(16.2)	(1.63)	(32.12)	(141.6)	(0.01)
a_pse	131 -200	4	19.7	1.48	164	2936.3	35.9	4.18	83.9	381	2.4	5	16.8	1.24	149.4	1592.2	32.6	3.5 (1.2)	57.41	349.2	2.23
			5	(0.21)	(13.19)	(933.4)	(6.73)	(1.2)	(33.12)	(138.2)	(0.01)		(2.28)	(0.15)	(10.48)	(510.1)	(18.9)		(16.55)	(103.4)	(0.0)
a_pse	201 - 500	5	22.8	1.97	262.8	5919.8	35.3	7.84	183.72	429	2.1	5	20.6	1.96	231.8	3736.2	23.1	10.01	194.13	298.6	2.53
			(3.83	(0.46)	(53.35)	(1323.9)	(10.39)	(2.43)	(86.56)	(264.1)	(0.01)		(7.77)	(0.43)	(30.38)	(2882.6	(17.6)	(5.91)	(100.37	(154.1)	(0.02)
f_syl	0 - 10	5	3.2	0.16	9.9 (5)	46.6	118.4	0.14	0.43	110	3.34	6	4.5	0.19	9.46	29.9	134.1	0.09	0.48	76.8	3.48
			(1.1)	(0.04)		(26.1)	(50.76)	(0.07)	(0.24)	(10.1)	(0.02)		(2.81)	(0.14)	(1.27)	(15.8)	(126)	(0.06)	(0.54)	(19.4)	(0.02)
f_syl	11 - 20	6	5.17	0.25	15.42	131.1	185.7	0.17	0.96	104	2.29	6	5.33	0.23	15.07	51.7	91 (49)	0.13	0.82	114.8	2.4
			(5.23	(0.13)	(3.56)	(100.6)	(71.41)	(0.05)	(1.04)	(36.9)	(0.01)		(2.34)	(0.04)	(2.66)	(33.2)		(0.08)	(0.75)	(27.9)	(0.01)
f_syl	21 - 35	7	8.57	0.39	25.86	434.4	154.5	0.4	3.02	164	3.9	9	10.78	0.44	26.39	143.6	65.9	0.33	3.87	151.5	3.09
			(3.15	(0.1)	(5.01)	(209.9)	(43.02)	(0.28)	(1.69)	(52.7)	(0.01)		(3.63)	(0.19)	(5.02)	(52.5)	(47.5)	(0.31)	(4.09)	(99.2)	(0.02)
f_syl	36 - 60	8	15.2	0.82	47.75	890.8	91.9	0.85	15.55	195	2.76	7	15	0.74	41.93	301.5	53.1	0.56	8.56	193.2	2.72
			5	(0.46)	(7.57)	(523.2)	(53.49)	(0.65)	(17.36)	(79.1)	(0.01)		(3.7)	(0.22)	(6.35)	(213.2)	(49.8)	(0.22)	(4.41)	(66.6)	(0.01)

			High-vitality									**Low-vitality**									
Sp	H class [cm]	N	Tree age	DRC [cm]	Height [cm]	LA [cm^2]	LAR [cm^2/g]	AGR [g/year]	Dry mass [g]	Ring width [µm]	ISF	N	Tree age	DRC [cm]	Height [cm]	LA [cm^2]	LAR [cm^2/g]	AGR [g/year]	Dry mass [g]	Ring width [µm]	ISF
f_syl	61- 90	7	15.5 7	0.96 (0.19)	70.14 (6.94)	2137.2 (1050.3)	87 (25.23)	1.63 (0.78)	24.68 (10.22)	208 (45.7)	2.32 (0.01)	4	23.25 (6.6)	0.96 (0.3)	73.25 (6.4)	2571.3 (1677)	71.2 (28.6)	1.62 (0.82)	39.75 (27.05)	271.7 (89.6)	2.27 (0.0)
f_syl	91 -130	5	23.2 (3.77	1.29 (0.22)	109.6 (5.32)	5521.8 (2445.2)	77.4 (28.5)	3.33 (1.84)	76.16 (42.31)	318 (126.4)	3.35 (0.02)	5	22.2 (3.42)	1.2 (0.19)	111.9 (12.58)	2260.3 (1416.5	47.1 (26.4)	2.62 (1.11)	60.01 (31.38)	232.9 (181.7)	1.78 (0.01)
f_syl	131 -200	8	26.5 7	1.69 (0.65)	165.75 (21.78)	9400.1 (4678.6)	49.5 (12.78)	8.21 (4.11)	206.08 (137.53	299 (104.8)	2.47 (0.0)	7	25 (3.27)	1.56 (0.33)	158.29 (20.77)	4576.5 (2707)	32.9 (19.9)	6.28 (3.04)	151.99 (68.35)	310.5 (67.2)	2.12 (0.01)
f_syl	201 - 500	5	30.6 (3.91	2.87 (0.9)	265.5 (43.01)	25983 (6692.8)	42.4 (10.02)	19.97 (7.89)	621.3 (285.26	195 (128.7)	2.28 (0.01)	5	29 (5.87)	2.17 (0.71)	268.6 (21.55)	6804.8 (4783.8	23.6 (11.1)	10.88 (7.54)	299.84 (219.73	215.8 (183.8)	2.81 (0.01)

Table S 2. Mean and standard deviation (in brackets) of the modelled height, leaf area (LA), dry mass and calculated LAR and AGR of dead trees (a_pla - A. platanoides; a_pse - A. pseudoplatanus; f_syl - F. sylvatica, LA – leaf area, LAR- leaf area ratio, AGR – absolute growth rate).

Sp	**H class [cm]**	**N**	**Tree age**	**DRC [cm]**	**Height [cm]**	**LA [cm^2]**	**LAR [cm^2/g]**	**Dry mass [g]**	**Ring width [μm]**
a_pla	11-20	2	8.5 (2.12)	0.23 (0.07)	19.03 (0.03)	108.84 (5.41)	65.54 (18.43)	1.72 (0.4)	200.32 (63.68)
a_pla	21-35	4	14.75 (6.45)	0.35 (0.06)	29.1 (3.98)	251.06 (51.6)	67.82 (4.86)	3.68 (0.55)	231.96 (79.28)
a_pla	36-60	21	12.19 (4.35)	0.59 (0.09)	48.14 (6.11)	391.46 (111.2)	46.64 (23.12)	9.47 (3.39)	252.55 (109.08)
a_pla	61-90	18	12.67 (4.51)	0.9 (0.2)	75.23 (10.23)	681.28 (164.53)	39.24 (29.66)	23.18 (10.91)	281.59 (153.73)
a_pla	91-130	9	14.11 (3.76)	1.28 (0.15)	107.87 (10.34)	1017.88 (324.55)	21.1 (5.63)	48.25 (9.13)	243.83 (58.62)
a_pla	131-200	4	15.50 (2.38)	1.46 (0.23)	141.58 (11.45)	2067.24 (625.8)	37.77 (32.85)	71.55 (28.25)	396.29 (190.34)
a_pla	201-500	2	24 (9.9)	1.57 (0.25)	235.93 (6.46)	4795.67 (5932.72)	29.45 (5.4)	195.14 (106.24)	316.26 (155.29)
a_pse	11-20	2	6.50 (0.71)	0.23 (0.03)	17.76 (0.36)	110.28 (42.82)	56.01 (19.69)	1.96 (0.08)	277.23 (116.59)
a_pse	21-35	5	9.8 (3.27)	0.37 (0.06)	29.1 (4.31)	133.52 (60.69)	48.46 (16.08)	2.76 (0.75)	188.45 (71.81)
a_pse	36-60	19	11.37 (2.97)	0.57 (0.09)	50.27 (7.52)	319.54 (82.73)	48.21 (21.06)	7.32 (2.48)	297.49 (104.71)
a_pse	61-90	28	13.86 (7.48)	0.83 (0.16)	76.14 (9.86)	655.35 (493.51)	36.36 (20.39)	18.54 (7.41)	293.3 (108.22)
a_pse	91-130	11	12.27 (4.56)	1.27 (0.17)	110.32 (8.81)	700.84 (151.57)	20.36 (9.16)	38.29 (11.56)	259.09 (113.25)
a_pse	131-200	5	15.2 (7.19)	1.49 (0.19)	149.54 (15.55)	1563.53 (682.49)	26.88 (15.87)	66.01 (29.9)	365.85 (176.81)
a_pse	201-500	2	23 (11.31)	1.65 (0.07)	234.38 (41.88)	3883.31 (0.00)	54.68 (0.00)	132.52 (86.97)	466.1 (268.92)
f_syl	11-20	2	10.5 (0.71)	0.23 (0)	18.26 (1.76)	95.01 (7.07)	110.69 (0.59)	0.86 (0.07)	352.55 (159.28)
f_syl	21-35	2	11 (4.24)	0.38 (0.04)	32.87 (0.54)	360.31 (118.39)	157.34 (118.13)	2.8 (1.35)	378.55 (246.03)
f_syl	36-60	12	23.92 (10.96)	0.52 (0.15)	51.26 (7.46)	1199.44 (879.84)	104.96 (47.44)	11.57 (5.26)	294.32 (126.87)
f_syl	61-90	8	17.75 (6.94)	0.8 (0.14)	70.74 (5.92)	925.94 (280.14)	55.56 (31.66)	18.78 (5.41)	259.27 (139.94)
f_syl	91-130	15	24.33 (8.57)	1.15 (0.25)	111.75 (12.62)	2226.9 (1121.61)	39.96 (17.56)	59.02 (22.82)	242.6 (97.02)
f_syl	131-200	6	30 (9.84)	1.48 (0.34)	163.33 (22.32)	5527.34 (4105.95)	37.3 (19.13)	148.93 (75.41)	266.34 (86.57)
f_syl	201-500	2	40 (0.00)	1.77 (0.25)	227.62 (11.85)	11916.81 (0.00)	39.49 (2.12)	306.37 (10.4)	308.46 (12.45)

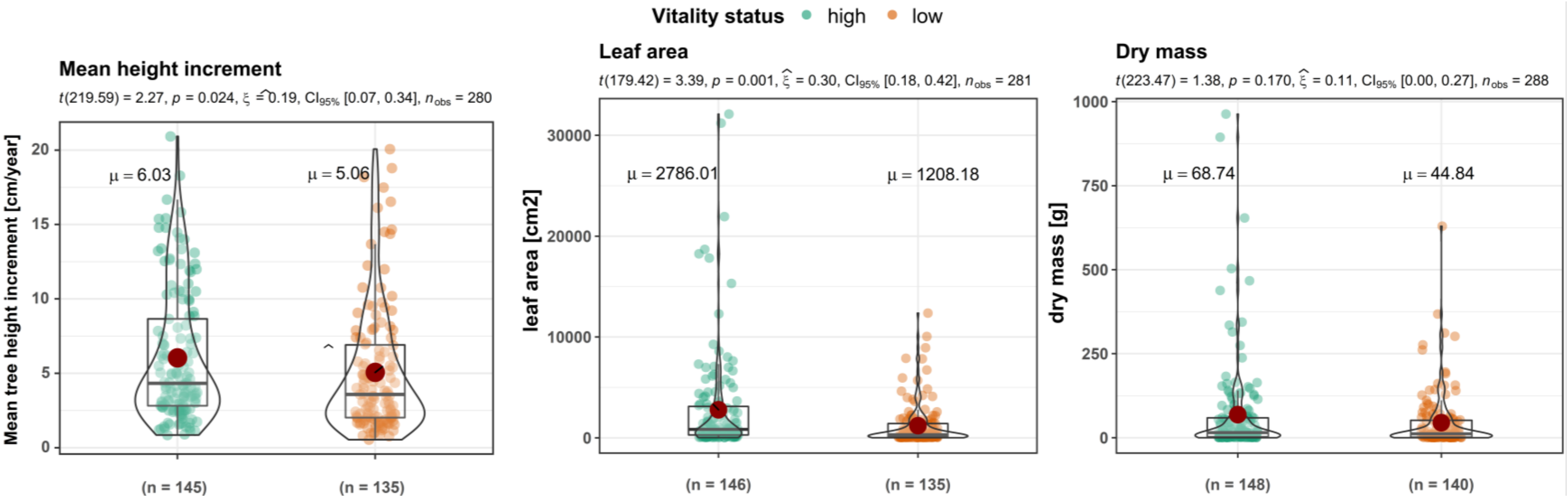

Figure S 1. Comparison of mean height increment, leaf area and dry mass of high and low vitality regeneration, Yuen's t-tests for trimmed means: red dots – mean, coloured dots – data, results of statistics are above.

Table S 3. Results of Cox proportional hazard test with Schoenfeld residuals

	χ^2	df	p
Species	6.29	2	0.043
Log (LAR) [cm2/g]	5.90	1	0.015
Log (avg. ring) [µm]	9.40	1	0.002
Height class [cm]	9.89	6	0.129
GLOBAL	26.32	10	0.003

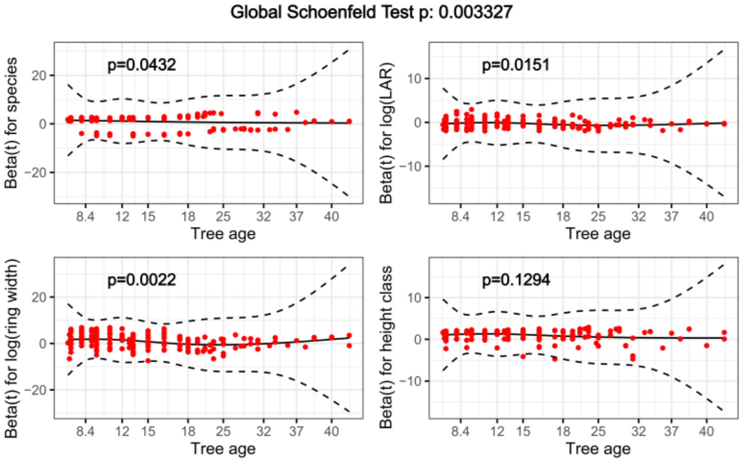

Figure S 2. Global and individual Schoenfeld tests per covariate including residuals plotted against tree age.

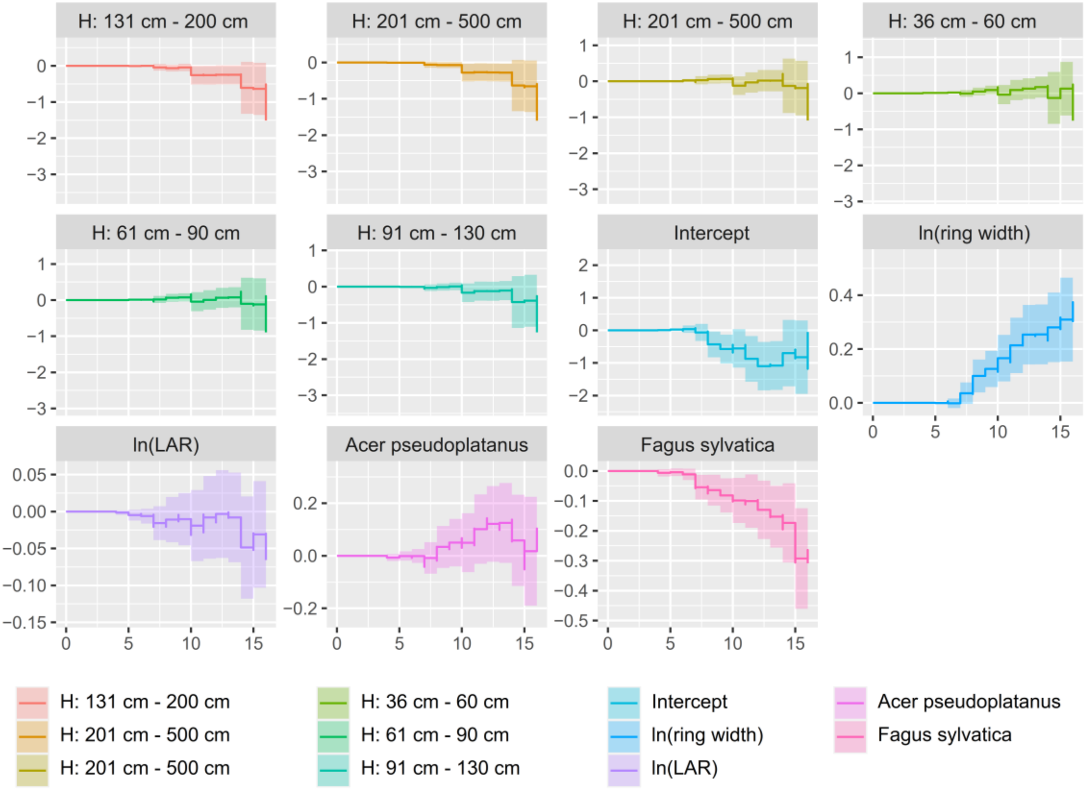

Figure S 3. Aalen additive regression with time-dependent covariates LAR and ring width.

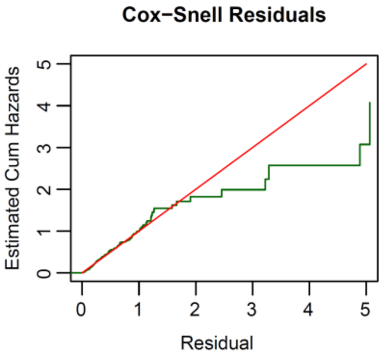

Figure S 4. Cox-Snell residuals: green line – estimated cumulative hazard of the of the Cox proportional hazard model, red line – a reference.

S 1.1 RESPONSE DISTRIBUTION, MODEL AND VARIABLE SELECTION

The variable LAR diminished with age because it depended on the tree mass while ring width increased with height class, hence the assumption of Cox proportional hazard rate was violated because of the time-dependant covariates (test with Schoenfeld and Cox-Snell residuals, Grambsch and Therneau (1994) (Figures S2, S3, S4). To check the goodness of fit of the AFT parametric survival model, the Kaplan–Meier estimates (Kaplan and Meier 1958) stratified by species were computed, and plotted against $log(t)$ (Figure S 5). As parallelism and linearity of the fitted data indicated goodness of fit to the lognormal distribution, we overlaid the estimated survival distribution with the theoretical one and did the same to check the residuals fit (package rms, Figure S 5). AIC (Akaike Information Criterion) among the fitted models (log-normal, Weibull, log-logistic and Gaussian) was the smallest for the log-normal model. The explanatory variables were selected with a fast backward step-down method (Figure S 6). Overfitting in the model was validated with bootstrapping (1000 iterations, package rms) and demonstrated low bias and good estimates of the future performance (Table S 5, Figure S 8).

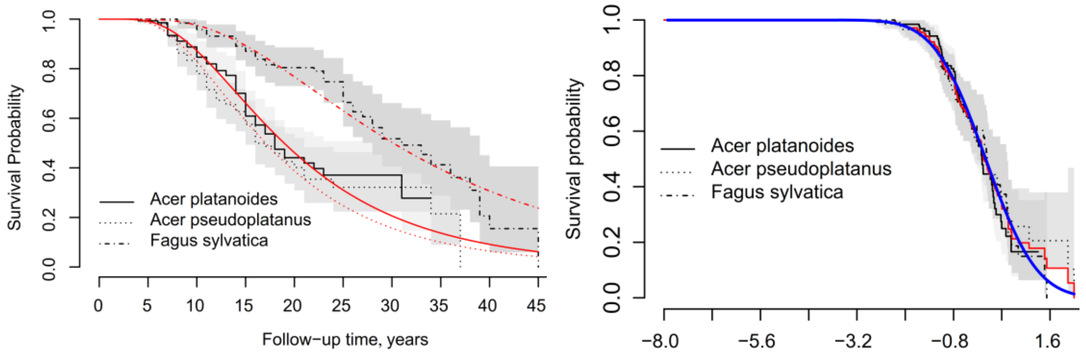

Figure S 5. Goodness of fit: left – normal inverse Kaplan–Meier estimates stratified by species overlaid by lognormal distribution (red lines). Linearity and semi-parallelism indicate a reasonable fit to the log-normal AFT model with respect to species. Right - Kaplan-Meier estimates of distributions of normalized, right-censored residuals from the fitted log-normal survival model. Residuals are stratified by important variables in the model (by quartiles of continuous variables). Left: theoretical standard log-normal distributions of residuals are shown with a blue solid line, red line – fitted data.

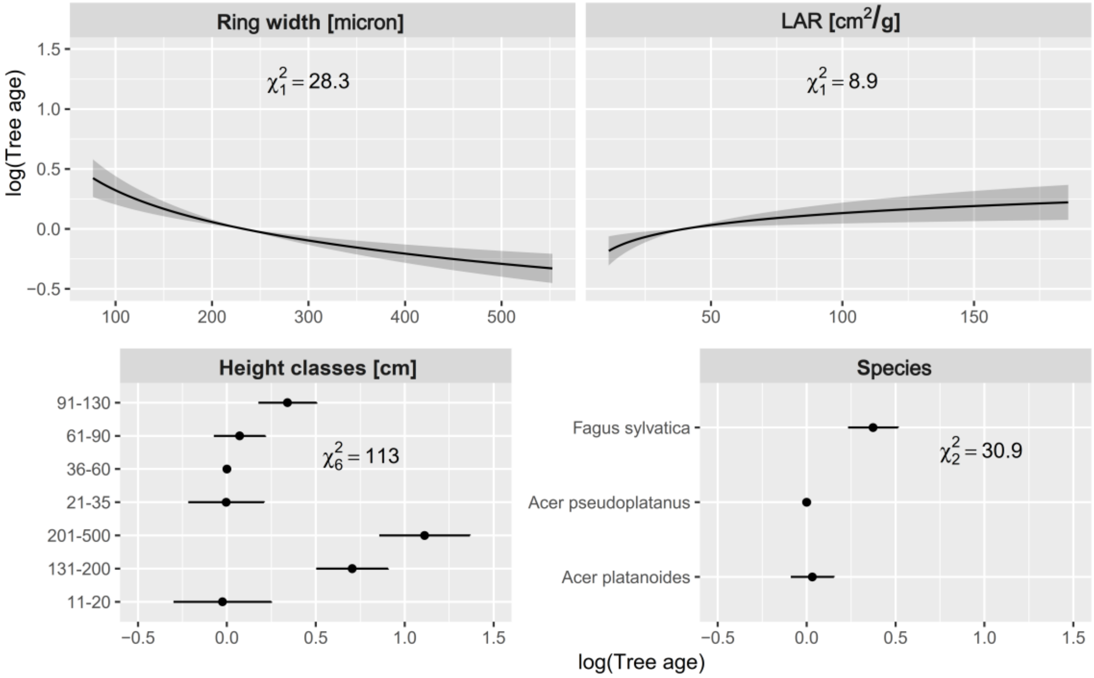

Figure S 6. Importance of covariates in AFT regression: ring width, LAR, height class, and species are the most important.

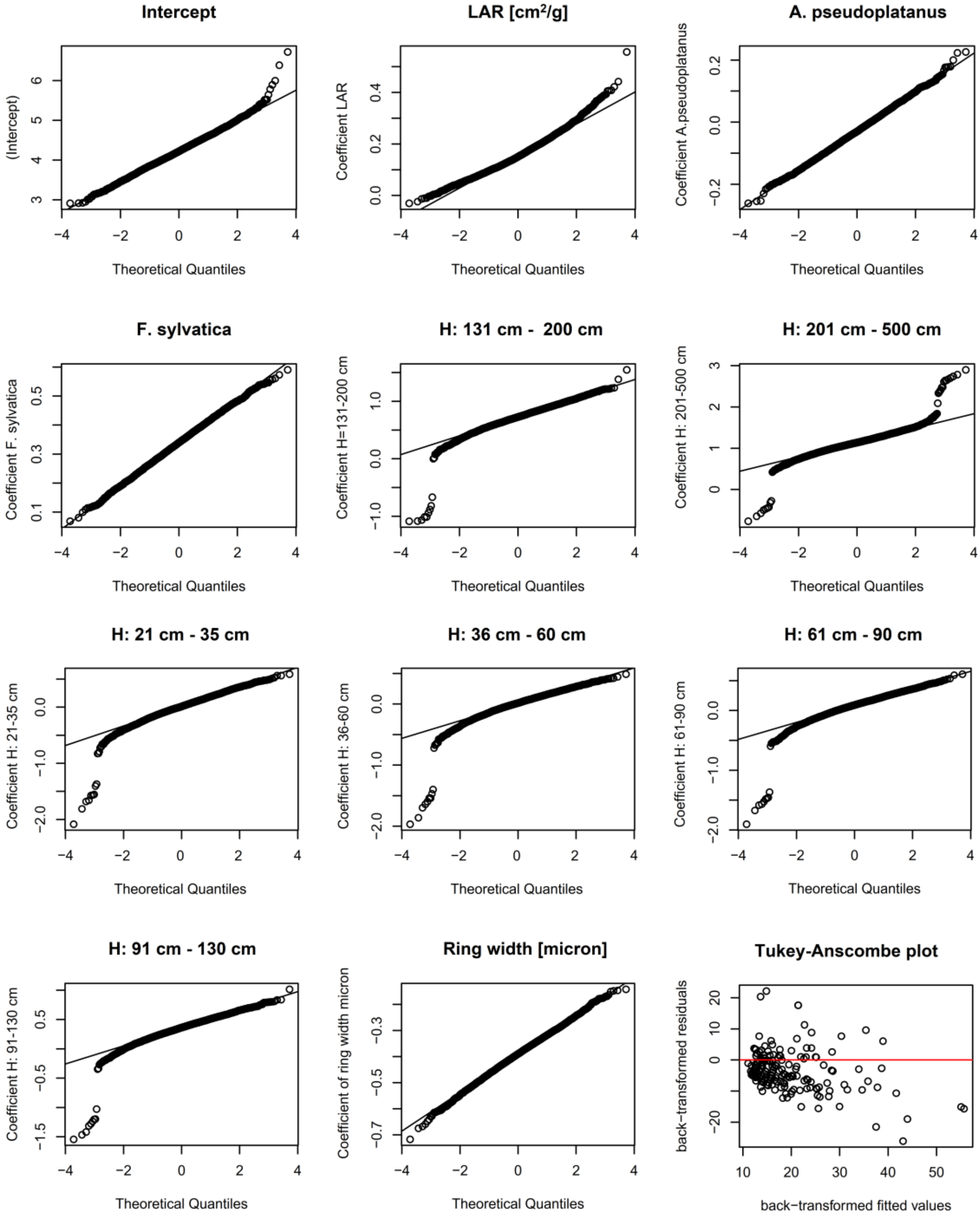

Figure S 7. Q-Q plot of standardized bootstrapped residuals in AFT log-normal model: all covariates' follow normal distribution except for the height class 201 cm - 500 cm (there are only two dead individuals per species in this class). Residuals are evenly distributed around zero at Tukey-Anscombe plot (right corner) except for some outliers.

Table S 4. Results of the log-rank (Mantel-Haenszel) test for the three species.

Species	**N sample**	**Observed number of events**	**Expected number of events**	**(O-E)^2/E**	**(O-E)^2/V**	**Chisq, p-value**
A. pseudoplatanus vs *F. sylvatica*	152 136	72 47	43.3 75.7	19.1 10.9	34.7 34.7	Chisq= 34.7 p= 4e-09
A. platanoides vs *A. pseudoplatanus*	142 152	60 72	65.7 66.3	0.49 0.49	1.04 1.04	Chisq=1 p= 0.3
A. platanoides vs *F. sylvatica*	142 136	60 47	37.5 69.5	13.47 7.27	24.2 24.2	Chisq= 24.2 p= 9e-07

Table S 5. Validating the AFT model for overfitting: Dxy of 0.53 changed only slightly after bootsrapping. It equals the difference between the probability of concordance and the probability of discordance of pairs of predicted survival ages and pairs of observed survival ages, accounting for censoring. Concordance = (Dxy+1)/2.

	Index.orig	**Training**	**Test**	**Optimism**	**Index.corrected**	**N**
Dxy	0.5627	0.5806	0.5509	0.0297	0.533	1000
R2	0.3427	0.3968	0.3604	0.0364	0.3062	1000
Intercept	0	0	0.1461	-0.1461	0.1461	1000
Slope	1	1	0.9517	0.0483	0.9517	1000

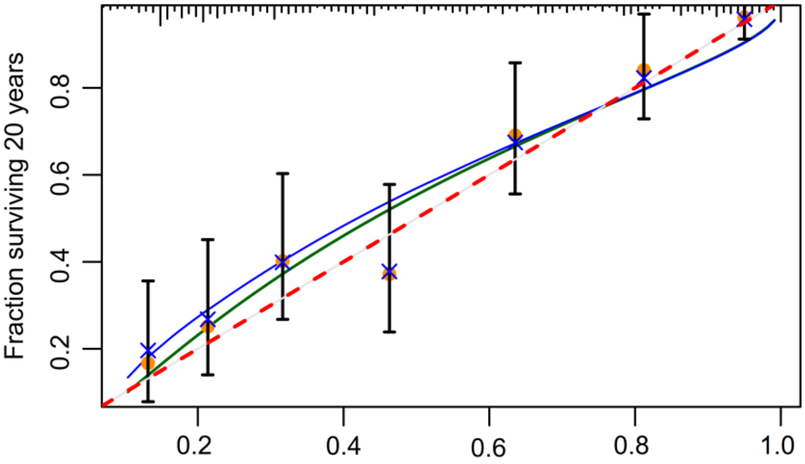

Figure S 8. Bootstrap validation of calibration curve of the survival model: orange dots represent calibration accuracy; crosses are bootstrap estimates corrected for overfitting. Blue curve is the estimated observed relationship and the green curve is the overfitting-corrected estimate. The red dotted line depicts the ideal relationship.

Chapter

3

Replace Me if You Can:

Abundance of Advance Regeneration Under Canopy Trees in a Primeval Beech Forest

To be submitted as:

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ABSTRACT

Tree replacement patterns strongly shape species coexistence and dominance in forest ecosystems. In mixed forests subject to a small-scale disturbance regime, dead canopy trees are often replaced by advance regeneration. Here, we study the abundance of saplings (6-10 cm dbh) and poles (10-25 cm dbh) under canopy trees based on four inventories on a 10-ha permanent plot in a large primary forest dominated by *Fagus sylvatica* in the western Ukraine. Saplings and poles of *Fagus sylvatica*, *Acer platanoides*, *A. pseudoplatanus* and *Ulmus glabra* were spatially linked to canopy trees ('hosts', dbh > 25 cm) based on the hosts' crown radius, and the hosts' neighbourhood was classified according to the presence of a lying or standing dead tree. The number of saplings and poles under hosts was modelled with a Bayesian hurdle Poisson model. Despite an increase over time of *Acer* spp. and *Ulmus glabra* saplings, *Fagus sylvatica* advance regeneration was much more numerous than that of the two minor species, in particular if a host was surrounded by other canopy trees. This indicates a high chance for recruitment of *Fagus sylvatica* into the canopy. *Acer* spp. had a chance to recruit a pole mostly in the vicinity of a dead lying tree or a gap. *Fagus sylvatica* poles were dominating even in gaps, thus further compromising the chances for *Acer* spp. and *Ulmus glabra* to reach the canopy. We conclude that almost all canopy trees of Acer spp. and *Ulmus glabra* are likely to be replaced by *Fagus sylvatica* if the current small-scale disturbance regime and single-tree mortality continue to prevail in this forest.

Key words: *Acer platanoides*, *Acer pseudoplatanus*, background mortality, dominance, *Fagus sylvatica*, abundance, replacement, *Ulmus glabra*

1 INTRODUCTION

An important process in forest succession is the replacement of a dead canopy tree by the tallest or fastest growing individual beneath it (Fox 1977), which may lead to a change in tree species composition. Canopy tree replacement has often been investigated in old-growth forests (Brewer and Merritt 1978; Poulson and Platt 1996; Woods 1979, 1984) as its patterns may provide insight into mechanisms of species coexistence or dominance (Busing 1996) and the nature of community dynamics (Horn 1975). In primary beech-dominated (*Fagus sylvatica* L., European beech) forests that are characterized by a small-scale disturbance regime (Hobi et al. 2015) and a canopy turnover time between 100 and 220 years (Drößler and Von Lüpke 2005; Valverde and Silvertown 1997), canopy tree replacement by poles (10-25 cm dbh, diameter at breast height) occurs mostly due to two processes, as explained below.

First, background mortality of individual trees (>25 cm dbh, Nagel et al. 2010), i.e. mortality that occurs in the absence of distinct disturbance events creating small gaps (<100 m^2), represents an important process that is structuring old-growth forests (Franklin et al. 1987, Korpel' 1995, Taccoen et al. 2019). Dying trees gradually lose crown biomass and let more light penetrate to the lower layers of the canopy, thus triggering the growth of advance (pre-established) regeneration beneath and facilitating subsequent replacement.

Second, intermediate wind disturbance events create mid-sized openings (100-1,500 m^2) that have no discrete edges and may contain surviving trees (Nagel and Diaci 2006; Woods 2000). Such openings stimulate the rapid growth of suppressed saplings (5-10.0 cm dbh) of *Acer platanoides*, *Acer pseudoplatanus* (Norway and sycamore maple), *Fagus sylvatica* and, occasionally, *Ulmus glabra* (wych elm) (Caquet et al. 2010; Feldmann et al. 2020; Janík et al. 2016; Kucbel et al. 2010).

To our knowledge, only two studies have reported reciprocal species replacement (i.e., saplings of two competing species are similarly able to replace dying canopy trees of the other species) between conifers and *Fagus sylvatica* in old-growth forests in Europe (Keren et al. 2014; Nagel et al. 2010), and there is no study on broadleaved species. In contrast, replacement among broadleaved species has often been studied in North America (Horn 1975; Poulson and Platt 1996; Woods 1979, 1984). While at the early sapling stage, *Fagus sylvatica* and *Acer* spp. often dominate in small and middle-sized gaps (Caquet et al. 2010; Feldmann et al. 2020), typically only *Fagus sylvatica* reaches the pole stage in small gaps (Feldmann et al. 2018). Such differences may maintain or reinforce an existing hierarchy, i.e. the dominant species in the shade will also show the highest growth rate after release among the poles located in small and mid-sized gaps. This superior performance is often tied to species-specific differences in shade tolerance (Firm et al. 2009; Lertzman 1992; Nagel and Diaci 2006; Webb and Scanga 2001). Given the strong differences in shade tolerance between the tree species in European broad-leaved primary forests (Ellenberg and Leuschner 2010), individual tree replacement may not be reciprocal under the current small-scale disturbance regime of these forests.

The number of poles that are being recruited for the eventual replacement of a broadleaved canopy tree in European temperate forests is poorly known. When a canopy tree is characterized by a long lifespan and slow senescence, a shade-tolerant pole will typically replace it because competing shade-intolerant poles tend to lag too far behind in size compared to shade-tolerant poles (Fox 1977). The mortality rate of canopy trees in *Fagus sylvatica* primary forests increases with tree size (Hülsmann et al. 2016). Therefore, the senescence of either individual canopy trees or tree cohorts is likely to favour their replacement by *Fagus sylvatica* rather than *Acer* spp. or *Ulmus glabra*. Consequently, the number of poles of the same or other species under canopy trees is likely an important element of species co-existence or dominance in primary forests. However, a quantitative understanding of (1) the likelihood of finding saplings and pole-stage trees under canopy trees in beech-dominated forests, and (2) the abundance of such sub-canopy elements is lacking. Here, we adopt an individual-tree perspective to evaluate tree-by-tree replacement (i.e., related to 'background mortality').

Primary *Fagus sylvatica* forests often show a striking dominance of beech (Korpel' 1995). For instance, in the Uholka-Shyrokyi Luh reserve (Ukraine), this species makes

up around 96% of the basal area (Commarmot et al. 2013). Taking into account the low abundance of the other tree species in this forest, our study focuses on the four most abundant species in this forest and aims to answer the following questions: i) What is the number of advance regeneration (saplings and poles) of *Fagus sylvatica, Acer platanoides, A. pseudoplatanus* and *Ulmus glabra* under mature canopy trees in this primary forest? ii) Which factors drive species presence and abundance?

2 MATERIALS AND METHODS

2.1 STUDY AREA

The Uholka-Shyrokyi Luh reserve (total area: 10,383 ha) in Ukraine is a beech-dominated primary forest, listed as a UNESCO World Heritage site. The Uholka part covers 4,729 ha and ranges between 400 and 1300 m a.s.l. in elevation. Mean annual temperature is about 8 °C at 430 m a.s.l. (-3 °C in January and 18 °C in July) and mean annual precipitation amounts to 1134 mm (Commarmot et al. 2013). The forest is subject to a small-scale disturbance regime, resulting in mainly small canopy gaps (98% are <200 m^2), and only few large stand-replacing events were detected using high-resolution satellite imagery (Hobi et al. 2015).

A permanent inventory plot of 10 ha (200 m × 500 m) was established in Uholka in 2000 as a collaboration project between the Swiss Federal Institute for Forest, Snow and Landscape Research WSL and the Carpathian Biosphere Reserve, Ukraine. It has since been re-measured at an interval of five years (Stillhard et al. 2019). It is located in an old-growth stand and is situated at 48.2695°N, 23.6207°E at an altitude of 700-800 m a.s.l. The plot faces mainly southeast with a grade between 20 and 40%. Soils consist mainly of dystric cambisols (Commarmot et al. 2005). The plot is dominated by *Fagus sylvatica* making up around 95% of the basal area (Stillhard et al. 2019), but it also includes tree species such as *Acer platanoides*, *A. pseudoplatanus*, *Ulmus glabra* and *Fraxinus excelsior.* Since plot establishment, two intermediate wind and heavy snowfall events occurred in 2007 and 2009, resulting in several larger canopy gaps (Figure 1, Stillhard et al. 2019).

The 10 ha plot is divided into 40 subplots of 50 m x 50 m to facilitate inventory work.

Within these subplots, all living and dead trees with a minimum diameter at breast height (dbh, height = 1.3 m) of 6 cm were numbered and mapped (Stillhard et al. 2019). Species identity and dbh of all these trees were recorded (2889 trees in total, inventory 2000) and four crown radii per tree were measured (2831 trees in total in 2000). While gaps were not delimited in the field, the mapping of dead trees enabled us to assume that their vicinity would be characterized by relatively high light levels. In addition, gaps were delineated based on LiDAR data in 2018 (cf. Supplementary materials S.7), resulting in gap area estimates between 100 and 2116 m^2 and an overall gap fraction of 7% (Hobi, *unpublished*).

2.2 SAMPLE DEFINITION

All saplings (6.0-10.0 cm dbh) and poles (10.1-25.0 cm dbh), jointly called 'advance regeneration' henceforth, were spatially related to canopy (host) trees (>25 cm dbh including dead standing trees). For this, the position of all canopy trees (focal points) was linked to saplings and poles with the method of k-nearest neighbours (k=10) based on Euclidian distances (R, package *FNN*, Beygelzimer et al. 2019). Among the linked advance regeneration (Figure 1), we selected only those located within the modelled crown radius (cf. eq. 1) of a host tree plus a 3 m buffer. When counting advance regeneration per host tree, each individual was counted only once by assigning it to the closest host tree. In addition, mature dead and living neighbours of host trees were identified with the same methods as explained above (k=10, crown radius + 3 m buffer as a cut-off). If a tree did not host advance regeneration at all, the count of advance regeneration was set to zero for each species and dbh class (saplings 6.0-10.0 cm and poles 10.1-25.0 cm). We excluded stand-alone advance regeneration (or advance regeneration cohorts) with no host tree from the model as their focal points (if any) most probably would be lying, decomposed or disappeared dead trees for which we could not model a crown radius.

All new standing dead trees (>25 cm dbh, Yamamoto 1996, Nagel et al. 2010) that appeared in any given inventory except for the inventory in 2000 (when we did not know for how long they had been dead) were considered as background mortality.

This included trees that had died because of biotic causes and either remained standing with an intact crown or still had a trunk with main branches. Standing hosts found dead in a former inventory did not qualify as hosts in subsequent inventories any more, i.e. dead standing trees were unique per inventory. Lying dead trees that had been uprooted (probably due to windstorm) were not included in the model, as they cannot be considered as background mortality (Larson and Franklin 2010). We repeated the above-mentioned procedure for each of the four inventories included in this analysis (2000, 2005, 2010 and 2015).

2.3 NEIGHBOURHOOD CLASSIFICATION

As gaps had not been delineated for every inventory, we were unable to determine whether they had existed before 2018, the year for which we had LiDAR data. Therefore, the host trees were classified according to their neighbourhood in four classes: i) host in canopy (if all neighbours were living canopy trees); ii) host adjacent to a standing dead tree, or iii) host adjacent to a lying dead tree, if at least one standing (>25 cm dbh) or lying dead tree (>25 cm dbh) was present within the modelled crown radius (plus 3 m buffer) of the host tree; and iv) stand-alone host, if there were no other living canopy trees or dead neighbours within the crown radius (plus 3 m buffer), which may occur in gaps (Figure 1).

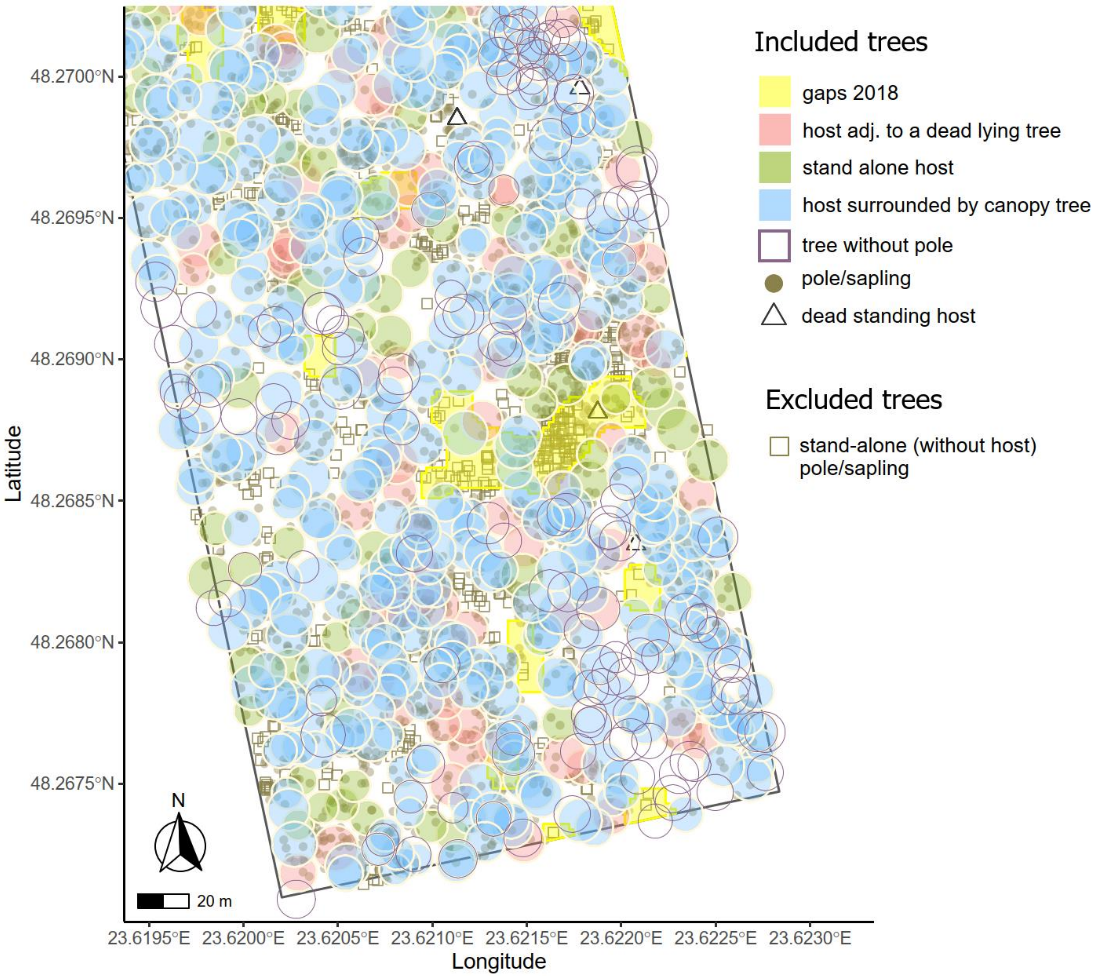

Figure 1. Spatially related advance regeneration (saplings and poles) and host trees (diameter of circles corresponds to their crown areas) on a fragment of the 10 ha plot. Selected and excluded trees are shown for the inventory 2015 (as an example). Mapped canopy gaps based on LiDAR data of the year 2018.

2.4 STATISTICAL ANALYSIS

2.4.1 MODELLING TREE CROWN RADIUS

Generalised linear models for the gamma distribution with a logarithmic link function (R, package *rms*, Harrell 2019) were applied to model the tree crown radius *cr*:

$$\ln(\mathrm{E}(cr)) = \beta_0 + \beta_1 \ln(dbh) + \beta_{2.1} species_1 + \beta_{2.2} species_2 + \beta_{2.3} species_3 + \varepsilon$$

(eq.1)

where E denotes expectation, β_0 = intercept, β_1 = coefficient of the covariate, and species$_{1,2,3}$ are three indicator (dummy) variables $\beta_{2.1-2.4}$ for the four tree species, ε = random error term asssumed to follow a standard normal distribution. The model assumed a linear relationship between the predictors and the link function. The statistical significance of the model coefficients was evaluated with the Wald Chi-squared test ($p<0.01$) and additionally checked by means of bootstrapping (1000 iterations). The model satisfied the assumptions of linearity between the predictors and the link function and showed no multicollinearity (variance inflation factor VIF cut-off set at 5). The root mean square error (prediction error) was 1.25 m (31%).

2.4.2 ABUNDANCE OF ADVANCE REGENERATION

A Bayesian hurdle Poisson model was used to estimate the mean number of advance regeneration per host tree (R, package *brms*, Bürkner 2020). The Bayesian approach works well with small samples, which occurred in the case of *Acer* spp*. and Ulmus glabra* in our analysis, and converges well using the gradient-based Hamiltonian Monte-Carlo sampler (Hoffman and Gelman 2014). The hurdle model has two parts: 1) a binary part that captures the absence/presence of advance regeneration with a response variable (y) as the probability of saplings or poles being absent (y = 0) or present (non-zero) based on a logit regression; and 2) a count part that models the estimated number of living advance regeneration (y >0) as a left-truncated Poisson regression. If saplings/poles are absent, the threshold ('hurdle') to the truncated count part is not crossed, and a zero is modelled. Otherwise, the hurdle to the truncated count part is crossed, and the amount of advance regeneration is modelled (cf. McElreath and Koster 2014). The parameter p_i indicates the probability of a zero value, and μ_i is the mean of non-zero outcomes. Then, the Poisson hurdle model is defined as:

$$f(y_i) = \begin{cases} (1 - p_i) Poisson(\mu_i), & if\ y_i > 0, \boldsymbol{counts}\ part\ of\ the\ model \\ p_i, & if\ y_i = 0,\ \boldsymbol{absence}\ part\ of\ the\ model \end{cases}$$

(eq. 2)

The presence/absence probability p_i was modelled as a linear combination of (1) the continuous predictor 'crown radius of the host tree' and the factorial predictors 'sapling/pole species' (*p.sp*, total 4 species), 'subplot' (40 subplots), 'inventory year' (4 inventories) and 'host tree ID' (*tree*, on average 600 trees per inventory) using a logit link (eq. 4). Here, host tree ID was used as a random effect because saplings/poles are nested under host trees. The ID of the host tree and the subplot-year interaction were used as random intercepts, allowing for correlation between year effects of the same subplot in both linear predictors. The counts μ_i are linearly connected via a log link and contain continuous predictors of stem diameter and factorial predictors including 'sapling/pole species' (*p.sp*), 'sapling/pole diameter class', and the 'neighbourhood classification of their host tree' (*neighb*, 4 classes, see Methods), 'subplot', 'year', and 'host tree ID' (eq. 5). The multicollinearity of crown radius and host dbh in either the count or logit part of the model was the main reason why we splitted these variables. In addition, the effect of host dbh on the abundance of advance regeneration is more straightforward to interpret, and thus we included 'host dbh' in the count part.

If we set $p.sp_i$ $(i = 1, \ldots, 4)$, $neighb_k$ $(k = 1, \ldots, 4)$, $year_l$ $(l = 1, \ldots, 4)$, $subplot_m$ $(m = 1, \ldots 40)$, $tree_n$ $(n = 1, \ldots, 600)$, then the multi-level model formulae are:

$$f(y_{ijklmn}) = \begin{cases} (1 - p_{ijklmn})Poisson(\mu_{ijklmn}), & if\ y_{ijklmn} > 0 \\ p_{ijklmn}, & if\ y_{ijklmn} = 0 \end{cases} \quad \text{(eq. 3)}$$

$$logit\ (p_{ijklmn}) = \gamma_0 + \gamma_1 radius_{ijklmn} + p.sp_i + year_l + c_{lm} + d_{n(jm)} \quad \text{(eq. 4)}$$

$$\ln (\mu_{ijklmn}) = \beta_0 + \beta_1 dbh_{ijklmn} + p.sp_i + dbh - class_j + neighb_k + year_l + a_{lm} + b_{n(jm)} \quad \text{(eq.5)}$$

where a_{lm}, $b_{n(jm)}$, c_{lm} and $d_{n(jm)}$ denote random effects with the following correlation structure:

$$\begin{pmatrix} \begin{pmatrix} a_{11} \\ \vdots \\ a_{41} \end{pmatrix} \\ \vdots \\ \begin{pmatrix} a_{140} \\ \vdots \\ a_{440} \end{pmatrix} \\ \begin{pmatrix} b_1 \\ \vdots \\ b_{600} \end{pmatrix} \end{pmatrix} \sim \mathcal{N}\left(\vec{0}, \begin{pmatrix} I_m \otimes \Sigma & 0 \\ 0 & I_m \sigma_b^2 \end{pmatrix}\right) \text{with } \Sigma =$$

$$\begin{pmatrix} \sigma_{a_{1m}}^2 & \cdots & \sigma_{a_{1m}}\sigma_{a_{lm}}\rho_{a_{1m},a_{lm}} \\ \vdots & \ddots & \vdots \\ \sigma_{a_{1m}}\sigma_{a_{lm}}\rho_{a_{1m},a_{lm}} & \cdots & \sigma_{a_{lm}}^2 \end{pmatrix} \qquad \text{(eq.6)}$$

and similarly for c_{lm} and $d_{n(jm)}$. The random effects are assumed to come from a multivariate normal distribution $\mathcal{N}$ with a mean of zero, Σ is the covariance matrix with diagonal elements of standard deviation σ, and I_m is the identity matrix.

Weakly informative priors were applied to the intercepts β_0, γ_0 and the coefficients $\beta_{1,2}$, γ_1 that follow a normal distribution $\mathcal{N}$ (μ, σ^2) with mean μ and variance σ^2. Weakly informative priors are preferable in the case of small samples (McNeish 2016) and restrict the parameter values to a reasonable range without strongly influencing the posterior distribution (Lemoine 2019). A half-t distribution (half-student distribution) with 4 degrees of freedom, mean and scale was applied for the intercepts and the standard deviations of the group levels (Gelman 2006):

$$\beta_0 \sim half - t(4, 0, 1)$$

$$\beta_{1,2} \sim normal(0, 0.3)$$

$$\gamma_0 \sim half - t(4, 0, 0.5)$$

$$\gamma_1 \sim normal(0, 0.5)$$

$$\sigma_{\alpha_{lm}} \sim half - t(4, 0, 0.5)$$

$$\sigma_{\beta_{n(jm)}} \sim half - t(4,0, 0.5)$$

$$\sigma_{c_{lm}} \sim half - t\ (4,0, 0.5)$$

$$\sigma_{d_{n(jm)}} \sim half - t\ (4,0, 0.5)$$

Additionally, to better understand the impact of the priors on the posterior results, we estimated the relative bias of the parameters for models with weakly informative vs. non-informative priors. In a sensitivity analysis, the mean of the weakly informative priors was varied upward and downward by 0.1. The model with non-informative priors had issues with multicollinearity, while the statistical findings from models with weakly informative priors were comparable for all models. This indicates that the parameter estimation was driven by the properties of the data rather than the nature of the priors (cf. Supplementary material).

The model fully converged and stabilized ($\hat{R} \leq 1$, Gelman and Rubin 1992) after running on 4 chains and with 4,000 iterations per chain plus 1000 iterations for warm-up. It did not show autocorrelation in the chains (cf. Supplementary materials). A relatively high effective sample size (ESS, Table 2) highlighted the ability of the draws to estimate the true mean values of the parameters (Gelman et al. 2013). The predictive accuracy of the posterior distribution was estimated with approximate leave-one-out cross-validation (LOO) based on Pareto smoothed importance sampling (Vehtari et al. 2017). Model choice was based on the highest expected log predicted density (elpd_loo) and the lowest LOO Information Criterion (looic). The Pareto k-values did not exceed 0.6 without influential observations (cf. Supplementary materials).

In Bayesian inference, goodness-of-fit is evaluated via posterior simulations, i.e. new data are simulated from the model with parameters from the estimated posterior distributions, and the simulated data are compared to the observed data. Therefore, we simulated new data based on 2000 draws from the parameters' posterior distribution and compared the mean and standard deviation with the observed data (cf. Supplementary materials). Model residuals were approximately normally distributed, random effects followed a normal distribution, and covariates showed no multicollinearity. The model showed no overdispersion either. The significance of the effects was tested with the full region of practical equivalence ROPE [full] (Kruschke 2018) based on high-density intervals (HDI). Values of the distribution both below and above the ROPE (-0.1, 0.1) indicate practical significance (Kruschke 2018; Makowski et al. 2019).

3 RESULTS

3.1 SAMPLES OF HOST TREES AND SPATIALLY RELATED SAPLINGS AND POLES

In the 2000 and 2005 inventories, only half of the host trees were spatially associated with advance regeneration. In contrast, in the 2015 inventory, 81% of the host tree

population was spatially associated with saplings or poles due to high ingrowth under host trees (Table 1). The storms in 2007 and 2009 had created gaps, thus allowing more light to penetrate below the canopy and raising the number of new saplings in the time between the inventories of 2010 and 2015. Advance regeneration under the host trees represented almost the entire population of saplings and poles, with only about 10% of the juvenile trees standing alone or as cohorts in gaps. In short, the sample used for this study consisted of most of the host trees and advance regeneration population which is present on the 10 ha plot.

Table 1. Samples of living host trees, living saplings and poles under host trees, and host trees without saplings and poles (all included in the model) relative to the total number of trees on the 10 ha plot (after /) per inventory. The mean dbh and crown radius of the host trees with standard deviation (sd) are given per species. Species: A. platanoides (A. pla), Acer pseudoplatanus (A. pse), Fagus sylvatica (F. syl), Ulmus glabra (U. gla).

Category	**Species**	**N'00/ total**	**N'05/ total**	**N'10/ total**	**N'15/ total**	**dbh (sd), [cm]**	**Crown radius (sd), [m]**
Host trees (dbh >25 cm)	A. pla	4 / 6	5 / 6	5 / 6	6 / 7	48.3 (15.4)	4.5 (0.6)
	A. pse	18 / 36	16 / 35	19 / 35	30 / 35	56.8 (15.5)	4.8 (0.5)
	F. syl	591 / 1,119	617 / 1,073	677 / 1,007	802 / 989	63.5 (22.4)	5.7 (0.8)
	U. gla	2 / 3	2 / 3	1 / 3	2 / 3	49.6 (10.4)	5.7 (0.5)
Saplings/ poles under host (dbh 6-25 cm)	A. pla	4 / 7	4 / 8	20 / 26	185 / 217	8.2 (3.5)	
	A. pse	6 / 8	9 / 18	29 / 44	129 / 212	8.0 (2.6)	
	F. syl	1,437 / 1,604	1,542 / 1,729	1,825 / 2,034	2,835 / 3,115	10.8 (4.4)	
	U. gla	4 / 5	6 / 7	15 / 16	87 / 104	8.8 (2.6)	

Fagus sylvatica featured a steady proportion of the number of advance regeneration to the number of host trees during the inventories 2000-2010 but showed a substantial increase in 2015 (Table 1). In contrast, *Acer* spp. had a negligible number of saplings and poles in 2000 and 2005, but after the storms their number went up strongly for the inventories of 2010 and 2015.

Surprisingly, mostly *Fagus sylvatica* poles appeared under *Acer* spp. or *Ulmus glabra* hosts while *Acer* spp. and *Ulmus glabra* poles grew mostly under *Fagus sylvatica* hosts (Figure 2). In 2000, almost all *Acer* spp. hosts were occupied by *Fagus sylvatica* poles, and a similar pattern was found in 2015. Comparing the inventories of 2000 and 2015, hosts in higher dbh classes (>85 cm) accumulated more poles of *Fagus sylvatica* with time or/and with higher light availability, while *Acer* sp. and *Ulmus glabra* poles competed more successfully among hosts in the lower dbh classes (<85 cm).

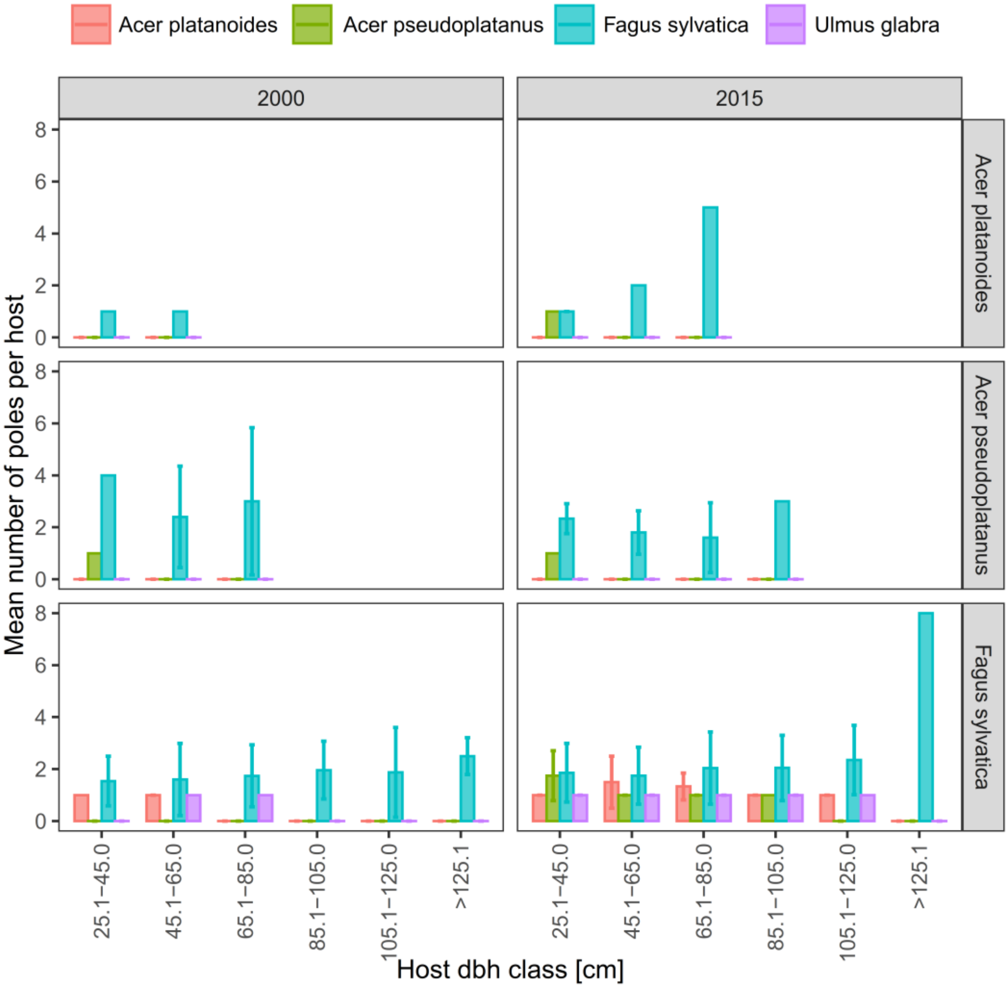

Figure 2. Mean number of poles (10.1-25.0 cm dbh) per host diameter class and host species (by row). Whiskers indicate one standard deviation. Note: two host trees of U. glabra were omitted here for readability.

A closer look at the location and neighbourhood of trees without advance regeneration revealed that they were growing mostly in dense clusters around dead lying trees in the inventory 2005 (Figure 3). These clusters created patches with low light availability and thus suppressed regeneration. However, after two windfalls some of these trees were killed, thus allowing for more light that triggered rapid sapling recruitment. Subsequently, most trees without advance regeneration became hosts in 2015 inventory.

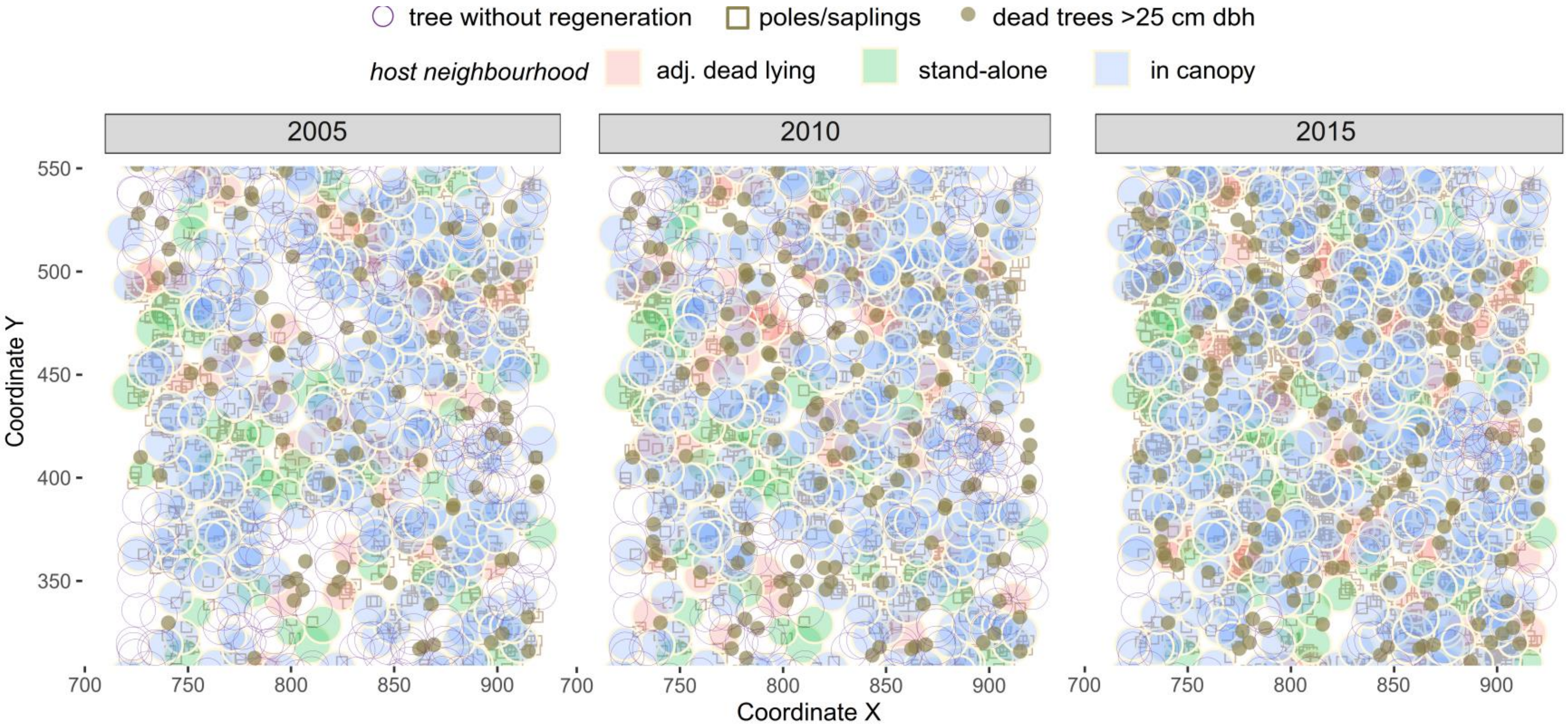

Figure 3. Fragments of 10 ha plot in 2005, 2010, 2015 showing clusters of trees without poles. Note: the inventory of 2000 was very similar to the inventory of 2005 in terms of number of trees without regeneration, and it is therefore not shown here.

The number of *Fagus sylvatica* stand-alone poles growing, presumably, in gaps (cf. Figure 1) increased from 2010 to 2015 (Figure 4). The rates of increase in saplings were quite similar for *Fagus sylvatica* and *Acer pseudoplatanus* but much lower at the pole stage for the latter. Interestingly, *Acer platanoides* was able to produce a similar number of saplings and poles as *Acer pseudoplatanus* in spite of much fewer hosts (Table 1, Figure 4 A).

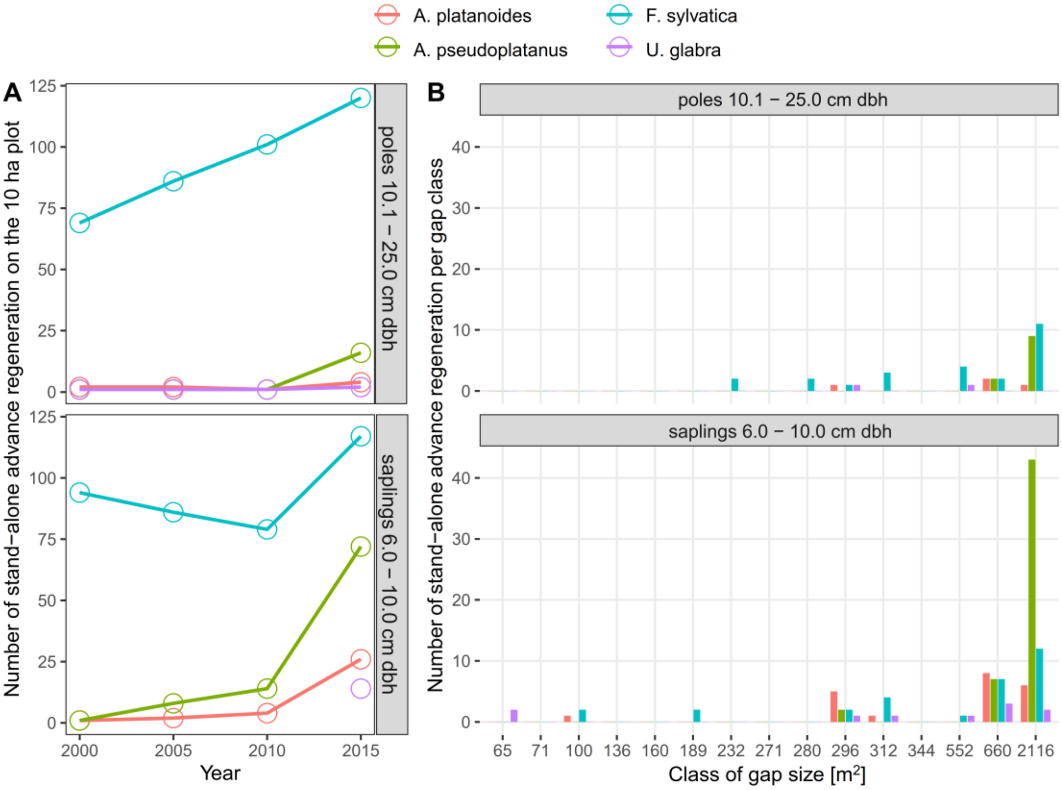

Figure 4. A: total number of stand-alone, i.e. host-free, saplings (dbh 6.0-10.0 cm) and poles (dbh 10.1-25.0 cm) in the four inventories 2000, 2005, 2010, 2015 on the 10 ha plot; B: advance regeneration in gaps delineated in 2018.

Only some gaps delineated based on LiDAR data from the year 2018 contained advance regeneration without hosts (Figure 4 B). It is noteworthy that the k-nearest neighbour method identified more gaps with stand-alone regeneration than LiDAR-derived gaps, but their size was impossible to determine. The number of saplings and poles in small gaps (<296 m^2) appeared to be negligible, but the amount of advance regeneration substantially increased in gaps >552 m^2. Saplings of *Acer pseudoplatanus* by far outcompeted *Fagus sylvatica* while keeping the same number of poles as dominant species in the gap size 2116 m^2.

3.2 SAPLING AND POLE ABUNDANCE AS AN INDICATOR OF HOST REPLACEMENT

In the hurdle model, the count and survival parts are separated, thus allowing the coefficients of the relationship between the predictor variables and the abundance of advance regeneration to be interpreted easily. An increase in one unit of host dbh (i.e., by 1 cm) increased the mean number (incidence rate) of advance regeneration by 1.04 points (cf. Table 2), respectively, for the same inventory period and subplot when holding the other covariates constant. This effect was not significant because the credible intervals were inside the ROPE indicator (see % inROPE [full], Table 2). When holding the other covariates constant, the mean number of advance regeneration was 1.29 points higher in *Acer pseudoplatanus* than in *A. platanoides* for the same year and subplot (difference not significant), while the number was significantly higher in *Fagus sylvatica* advance regeneration (by 1.76 points) and lower in *Ulmus glabra* (by 0.56 points).

Regarding neighbourhood effects, trees in the vicinity of a standing dead tree or those that were surrounded by other living canopy trees were less likely to host advance regeneration compared to hosts adjacent to lying dead trees, while stand-alone hosts had the highest number of saplings and poles underneath. The model predicted an increase in the mean abundance of advance regeneration compared to the 2000 inventory for the inventories after the storms in both 2010 (by 1.1 points, not significant) and 2015 (by 1.6 points, significant).

Table 2. Results of the hurdle Poisson model indicating the number of tree regeneration in the counts part (left) and the likelihood of its presence in the logit part (right). Exp coef - exponentiated coefficients, sd – standard deviation, %in ROPE [full] - percentage in ROPE as an index of significance, ESS – effective sample size, AR – advance regeneration, A. pla – A. platanoides, A. pse – A. pseudoplatanus, F. syl – Fagus sylvatica; Bayesian significance is marked as (*). Total number of observations: 4,275.

Parameter	Incidence rate (sd)	% inROPE [full]	$\hat{R}$	ESS	Odds ratio(sd)	% inROPE [full]	$\hat{R}$	ESS
	Counts part					**Logit part**		
Intercept	0.44 (1.15)	0.0	1.0	9,290	0.01 (1.82)	0.0*	1.0	10,310
Host dbh [cm]	1.04 (1.15)	65.7	1.0	20,394				
Host crown radius [m]					0.83 (1.6)	43.1	1.0	12,187
A. pla (AR)	*reference*							
A. pse (AR)	1.29 (1.15)	14.3	1.0	22,837	1.24 (1.56)	40.3	1.0	10,707
F. syl (AR)	1.76 (1.11)	0.0*	1.0	24,129	0.47 (1.58)	7.5*	1.0	9,725
U. gla (AR)	0.56 (1.19)	0.2*	1.0	19,529	1.29 (1.57)	35.9	1.0	10,178
Dbh class of AR [10.1-25.0 cm]	*reference*							
[6.0-10.0 cm]	1.19 (1.03)	2.0*	1.0	8,209				
Host adj. lying dead	*reference*							
Host adj. dead standing	0.81 (1.22)	29.8	1.0	17,745				
Host in canopy	0.93 (1.06)	68.2	1.0	10,544				
Host standing alone	1.40 (1.09)	0.3*	1.0	9,807				
Inventory 2000	*reference*							
Inventory 2005	0.98 (1.06)	92.4	1.0	25,981	1.00 (1.56)	57.8	1.0	8,512
Inventory 2010	1.11 (1.06)	52.0	1.0	16,048	0.83 (1.65)	43.4	1.0	7,885
Inventory 2015	1.60 (1.07)	0.0*	1.0	10,126	0.83 (1.68)	43.1	1.0	8,021

**Note: Bayesian statistical significance is not directly comparable to significance in frequentist statistics.*

In the logit part of the model (Table 2), an increase in the crown radius of a host tree by one unit led to a decrease of the adjusted odds of advance regeneration to be absent by a factor of 0.83 for the same year and subplot. Compared to *A. platanoides*, advance regeneration of both *Acer pseudoplatanus* and *Ulmus glabra* had lower chances to be hosted than that of *Fagus sylvatica*. Due to improved light conditions after the windstorms, the likelihood of advance regeneration being absent decreased in 2010-2015 compared to 2000, confirming the similar effect in the counts part of the model (Table 2).

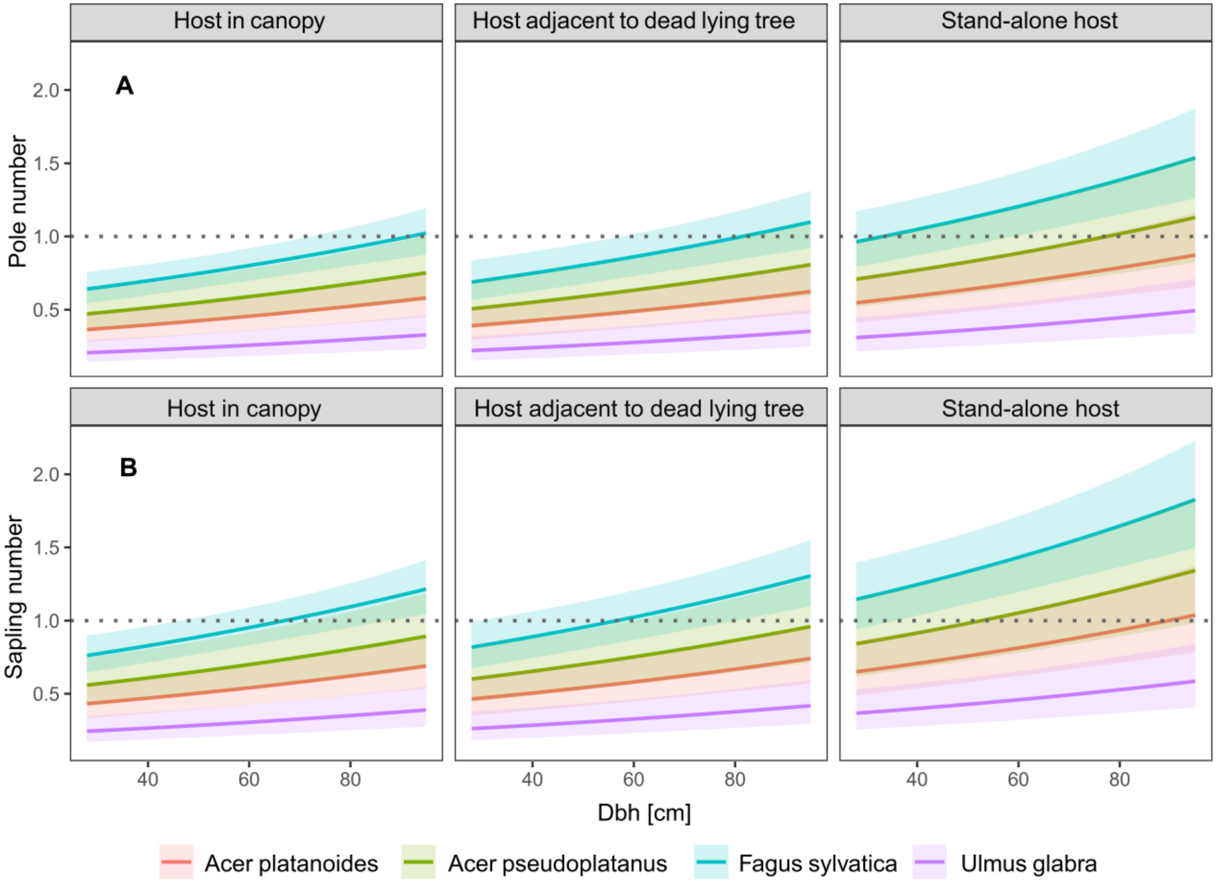

Figure 5. ***A****: Number of poles (dbh 10.1-25.0 cm) and* ***B:*** *saplings (6.0-10.0 cm) under a host tree in different host neighbourhoods. Thick lines are marginal means averaged for the four periods, shaded regions 95% credible intervals (CI) for the marginal means, and the grey dotted horizontal line indicates the threshold for potential replacement by at least one pole.*

Generally, the number of advance regeneration hosted under trees in different neighbourhoods was lower for poles (Figure 5A) than for saplings (Figure 5B). Also, there was a clearly higher number of advance regeneration under hosts with increasing diameter. The availability of poles under hosts in different host neighbourhoods and in dependence of host dbh mirrored the presence of saplings, but at clearly lower levels (Figure 5A). At host dbh 40 cm, the number of *Fagus sylvatica* poles in shaded conditions (i.e., host in canopy) was low (mean=0.6, CI [0.4, 0.8]) and increased to one pole under hosts > 80 cm dbh. Moreover, hosts in the vicinity of dead lying trees or stand-alone hosts showed an intermediate abundance of *Fagus sylvatica* poles (mean=0.9 and 1.2), suggesting realistic chances for a successful replacement. Unlike in *Fagus sylvatica*, the low numbers of *Acer spp. and Ulmus glabra* poles in shaded conditions most likely render replacement a rare event. Only near a dead lying tree, *Acer pseudoplatanus* hardly achieved an abundance of one pole at host dbh values larger than 80 cm. Finally, in gaps both *Acer spp.* were able to compete to a certain degree with *Fagus sylvatica* poles (Figure 5B).

Under low light levels (i.e., host in canopy), one sapling of *Fagus sylvatica* (mean=0.96, CI [0.8, 1.1]) was present as a potential replacement for one host of 60 cm dbh, or for one host adjacent to a dead lying tree (mean=1.0, CI [0.9, 1.2]; Figure 5A). If a host was in a gap (stand-alone host), up to two *Fagus sylvatica* saplings were available as potential replacement for hosts with a dbh > 60 cm. The number of saplings potentially replacing a host was lower in *Acer pseudoplatanus* than in *Fagus sylvatica,* and close to 1 only if the host was large (dbh > 60 cm), either in the vicinity to a dead canopy tree or standing alone in a gap (mean= 1.1, CI [0.8, 1.4]). In contrast, at these locations neither *Acer platanoides* nor *Ulmus glabra* seem able to recruit a sapling for replacement of a host (60 cm dbh), although proximity to a gap increased the chances for replacement in *Acer platanoides* saplings (mean=0.8, CI [0.6, 1.1]).

4 DISCUSSION

4.1 ABUNDANCE OF POTENTIAL RECRUITS TO CANOPY

We studied the abundance of potential recruits to the canopy under hosts, not recruiting events over time. However, we were able to infer from the number of recruits under a host whether a replacement is likely to occur in case the host dies. A higher number of recruits of a given species under a host makes an actual replacement more likely, and vice versa. As poles have a higher chance than saplings to reach the canopy, we assume that the number of poles per host in the model corresponds with the actual replacement events. Unlike previous studies (e.g., Busing 1996; Nagel et al. 2010), we did not assume that the presence of one successor sapling/pole underneath a host tree suggests that this sapling/pole will indeed replace the host. Instead, we accounted for the population of all saplings and pole-stage trees, thus yielding a more accurate estimation of the successor species based on Bayesian statistics. On this account, our study is close to Horn's (1975) model where the proportion of saplings under a host tree was used to derive the probability of replacement. The quality of Bayesian inference (McNeish 2016) about model parameters is not controlled by sample size, as in frequentist statistics (i.e., a small sample implies a high bias), but rather by the number of samples simulated (ESS in Table 2). The simulated effective samples were sufficient to draw conclusions on potential replacement event not only for the dominant species *Fagus sylvatica*, but even for the minor species *Acer* spp. and *Ulmus glabra*.

Our study provides no indication of reciprocal canopy replacement between *Fagus sylvatica* and *Acer* spp. or *Ulmus glabra*, as was observed between *Fagus sylvatica* and *Abies alba* poles (Nagel et al. 2010), between *Fagus sylvatica* and conifer species (Keren et al. 2014), or between *Fagus grandifolia* and *Acer saccharum* (Poulson and Platt 1996; Woods 1984) in North America. Similar to European *Acer pseudoplatanus*, *Acer saccharum* is considered a less shade-tolerant species than *Fagus grandifolia* (Beaudet et al. 1999; Beaudet and Messier 1998; Canham 1988; Collin et al. 2017; Kobe et al. 1995), however it shares a dominant position with the latter due to higher frequency and larger scale of

disturbance in North America compared to Europe (Marshall and Camp 2013). Reciprocal replacement of *Abies alba* and *Fagus sylvatica* was explained by gap size, i.e. the former was able to reach the top canopy in small and mid-sized gaps while the latter occurred mainly in gaps >400 m^2 (Nagel et al. 2010). On the contrary, we found competitive replacement of heterospecific host trees by *Fagus sylvatica* advance regeneration (Figure 2) irrespective of the neighbourhood (Figure 5), whereas the self-replacement of *Acer* spp. occurred only in the proximity of lying dead trees, and for *Ulmus glabra* in gaps. Hence, given the prevailing single-tree mortality in our study area and the overall low gap fraction (7% in year 2018), canopy replacement benefits mostly *Fagus sylvatica*.

In previous research, the probability of replacement was typically derived from cross-sectional rather than longitudinal data (Fox 1977; Nagel et al. 2010; Poulson and Platt 1996; Woods 1984). We used longitudinal data and allowed for correlation between year effects of the same subplot in both linear predictors, which is why the number of advance regeneration available for replacement and also their absence differed between periods (Table 2). We found that the number of advance regeneration under a host significantly increased during the inventory period 2010-2015, especially in the vicinity of dead lying trees and gaps. However, between 2010 and 2015 the number of host trees increased substantially as well, maintaining a similar amount of advance regeneration per host as before.

The stand structure on the 10 ha plot studied here differs from that of the entire reserve, e.g., the 10 ha plot has higher basal area, host tree diameters (Peck et al. 2015), abundance of small saplings (up to 1.3 m in height) of *Acer* spp. and *Ulmus glabra* (Commarmot et al. 2005; Stillhard et al. 2019), and a higher gap fraction (Hobi et al. 2015). Nevertheless, neither the high gap fraction nor the higher frequency of windfalls stimulated significant recruitment to poles of *Acer* spp. and *Ulmus glabra* compared to *Fagus sylvatica* stand-alone advance regeneration on the 10 ha plot (Figure 4). Stillhard et al. (2022) reported a 97% share of *Fagus sylvatica* in the sapling class (0-5.9 cm dbh) for the entire Uholka-Shyrokiy Luh reserve. This suggests that replacement on the 10-ha plot occurs mostly under the single-tree mortality scenario (Figure 5) and follows the same pattern as in the entire reserve, thus explaining the strong *Fagus sylvatica* dominance in this forest.

4.2 FACTORS AFFECTING ABUNDANCE OF ADVANCE REGENERATION

We studied two situations of tree-by-tree replacement: i) the replacement of canopy trees in a matrix of other living canopy trees, based on spatial associations between overstory and understory trees (Culver 1981; Fox 1977; Horn 1975; Woods 1984); and ii) the replacement of canopy trees that are adjacent to or in gaps (in the vicinity of lying dead trees or stand-alone host trees) (Lertzman 1992, 1995; Runkle 1981). Some studies (Ammer and Weber 1999; Busing and White 1997; Denslow 1995) suggested that gaps are not necessarily the primary sites of successful regeneration of shade-tolerant species. Yet, in our study the number of advance regeneration per host was higher for hosts in the vicinity to lying dead trees and gaps (Table 2), and significantly lower for hosts surrounded by neighbouring canopy trees. Our findings are thus in line with those of Feldmann et al. (2018, 2020), who reported the density of *Fagus sylvatica* saplings (≥0.5 m height and dbh <7 cm) to be five times higher in gaps than under the closed canopy. However, our findings here contradict those of Nagel et al. (2010), who found that the density of *Fagus sylvatica* advance regeneration was largely decoupled from light levels. We found that host neighbourhood (only living canopy trees vs. at least one dead tree vs. no neighbours, suggesting a gap) as an indicator of local light availability is pivotal for *Acer* spp. and *Ulmus glabra* as it substantially increases the recruitment of saplings to poles and, subsequently, the number of poles in higher dbh classes (Figure 5).

In our study, the dbh of a host tree did not have a significant effect on the amount of advance regeneration underneath it, although hosts in high dbh classes accumulated advance regeneration with time (Figure 2) and increasing light availability. Indeed, since 2007 the neighbourhood of many hosts had changed, and we assume that the additional light becoming available promoted the growth of seedlings to saplings and poles. This process went along with the ingrowth of host trees into high dbh classes. Hence, we surmise that the increase in the amount of advance regeneration under hosts in high dbh classes is related to (i) processes depending on time (e.g., increasing crown senescence and disintegration) and (ii) changes in host neighbourhood (e.g., increasing light availability). We cannot, however, exclude an effect of the crown area geometry because

trees with larger dbh have also larger modelled crown radii.

Several studies reported different relations between *Fagus sylvatica* poles and hosts of conifer and broadleaved species in old-growth European forests. *Fagus sylvatica* poles alone were negatively spatially related to conspecific adult trees (Janík et al. 2014) and the probability of replacement of dead *Abies alba* trees by *Fagus sylvatica* poles was higher than of dead *Fagus sylvatica* trees (Nagel et al. 2010). A negative correlation between *Acer pseudoplatanus* poles and *Fagus sylvatica* hosts up to 6–7 m in distance was found by Janík et al. (2016), whereas *Fagus sylvatica* poles showed no or only a weak positive correlation to *Acer pseudoplatanus* hosts. Although we did not include host identity in the final model, one of the preliminary models was built with this explanatory variable. The amount of advance regeneration was slightly lower under *Fagus sylvatica* than under *Acer pseudoplatanus* hosts, even though this effect was not significant. Our results show that the host neighbourhood, rather than its species identity, plays a crucial role in the accumulation of poles. *Fagus sylvatica* canopy trees can host numerous heterospecific poles (Figure 2) provided the hosts are located near dead lying trees or gaps.

We did not consider host-free advance regeneration in our analysis. Could these individuals make a difference, and in particular explain why *Fagus sylvatica* is not entirely excluding the minor species from reaching the canopy at larger scales? The analysis of sapling (< 4 cm dbh) and pole recruitment (4-12 cm dbh) after wind disturbance on permanent plots over 25 years showed that both regeneration classes of *Fagus sylvatica* successfully recruited in high amounts after disturbances while the number of *Acer* spp. saplings decreased and the number of poles lagged behind those of *Fagus sylvatica* (Scherrer et al. 2022). Although in our study the number of *Acer pseudoplatanus* saplings without hosts increased presumably in gaps (Figure 4), they did not respond with strong growth and recruitment to poles after wind disturbances, supporting the proposition that shade negatively influences the height and diameter increment of *Acer* spp. regeneration with increasing age (Brüllhardt et al. 2020; Schmidt and Roloff 2014). This provides support to the notion that *Acer pseudoplatanus* may be able to maintain its presence in the canopy only when two circumstances coincide: i) saplings are still able to react strongly in their growth when light levels increase; ii) a canopy opening is big enough so as to provide the time required for the recruitment to pole. This suggests that *Acer* species regenerate in some pulses (Jentsch and White 2019) with low probability of the coincidence of factors mentioned above and thus of recruitment to the canopy, confirming the interpretation of the statistical model of pole number. In contrast, *Fagus sylvatica* is able to grow not only to higher dbh classes (Nagel et al. 2010) but also in higher numbers in gaps due to lower mortality in the shade compared to *Acer* spp. (Kunstler et al. 2005; Petriţan et al. 2007; Petrovska et al. 2021). The number of *Fagus sylvatica* stand-alone saplings and poles increased at a higher rate than those of *Acer* spp., and they became more numerous especially at the pole stage (Figure 4). To conclude, gaps have an important role for long-term species coexistence, and they can become dominated by pure *Fagus sylvatica* advance regeneration (Feldmann et al. 2018; Jaloviar et al. 2020; Kramer et al. 2014), or they may harbour occasional *Acer* spp. and – even more rarely – *Ulmus glabra* advance regeneration, be it as single poles or as cohorts.

The occurrence of canopy trees that do not host advance regeneration can partly be explained by the calliper threshold. Also, the method of k-nearest neighbours assigns a sapling or pole to a host based on the nearest distance inside perfect circular crown projection, even though a pole may grow outside of its host's irregular crown projection in a real forest. Hence, the distribution of advance regeneration is more clustered for some hosts, leaving some mature trees without advance regeneration. In addition, increased mortality of poles, especially *Fagus sylvatica,* due to windthrow on the 10 ha plot was also observed in other temperate forests, where regeneration at the pole stage showed the largest decrease in density (Gabrysiak et al. 2021), and in boreal forests at a range of storm intensities (Rich et al. 2010; Shorohova et al. 2008). However, the rapid recruitment of advance regeneration in the inventories of 2015 vs 2010 (Figure 3) suggests that its absence under some trees was mainly due to the callipering threshold and method used for the spatial identification of host and its advance regeneration.

4.3 MANAGEMENT IMPLICATIONS

The maintenance of minor broadleaved species such as *Acer spp.* and *Ulmus glabra* in stands dominated by beech is an important management question. Previous research on *Acer* spp. saplings showed their ability to survive in deep shade (mean 2-3% of diffuse

light) up to 48 years (Petrovska et al. 2021). However, shade negatively influences the height and diameter increment of these species with increasing age (Brüllhardt et al. 2020; Hein et al. 2009; Mosandl and El Kateb 1988; Schmidt and Roloff 2014). Some silvicultural guidelines recommend an opening of the canopy as soon as *Acer pseudoplatanus* reaches 2-4 m in height (Leder 2009). However, already 1-2 m tall saplings growing in the shade may stagnate in height growth (Schmidt and Roloff 2014). Therefore, it is critical to open the canopy at 1-2 m sapling height to maintain *Acer* spp. at sufficient density, i.e. before their mortality sharply increases (Petrovska et al. 2021), so as to stimulate their diameter and height growth at an early age (Brüllhardt et al. 2020; Hein 2003).

Canopy openings that are as large as the crown projection of a mature beech tree (≤184 m^2, modelled max. crown area in this study) are clearly insufficient for *Acer* spp. recruitment. In our study, a canopy opening equivalent to at least 3-4 tree crowns (about 550-736 m^2) strongly accelerated the recruitment of *Acer* spp. and *Ulmus glabra* saplings to poles (Figure 4B) and increased the chances for replacement of host trees by *Acer* spp. and *Ulmus glabra* in the vicinity to gaps (Figure 5, Brüllhardt et al. 2020). If the goal is to retain *Acer spp.* and *Ulmus glabra* poles, one should pay special attention to the often numerous advance regeneration of *Fagus sylvatica*. One option is to create canopy openings together with a thinning from below in advanced *Fagus sylvatica* saplings/poles, so as to reduce their competition.

Due to Dutch elm disease, *Ulmus glabra* is of low interest to forest managers today, but still important for conservation as a threatened species (Thomas et al. 2018). In some mixed forests without *Fagus sylvatica*, *U. glabra* was the third most abundant species before elm disease (Puspure et al. 2016). We found that the species' pole number increased substantially in the vicinity of gaps, suggesting that it depends on the presence of larger gaps (Lygis et al. 2014), although it was found to recruit well in openings <200 m^2 in rather open boreal *Picea abies* forests (Drobyshev 2001). Taking into account the fast closure of small gaps in *Fagus sylvatica* dominated forests (Madsen and Hahn 2008), larger gaps and an early release are needed to maintain *Ulmus glabra* as well as *Acer* spp. in these forests. Consequently, single-tree selection management is unsuitable for maintaining *Acer* spp. and *Ulmus glabra*, as found by Brüllhardt (2021) and Péter-Contesse (1972), and silvicultural systems with larger gaps such as irregular shelterwood are required (Ammer and Weber 1999, El Kateb et al. 2006).

5 CONCLUSION

Under the prevailing single-tree mortality, *Fagus sylvatica* poles replace hosts of its own species (self-replacement) as well as heterospecific hosts such as *Acer* spp. and *Ulmus glabra* in the Uholka forest. This process does not depend on neighbourhood. In contrast, *Acer platanoides* and *U. glabra* are not capable of self-replacement and cannot replace a heterospecific host, while this is possible, to a low degree, for *Acer pseudoplatanus*. The stem diameter of host trees correlates slightly but insignificantly and positively with the number of advance regeneration, while properties of the host neighbourhood, particularly the proximity to dead lying trees and gaps, significantly increases the number of poles and thus the chance for successful replacement of all species. For *Acer* spp. and *U. glabra* saplings, the proximity to dead lying trees and gaps is crucial for successful growth to the pole stage. This implies that in the absence of gap-creating disturbances, the existing population of mature *Acer* spp. and *U. glabra* will be replaced by *F. sylvatica* on the 10-ha plot, and likely also in the Uholka-Shyrokyi Luh reserve as a whole.

As a case study, our results represent a stepping stone towards a more general understanding of beech dominance in primary beech and mixed old-growth forests. Periods of closed canopy conditions filter the regeneration against species with intermediate shade tolerance and progressively enrich the understory with shade-tolerant *F. sylvatica*. Single-tree background mortality is insufficient to foster coexistence in the tree community since it primarily strengthens the status of pre-existing *F. sylvatica* saplings and poles, rather than facilitating the recruitment of mid-shade tolerant species to the canopy. Only disturbances affecting several canopy trees or creating large gaps can ensure that mid-shade tolerant *Acer* spp. and *Ulmus glabra* can grow up and reach the canopy.

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ELECTRONIC SUPPLEMENTARY MATERIAL

S 1. CONVERGENCE DIAGNOSTICS

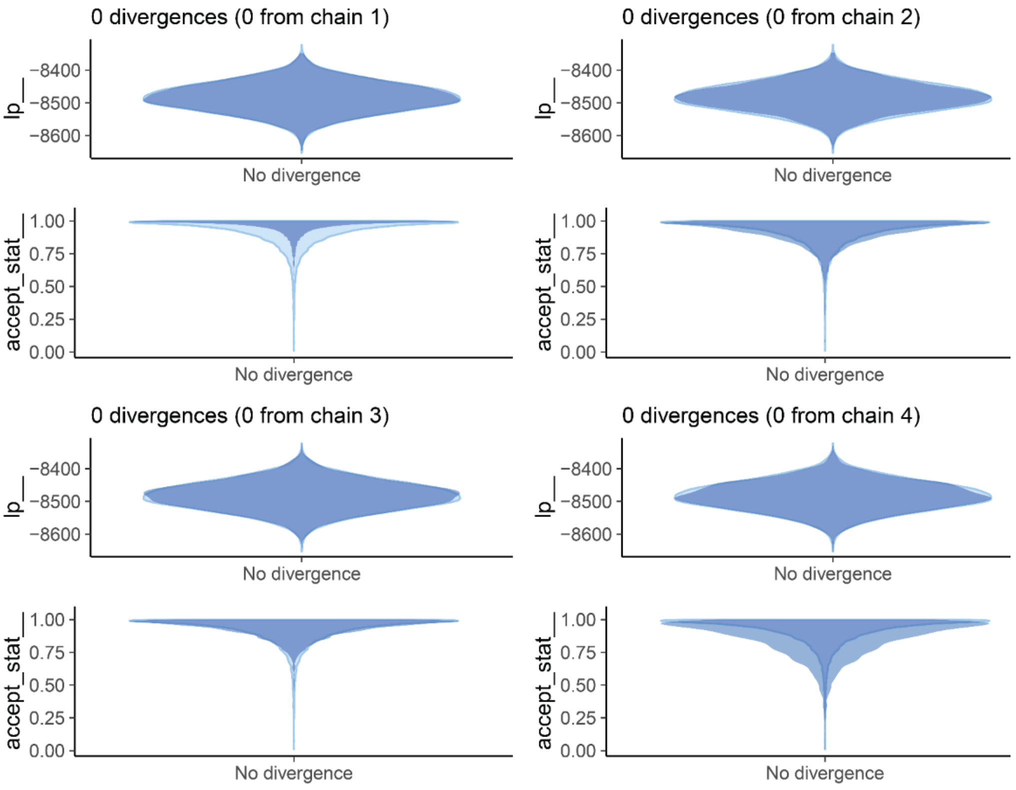


Figure S 1. Zero chains' divergences indicate that all parts of the posterior are being explored.

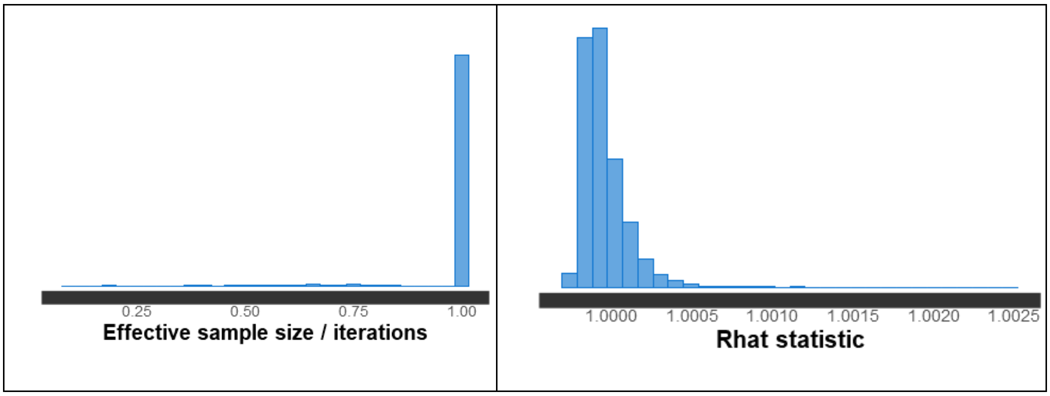


Figure S 2. Left:- effective sample size (N_{eff}) > 0.5 (the larger the ratio of N_{eff} to sample size N the better); right: $\hat{R} \leq 1.1$ indicates that chains have converged to a common distribution.

S 2. AUTOCORRELATION OF CHAINS

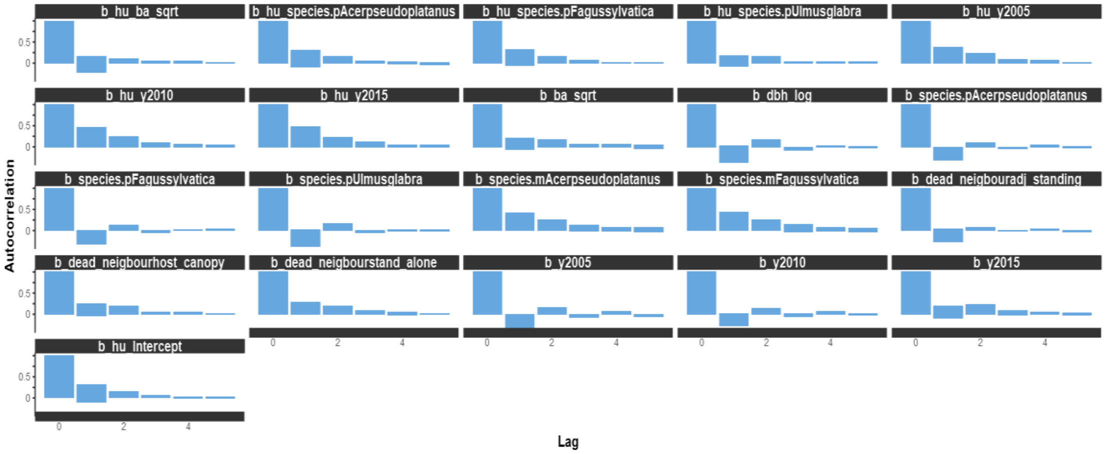


Figure S 3. Autocorrelation of combined chains per model parameter disappears after second lag proving samples independence. Negative autocorrelation is possible as it indicates fast convergence of sample mean towards true mean.

S 3. OVERDISPERSION & ZERO INFLATION

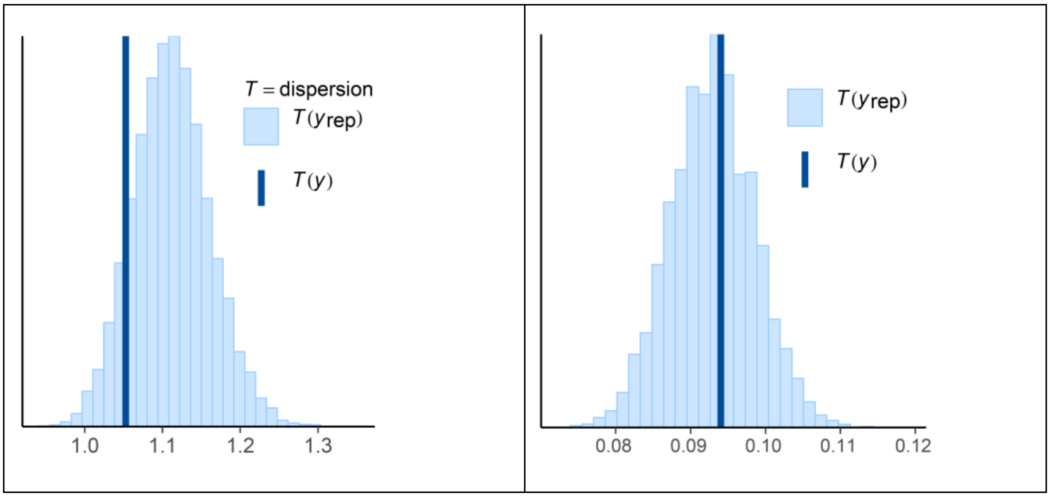


Figure S 49. Left: observed (T(y)) and posterior (T (y_{rep})) dispersions are less than 1.15 that is acceptable for Poisson models (Payne et al. 2018); Right: small zero-inflation of the observed and posterior data.

S 4. MODEL RESIDUALS

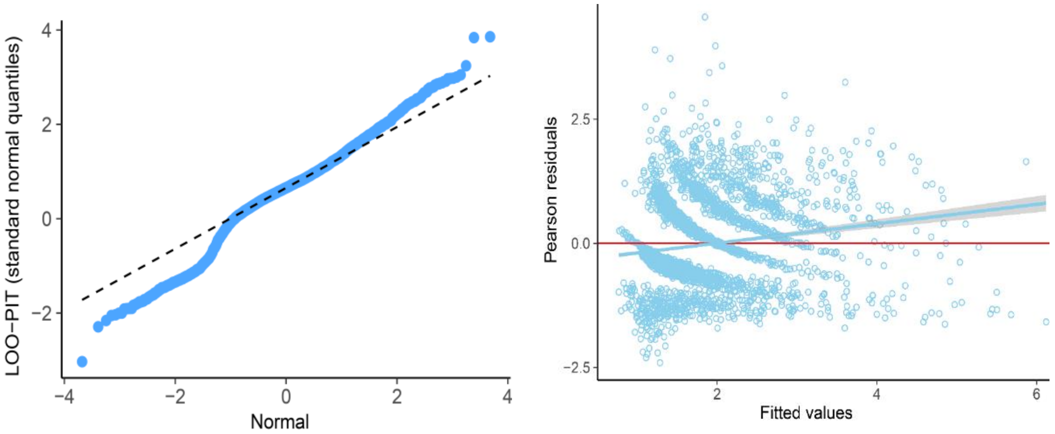


Figure S 5. Left: QQ plot of standardized residuals shows that residuals approximate normal distribution; right: Pearson residuals vs fitted values deviate around zero (red line).

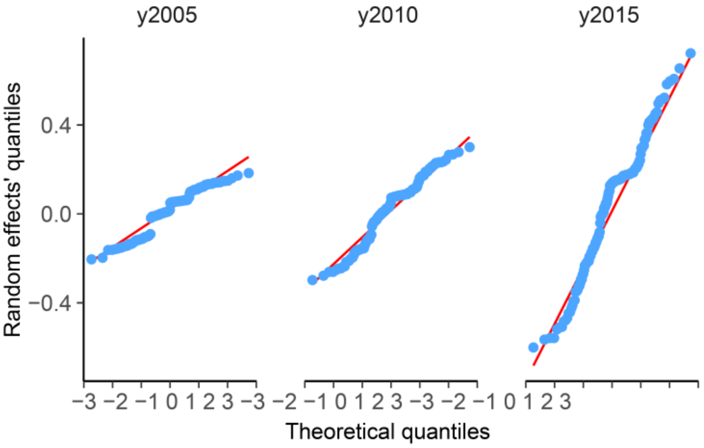
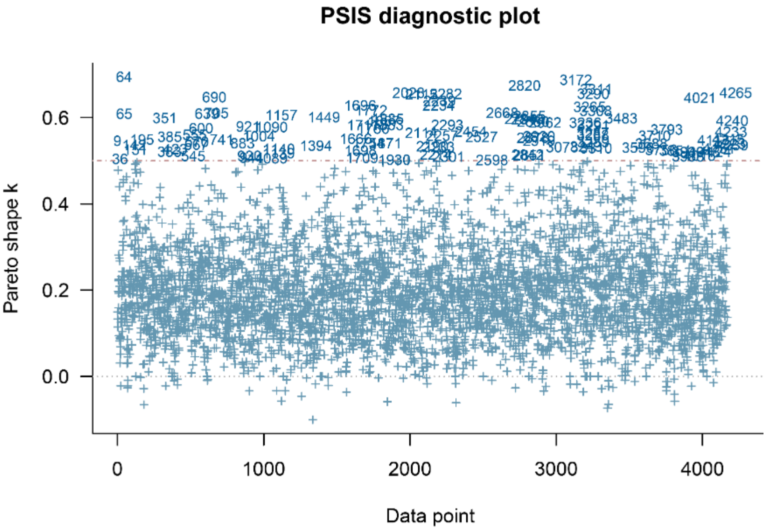


Figure S 6. Residuals of random effects

S 5. MODEL FIT



S 7. The model reliability with Pareto smoothed importance sampling: no overly influential outliers, Pareto shape k is within 0.6 and no more than 0.7. The model is well specified, with useful convergence rates and small Monte Carlo (0.4) error estimates.

S 6. POSTERIOR ANALYSIS

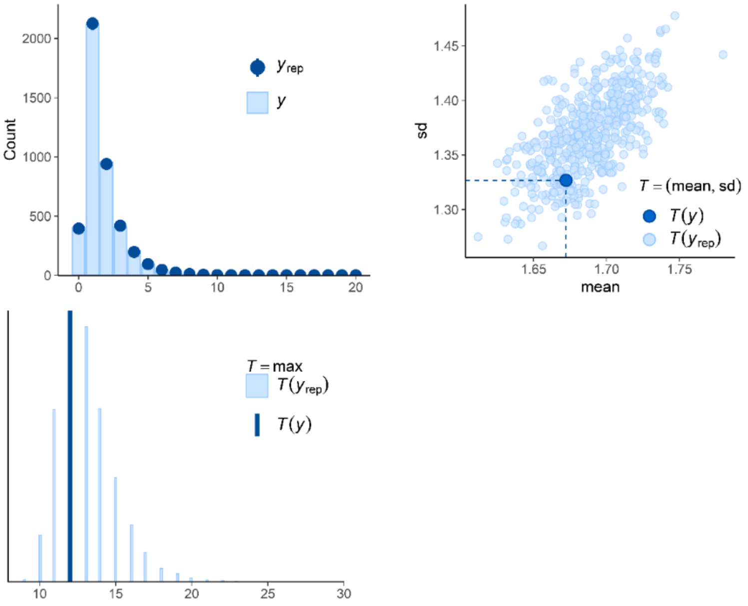


Figure S 8. Upper left: simulated posterior (yrep) fits observed count data (y) well but overestimate number of poles >12; upper right: mean and standard deviation (sd) of posterior overlap observed mean and sd suggesting good model accuracy; bottom left: posterior maximum values are higher than observed maximum values.

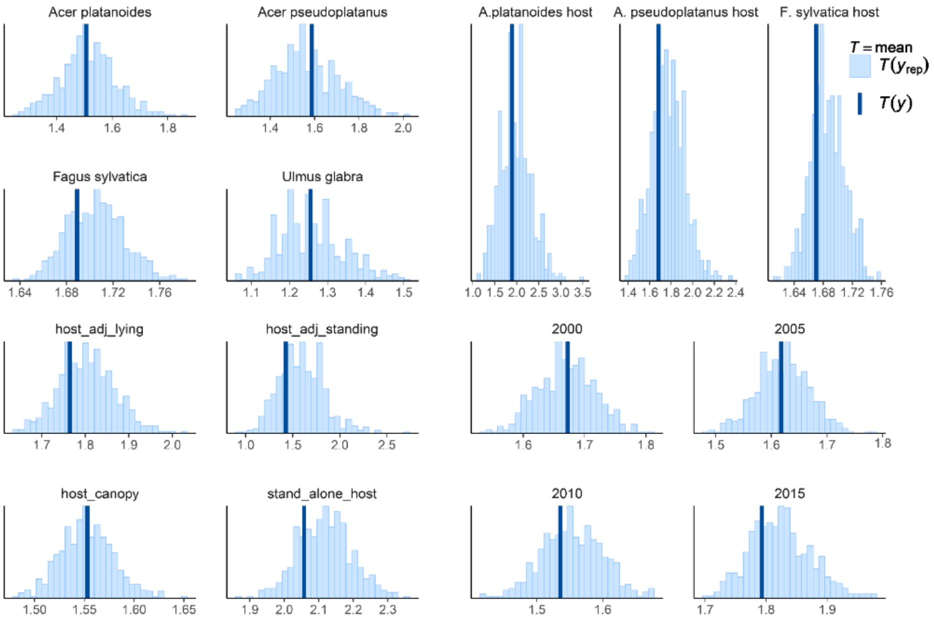


Figure S 9. Posterior means of model parameters (fixed effects) correspond well with observed means indicating a good fit.

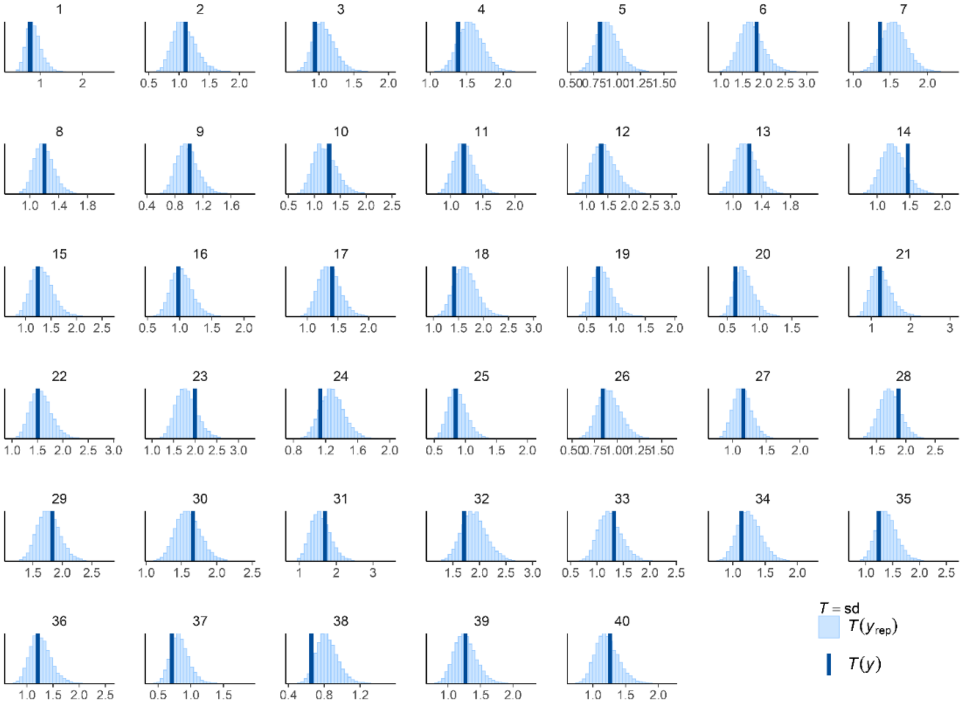


Figure S 10. Posterior standard deviations per subplot correspond to observed deviations suggesting good model accuracy in random effect estimation.

S 7. GAP CLASSIFICATION

For the classification of canopy gaps on the 10 ha plot LiDAR data with a point density of 30 points/m^2 acquired in May 2018 was used. In a first step a vegetation height model (VHM) was calculated based on the subtraction of a digital terrain model (DTM) from a digital surface model (DSM) of the area. Using a canopy height threshold of 15 m the gaps in the area were classified. Meaning that all vegetation below a height of 15 m was classified as a gap.

SYNTHESIS

This thesis focuses on the shade tolerance of juvenile broadleaved trees in deep-shade environments (Figure 2, Introduction). Using the largest remaining primary *Fagus sylvatica* forest as a case study, a comprehensive picture of the traits underlying shade tolerance, and their role in beech dominance in temperate forests, was developed. The approaches applied were the sampling and excavation of juvenile trees on small sampling plots established for this research, which were analysed with dendroecological and chemical methods, and the analysis of the patterns of abundance of tree regeneration under canopy trees on a 10-ha permanent plot. More specifically, i) the effect of species identity, tree age and biomass partitioning to leaves/branches on leaf area ratio, absolute growth rate of tree biomass and storage in stems and roots of naturally regenerated seedlings and saplings growing in deep shade was investigated; also, the impact of the trade-off between absolute growth rate and storage on survival times of three species was studied. Moreover, ii) species-specific mortality rates and survival times of young trees and iii) relative abundance of tree regeneration under canopy trees was assessed as a proxy for the replacement of mature trees by poles. Shade tolerance was studied in all chapters in three species (the dominant *Fagus sylvatica*, and the competitor species *Acer pseudoplatanus* and *A. platanoides*), to which in chapter 3 *Ulmus glabra* was added as a fourth species.

SHADE TOLERANCE IN BROADLEAVED TREES

Shade tolerance is estimated in a wide variety of ways on many different scales, making comparisons difficult (Miyashita and Tateno 2014; Niinemets and Valladares 2006). A high survival rate in deep shade is one of the widely used indicators of shade tolerance (Kobe et al. 1995), but this thesis suggests that survival time is a more universal indicator as it embraces the whole ontogenetical development of a young tree in the understory in contrast to the survival rate that changes over tree size and with age (Seiwa 2007; Walters and Reich 1996) and may be similar for shade- and mid-tolerant species at the seedling stage (Canham et al. 1999; Walters and Reich 1996, 2000). Moreover, a tree-by-tree replacement rate implicitly links shade tolerance to successional processes and dominance of shade-tolerant species.

There is consensus on the traits that influence shade tolerance, but the debate over their relative importance continues (Valladares and Niinemets 2008). In this study, leaf area ratio was found to be suited better than other leaf traits to explain constraints of photosynthate supply to growth and storage in deep shade. The trade-off between growth rate and storage leading to carbon starvation is much debated in studies on drought but was not fully explored in research on shade tolerance, particular in ontogeny (Valladares and Niinemets 2008; Weber et al. 2018, 2019). Today, the shade tolerance of a plant is usually defined as the minimum light under which it can survive (Valladares et al. 2016) or features low mortality at slow growth (Pacala et al. 1996). However, my findings suggest that shade tolerance involves a more complex interplay, i.e. a balancing act between leaf area ratio, growth rate, and storage during ontogenetical development.

TRAITS DEVELOPMENT IN SHADE

High leaf area ratio, low absolute growth rate, and storage in stems and roots are well-known traits associated with shade tolerance (Valladares and Niinemets 2008) in juvenile trees facing deep shade (mean diffuse light 2-3%). My investigations were based on a relatively large sample of fully excavated juvenile trees in the height range from 0 to 5 m, thus not only using seedlings, which is done in 75% of the papers on biomass development in juvenile trees (Gibert et al. 2016). Furthermore, while previous studies have focused on one or two shade tolerance traits (Valladares and Niinemets 2008), I combined leaf, growth and storage traits and studied their development to arrive at a more comprehensive assessment.

Fagus sylvatica pursues a light-harvesting and space occupation strategy, allocating more biomass to leaves and branches to create a high leaf area and large crown, while keeping a low absolute growth rate, and consequently allocating less biomass to the storage in the stems and roots. As a result, it maintains a high ratio of leaf area to biomass and its capacity to produce photosynthates is well balanced and allows capturing carbon for both growth and storage. Consequently, the trade-off between growth and storage, which may occur in plants surviving in the shade for decades (Palacio et al. 2014), does not occur or is avoided in time.

High biomass allocation to leaves and branches was also found for *Fagus grandifolia* saplings

(Messier and Nikinmaa 2000; Takahashi and Lechowicz 2008) in eastern North American forests. Like European beech, *Fagus grandifolia* saplings allocate less biomass to stem with height when growing in shade (Messier and Nikinmaa 2000). Similar patterns of biomass allocation were observed in *Fagus crenata*, a dominant species in northeastern Japanese forests. In the shade, its seedlings showed the lowest total biomass growth and storage content at comparatively high leaf area when compared with mid-shade tolerant species (Takahashi and Goto 2012). This suggests that the low light environment drives similar biomass allocation patterns to leaves/branches and growth rate in ontogeny across the *Fagus* genus, resulting in a generally high survival time of juvenile trees in the understory.

In Chapter 1, the survival time of *Fagus sylvatica* juveniles was projected to be more than two decades longer than that of its competitor species. By applying survival analysis in Chapter 2, the mean survival time of *Fagus sylvatica* was estimated at 72 years, while that of *Acer* spp. was 47-48 years, which was in line with projections of *Acer* spp. survival times in Chapter 1. While survival time can be estimated by two methods, both are somewhat biased: The method in Chapter 1 used subjectively chosen saplings of high and low vitality, while the Survival analysis in Chapter 2 was based on the reconstructed leaf area ratios of low vitality trees. Both approaches were used in a complementary fashion to make up for the fact that long-term plots in which regeneration is tracked individually, which would enable the direct measurement of mortality and survival time, are very rare in European old-growth forests (but cf. ForestGEO 2021).

In the understory, the survival time of juvenile *Fagus grandifolia* was estimated on average at 66-80 years (Canham 1990) and ranging up to 121 years (Poulson and Platt 1989, 1996). The same pattern was shown for modelled survival time (125 years) at low radial growth (Lin et al. 2001). *Fagus crenata* on average persisted up to 120 years in the understory before canopy release (Peters et al. 1992). High survival times of juvenile trees in the Fagus genus may be caused by similar biomass allocation patterns in ontogeny and the absence of carbon limitation in deep shade.

REGENERATION MORTALITY IN THE SHADE

In this study, the mortality and survival times of juvenile trees (*Acer platanoides*, *A. pseudoplatanus* and *Fagus sylvatica*) were assessed from the seedling to the sapling stage based on leaf and growth traits associated with shade tolerance. In previous studies, models of regeneration mortality had been based on a retrospective approach and the assumption of decreased radial growth of a juvenile tree prior to death (Dekker et al. 2009; Kunstler et al. 2005; Petriţan et al. 2007). For the first time, in this study not only radial growth but also leaf area ratio was used as a covariate, providing more comprehensive insights into the complex mechanisms underlying mortality. In *F. sylvatica*, the age-specific mortality rate over 3 years increased slowly, reaching 0.036 events (i.e., the conditional probability of death was 3.6%) at 40-50 years. In contrast, the age-specific mortality rate over three years for *Acer* spp*.* increased rapidly, reaching 0.07-0.08 events at an age of 40-50 years. A lower age-specific mortality rate in *Fagus sylvatica* corresponded to a higher leaf area ratio and height, while higher mortality rates in *Acer* spp. were related to higher allocation of biomass to radial growth, and lower allocation to leaves (lower leaf area ratio). These findings contradict earlier research that reported increased survival with increased radial growth at light levels higher than 3% of diffuse radiation (Kunstler et al. 2005; Petriţan et al. 2007). In my study, slow growth was found advantageous in the long-term at mean diffuse radiation (2-3%) due to low maintenance and respiration costs. Thus, shade-tolerant species are able to reduce growth (and respiration) more efficiently than shade-intolerant ones (Rodríguez-Calcerrada et al. 2019; Valladares and Niinemets 2008).

In contrast, a weak correlation between juvenile *Fagus grandifolia* growth and mortality has been reported in several studies conducted along a wide light gradient. Its probability of mortality was estimated at 1% at low radial growth (Lin et al. 2001) and varied from 1.4% to 10% for 2.5 years (Kobe et al. 1995) or from 0% to 1.8% over 10 years (Duchesne et al. 2005). Low mortality at low and high light levels implies that both *Fagus* species may have similar light thresholds that result in a strong control of radial growth and the maintenance of high leaf area at low light but relatively high growth at high light when there is no need to save on carbon.

ABUNDANCE OF ADVANCE REGENERATION UNDER CANOPY TREES

The absolute and relative abundance of advance regeneration of different species under a canopy tree is implicitly related to the probability of replacement of the canopy tree in forests

with small-scale disturbances. In chapter 2, the mortality rate of *Fagus sylvatica* was estimated only for juvenile trees, while chapter 3 evaluated the probability of absence/presence of living and dead saplings and poles, and thus sought to identify the average number of potential successor trees of each species for a canopy tree, thus approximating a replacement probability. The abundance of advance regeneration was assessed for *Fagus sylvatica* and its competitor species *Acer platanoides*, *A. pseudoplatanus,* and *Ulmus glabra* based on longitudinal data from a permanent 10 ha plot.

In this study, the position of all canopy trees ('host', dbh >25 cm) was linked to saplings and poles growing below or around that tree. Also, the position of hosts was linked to living/dead neighbouring trees (>25 cm dbh). Depending on the neighbourhood, a pole beneath a host tree may grow better if more light was available, i.e. when it is located near a dead lying tree or under a stand-alone host, and less if surrounded by living mature trees. Therefore, this study modelled the replacement of a host tree i) in the canopy, ii) in vicinity to lying/standing dead tree(s), or iii) in a gap if there are no living/dead neighbouring trees. This provided more comprehensive results than previous research that had focused either on tree replacement under the canopy (Culver 1981; Fox 1977; Horn 1975; Woods 1984) or in gaps only (Lertzman 1992, 1995). Unlike previous studies (e.g., Busing 1996; Nagel et al. 2010), I did not assume that the presence of one successor sapling/pole underneath a host tree suggests that this sapling/pole will indeed replace the host. Instead, I accounted for the population of all saplings and pole-stage trees, thus yielding a more accurate estimation of the successor species based on Bayesian statistics.

In general, a tree replacement event assumes the presence of at least one sapling/pole under a host, depending on its neighbourhood. The amount of advance regeneration under trees in different neighbourhoods was found to be lower for poles than for saplings. Also, there was a clearly higher amount of advance regeneration under hosts with increasing diameter. In shaded conditions, *Fagus sylvatica* poles have the highest chances to be a successor in the canopy if its host has a dbh >80 cm, while neither *Acer* spp. nor *Ulmus glabra* saplings can recruit to the pole stage under these conditions. Moreover, *Fagus sylvatica* poles have also a high chance to replace a host when it is adjacent to a dead lying tree or under a stand-alone host that is presumably located in a gap. Currently, only *Fagus sylvatica* poles are growing under heterospecific hosts on the 10-ha plot. Hence, competitive replacement of heterospecific hosts by *Fagus sylvatica* advance regeneration is likely to occur, irrespective of the neighbourhood. Unlike in *Fagus sylvatica*, the low numbers of *Acer spp. and Ulmus glabra* poles in shaded conditions most likely render replacement by these species a very rare event. By contrast, *Acer* spp. can recruit to the pole stage and be successful in canopy replacement only if a host has a dbh >80 cm and is adjacent to a dead lying tree or a stand-alone host. Therefore, beech poles will replace most mature competitor trees currently growing on the 10-ha plot. Nevertheless, poles of competitor species that established in gaps are at least partly able to grow into the canopy at the current disturbance rate of 7% after two subsequent windfalls, which will maintain a small population of minor species in the long-term.

In short, autogenic succession with anthropogenic influence is generally observed in European old-growth forests (Vrška et al. 2009), where *Fagus sylvatica* dominates in the understory (chapters 1, 2) and excludes other species from the canopy (chapter 3) under low canopy disturbance rate (Figure 2, Introduction). On the contrary, tree-by-tree replacement of *Fagus grandifolia* in northeastern America for the last 100 years of twenty century was characterized by allogenic co-existence with anthropogenic influence (McLachlan et al. 2000; Poulson and Platt 1996), where species abundance changes with intensive and more frequent canopy disturbance, thus enabling less shade-tolerant *Acer saccharum* to replace *Fagus grandifolia* and vice versa (Woods 1979). However, more recently, several studies have reported an abrupt increase in *Fagus grandifolia* regeneration and pole density as a response to the rising frequency of release events during 1990–2000 and *Acer saccharum* regeneration failure 40 years ago (Beaudet et al. 1999, 2007; Duchesne et al. 2005; Gravel et al. 2010, 2011). A double increase in *Fagus grandifolia* pole density (ibid.) suggests that this species may use similar competitive mechanisms described in the three chapters of the thesis, and respond quickly to the change in the canopy light regime.

IMPLICATIONS OF THE FINDINGS FOR BEECH FORESTS IN A CHANGING CLIMATE

Overall, this thesis highlights a set of external factors, such as low canopy disturbance and short- and long-term human impacts (Figure 2, Introduction) that may exacerbate adverse environmental conditions for competitor species and promote the competitiveness of dominant species. However, anthropogenic climate change (IPCC 2018) may downscale the

importance of shade tolerance and the competitive advantage of *Fagus sylvatica*. Specifically, under enhanced drought and shade, tree replacement may slow down or fail due to an overall lower growth of *Fagus sylvatica* regeneration or a low abundance of saplings and a lower recruitment rate of saplings to pole size.

Microclimatic buffering in the understory (De Frenne et al. 2013, 2021; Von Arx et al. 2013) and the high phenotypic plasticity of *Fagus sylvatica* (Robson et al. 2012; Wang et al. 2020) as a result of its stress-memory (past experiences of an individual that influence resistance, resilience and recovery) and priming (phenotypic adjustment of an organism which confers it an improved response to future stress, Gessler et al. 2020) enables juvenile trees to acclimate to multi-year droughts such as 2018-2019 (Beloiu et al. 2020) and to resist to climatic stress e.g. at the species' southern distribution limit (Čater and Levanič 2019). Under drought, the leaf area of *Fagus sylvatica* strongly decreases (defoliation and crown dieback, Chakraborty et al. 2013; Kohler et al. 2006), its metabolism slows down (Barigah et al. 2006, 2013; Goisser et al. 2013) storage increases reducing growth (Liu et al. 2017; Zang 2014). In fact, after subsequent droughts, xylem conduits in saplings become narrower in diameter to avoid hydraulic failure, resulting in lower radial growth (Schuldt et al. 2016). This implies that the trade-off between growth and storage, as assumed in Chapter 1, can in fact hardly occur under drought and shade as growth is under strong adaptive control. The changes in xylem anatomy and the strategy to preserve storage pools to the detriment of growth could explain the low annual mortality of *Fagus sylvatica* saplings (4.8%) after 3 years in an experiment with severe soil water deficit (Chuste et al. 2020) and after the strong drought of 2003 (5%, Czajkowski et al. 2005). Hence, the survival time and mortality of *Fagus sylvatica* would largely depend on storage and the recovery of leaf area. However, crown dieback (Chakraborty et al. 2013) can hamper the recovery of leaf area, thus undermining vitality and storage replenishment, eventually shortening the survival time of juvenile trees under drought and shade.

Seedlings of *Acer platanoides* were reported to invest more biomass in stem and root growth under drought than *A. pseudoplatanus* (Carón et al. 2015), which confers them a higher drought tolerance. However, faster growth requires more carbon and water (Goisser et al. 2013) under drought and shade. Thus, in the long-term, allocation in favour of growth and storage at the expense of leaf area leads to the trade-off proposed in Chapter 1, and would diminish the survival time of *Acer* spp. compared to *Fagus sylvatica* under drought and shade.

Although the replacement of individual canopy trees is an important mechanism of *Fagus sylvatica* dominance, under climate change its competitive strength may change, promoting species with higher growth under frequent canopy disturbance (Cavin et al. 2013). Frequent abiotic disturbance in combination with drought-induced canopy dieback (Carnicer et al. 2011; Senf et al. 2018) and forest management (e.g. shelterwood or salvage logging) may create canopies that are more open than under the current disturbance regime. So far, the climate-driven tree mortality seems to be relatively low (NW-FVA 2018, 2019) and recovery times are remarkably short (on average 4 years, Anderegg et al. 2016; Fischer et al. 2009; Lakatos and Molnár 2009). The mean mortality of 1.3% of *Fagus sylvatica* under multi-year droughts (1947-49, 1959-61, 1989-91, 2001-03, Moravec et al. 2021) in Switzerland (Etzold et al. 2019) or the highest regional mean mortality of 1.9% in the canton Basel (Wohlgemuth et al. 2020) suggests rather small canopy openings, on average ca. one dead tree per 200 living trees (Braun et al. 2020; Denzler et al. 2019) or maximum 3-4 dead trees per 200 living trees at the highest known regional mortality (Wohlgemuth et al. 2020). However, the tree size and crown dimension of the dying trees is likely to affect potential changes in species composition in mature *Fagus sylvatica* stands. A cohort mortality of 3-4 old trees with a mean crown area 184 m^2 (Chapter 3) each would create a medium-size interconnected gap, suitable for the recruitment to the canopy of all four species studied here (*Fagus sylvatica*, *Acer* spp. and *Ulmus glabra,* Chapter 3). However, in younger stands (mean tree crown area 68 m^2, Chapter 3), the canopy openings would tend to be smaller and diffuse, favouring the replacement mostly by *Fagus sylvatica.* Therefore, patchy die-off of *Fagus sylvatica* may not lead to a shift in canopy dominance or species composition in the core habitats of *Fagus sylvatica*, provided recurrent intensive fires or large-scale wind disturbances do not occur.

To summarize, this thesis highlights the importance of shade tolerance for the dominance of *Fagus sylvatica* and the compatitive advantages of this species in European temperate forests, i.e. i) long survival time, ii) low mortality; iii) high abundance of advance regeneration suggesting not only self-replacement but also replacement of heterospecific tree species. In a changing climate these competitive mechanisms may not play out as much as in the past. Climate change may reduce fecundity (Clark et al. 2021) and germination

rate (Classen et al. 2010; Muffler et al. 2021), thus increasing the importance of specific mycorrhiza and root traits (Swaty et al. 2004) in drought resistance. To conclude, such effects of climate change have the potential to reduce the importance of shade tolerance in species dominance (Figure 2, Introduction), especially in the case of frequent and severe canopy disturbance.

RECOMMENDATIONS FOR FURTHER RESEARCH

Specific recommendations were made in each chapter of this thesis. Here, I would like to emphasize the most important issues.

i. Long-term regeneration plots with labelled seedlings and saplings are needed to improve mortality predictions and foster the understanding of juvenile tree health, mortality and survival times under climate change. Hülsmann et al. (2016) has already addressed this issue in detail. Within the ForestGEO network (ForestGEO 2021), there are four plots with labelled regeneration of > 1 cm dbh in Europe. However, only one of them represents old-growth forests, while the others are in different stages of transition to old-growth forests. Furthermore, the height treshold >50 cm can be a compromise between the amount of field work needed to tag regeneration and important data on seedling dynamics.

ii. The monitoring of understory microclimate and soil moisture (De Frenne et al. 2013, 2021; Harwood et al. 2014) is critical to better understand regeneration mortality, health status, and abundance dynamics under drought and shade. In addition to the more intensive monitoring of juvenile trees (see point i), this would require the establishment of a network of meteorological stations under canopy in different forest types. In Switzerland, stand microclimate is already measured on eleven Level II monitoring plots in different forest types (Von Arx et al. 2013). This also implies that the mortality of juvenile trees observed in greenhouse experiment (Bolte et al. 2016) or at the forest edge (Von Wühlisch 2012) may be systematically biased as such approaches do not account for understory microclimates.

iii. Mimicking microclimate data is urgently needed in long-term greenhouse and forest experiments where the sensitivity of several species to drought and shade is tested. Numerous short-term experiments had several systematic biases in their design setup.

First, almost all of them did not provide shade (if provided, >30% of diffuse light is too high for mean light levels in forests) when testing for germination and survival of *Acer* spp. seedlings (Carón 2014), phenotypic plasticity of *Fagus sylvatica* provenances (Bolte et al. 2016; Harter et al. 2015; Rose et al. 2009; Thiel et al. 2014; Tognetti et al. 1995; Varsamis et al. 2019) or its water-deficit tolerance (Pšidová et al. 2015). Second, most of such experiments did not provide time for root acclimation when re-potted seedlings from open-air nurseries were used; therefore, tests were run on already stressed plants. Goisser et al. (2013) has addressed this problem in detail. Third, all afore-mentioned experiments focused exclusively on the seedling stage, without comparison with other species, except for (Carón 2014), and were short-term. For example, the long-term forest study with throughfall manipulation by Hanson et al. (2001) targeted several species in the sapling and pole stages.

iv. To understand the combined effects of drought and shade on juvenile trees in the forest understory and in gaps of different size, and thus in a management context, new experiments with canopy openings of different size should be established in conifer and broadleaved forests on a long-term basis. Here, regeneration abundance and mortality should be evaluated both in understory and gaps in the absence and presence of drought. Drought- and shade-acclimated advance saplings may be sensitive to change in the light environment, which may induce a sharp increase in transpirative demand. It is important to study both conifer and broadleaved forests since they mediate drought effects on stand microclimate to a different extent (Von Arx et al. 2013).

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Education

2017- till present	PhD in Environmental Systems Science, ETH Zurich, Switzerland
2014-2016	MSc in Tropical Forestry and Management, Dresden University of Technology, Germany
2000 - 2002	MSc in Environmental Science, National University of Kyiv-Mohyla Academy, Ukraine
1995 - 1999	BSc in Biology, National University of Kyiv-Mohyla Academy, Ukraine

Background

10.2017 - till present

PhD, Swiss Federal Institute for Forest, Snow and Landscape Research WSL and ETH Zurich

- Lead research on beech dominance in prime and old-growth forests of Europe
- Assist in the organization of the international conference on old-growth forests.

03.2017-10.2017

Project co-ordinator, Institute of International Forestry and Forest Products, Dresden University of Technology, Germany

- Liaise the research team on technological, genetical and production improvements in bamboo value chains in Vietnam
- Draft an application for a grant and submit it to the Ministry of Education and Research, Germany
- Report budget changes to the Ministry

10.2010 – 09.2014

Group brand manager, First Private Brewery, Kyiv, Ukraine

- Define strategy for incumbent brands, based on the market data and in line with the company strategic planning
- Plan and implement brands budgeting. Control budget spending, take corrective actions
- Verify developed strategies with the changing market environment and adapt them respectively, under the supervision of Marketing Director

- Liaise with suppliers and departments (Production, Trade Marketing, Procurement, Finance, etc.) to ensure timely and high-quality implementation of marketing campaigns
- Brief external business partners i.e. agencies for brand objectives and control implementation of brand activities
- Coach and supervise the team of 2 persons.

07.2007-09.2010

Marketing Director, Mareven Food Ukraine, Kyiv, Ukraine

- Develop annual brands & product strategy in accordance with targets set for the brands
- P&L responsible: run product portfolio analysis to identify gaps, weak performers, initiate appropriate actions
- Lead & coordinate cooperation with R&D and Production departments
- Adapt procedures and processes for ISO 9001:2008, ISO 22000:2005
- Initiate and conduct consumer and retail studies in cooperation with research agency, report results and take appropriate actions
- Supervise the team of 2 persons.

01.2002 – 06.2007

Brand Manager for Family Care (Kleenex brand), Kimberly-Clark Ukraine, Kyiv, Ukraine

- Maximize brand value by developing and executing effective brand initiatives, positive market share development vs. competition
- Agree on financial and brand health targets, deliver volume, share, market profit and brand health targets consistent with the Plan
- Manage product marketing mix within the brand, P&L responsible, run product portfolio analysis to identify gaps, weak performers, initiate appropriate actions
- Liaise with advertising agencies to develop media strategy, provide input into media planning and buying
- Conduct in-depth analysis of the category, the brand, consumers, and competitors
- Translate specific tasks into creative, media, BTL brief; cooperate with Sale and Trade Marketing to ensure excellent execution; assess results
- Developing additional business opportunities to generate upsides to the Plan
- Coach distributors’ teams and the promo-coordinators team.

01.1999 – 12.2001

Account Manager (P&G’s brands: Ariel, Pampers, Comet), Saatchi & Saatchi advertising agency, Kyiv, Ukraine

- Develop creative strategy for local initiatives of Procter & Gamble brands

- Produce local TV commercial, print layouts, POP materials production.
- Adapt TV, print, and POP materials
- Conduct in-depth analysis on brands’ health, consumers, and competitors
- Liaise with the non-government organization (Association of Pediatrics) for development of the local brand initiatives.

Languages	**Ukrainian** – native **English** – advanced **German** – intermediate	**French** - basic **Russian** – fluent

Professional courses

1. Carbon Forestry at the University of Freiburg (2018, Germany)
2. FSC Forest Management course for auditors (2020, NEPCon/Forest Alliance)

Skills and abilities

Fast learner, good organisational and time management skills with an eye for detail, communication and inter-personal skills. Advanced user of PC, R, ArcGIS, basics of Python, driver license category B.

Birmensdorf 2021