Waldökologie, Landschaftsforschung und Naturschutz	Heft 24 (2026)	S. 61–84	6 Fig. 5 Tab. + Anhang
			urn:nbn:de:0041-2511131855338.955343304039

Scopus Indexed Journal

Waldökologie, Landschaftsforschung und Naturschutz – *Forest Ecology, Landscape Research and Nature Conservation*

www.afsv.de/index.php/waldoekologie-landschaftsforschung-und-naturschutz

Long-term development of light-demanding tree species in unmanaged forests

Langfristige Entwicklung von Lichtbaumarten in unbewirtschafteten Wäldern

Markus Blaschke, Klaus Striepen, Andreas Mölder, Marcus Schmidt, Anne Wevell von Krüger and Peter Meyer

Abstract

The differing capacities of trees and shrubs to create and tolerate shade have been recognized for centuries and are currently integrated into silvicultural concepts. Due to the long history of forest management in Central European forests, little is known about the long-term development of light-demanding tree species in unmanaged forests. We provide an updated categorization of light-demanding tree species through a literature review and then analyze their development in strict forest reserves as a function of forest type and site conditions.

We analyzed tree inventory data from 219 strict forest reserves, mainly mixed stands, from ten federal states, covering a wide range of time since abandonment (13–167 years) and site conditions. The analysis was restricted to the first and the last inventory to maximize the time span of the analysis (6–43 years). We calculated the net annual rates of change in basal area and stem number for each tree species and summarized them according to their assignment to the light species class.

The development of light-demanding tree species lagged behind that of shade-tolerant tree species. The stem number of light-demanding species decreased faster than that of shade-tolerant species, and there was no significant annual increase in basal area of light-demanding species, whereas the basal area of shade-tolerant species increased by about 1% per year. This resulted in a decreasing proportion of light-demanding tree species over time. Based on the large number of forests studied at different sites and with different tree species composition, we interpret the increasing dominance of shade-tolerant species as a major successional trend in strict forest reserves after management cessation. We found no clear evidence for a differential development of light-demanding species along nutrient or moisture gradients.

Surprisingly, the displacement of light-demanding tree species in unmanaged mixed stands appears to be rather slow. However, the general trend supports the view that active forest management is needed to maintain light-demanding tree species in mixed stands with shade-tolerant tree species.

Keywords: *Long-term research, Forest ecology, Forest inventory, Close-to-nature forest management, Nature conservation, Natural forest development, Strict forest reserves*

Zusammenfassung

Die unterschiedliche Fähigkeit von Bäumen und Sträuchern, Schatten zu spenden aber auch zu tolerieren, ist seit Jahrhunderten bekannt und wird in vielen waldbaulichen Konzepten berücksichtigt. Trotz der langen Geschichte der Waldbewirtschaftung in mitteleuropäischen Wäldern ist allerdings wenig über die langfristige Entwicklung von Lichtbaumarten in unbewirtschafteten Wäldern bekannt. Vor diesem Hintergrund wurde zunächst durch eine Literaturstudie eine aktualisierte Kategorisierung der Lichtbedürfnisse der mitteleuropäischen Baumarten vorgenommen. Anschließend wurde die Entwicklung der Baumartenanteile der einzelnen Lichtklassen in Naturwaldreservaten in Abhängigkeit vom Waldtyp und den Standortbedingungen analysiert.

Zur Verfügung standen Bestandesinventurdaten von 219 Naturwaldreservaten aus zehn Bundesländern, in denen seit 13 bis 167 Jahren auf die Nutzung verzichtet wird und die zahlreiche Standorte umfassen. Die Analysen schlossen jeweils die erste und die letzte Bauminventur für jede Fläche mit einer Zeitspanne von 6 bis 43 Jahren ein. Die jährlichen Nettoveränderungsraten von Grundflächen und Stammzahlen jeder Lichtartenklasse wurden einander gegenübergestellt.

Die Ergebnisse zeigen, dass die Entwicklung der lichtbedürftigen Baumarten hinter der der schattentoleranten Baumarten zurückblieb. Die Anzahl der Stämme lichtbedürftiger Arten nahm stärker ab als die der schattentoleranten Arten, und ihre Grundfläche stagnierte, während die Grundfläche der schattentoleranten Arten um etwa 1 % pro Jahr zugenommen hatte. Dies führte dazu, dass der Anteil der lichtbedürftigen

Baumarten im Laufe der Zeit abnahm. Aufgrund der großen Anzahl von Wäldern, die auf verschiedenen Standorten und mit unterschiedlicher Baumartenzusammensetzung untersucht wurden, interpretieren wir die zunehmende Bedeutung schattentoleranter Arten als einen wichtigen Sukzessionstrend in Naturwaldreservaten nach Einstellung der Bewirtschaftung. Im Zusammenhang mit verschiedenen Nährstoff- und Feuchtigkeitsklassen zeigte sich keine unterschiedliche Entwicklung der lichtbedürftigen Arten.

Die Verdrängung von lichtbedürftigen Baumarten scheint in Mischwäldern mit natürlicher Entwicklung eher langsam zu verlaufen. Der allgemeine Trend spricht jedoch dafür, dass die Erhaltung von lichtbedürftigen Baumarten in Mischbeständen mit schattentoleranten Baumarten eine aktive Waldbewirtschaftung und damit eine Steuerung der Baumartenzusammensatzung erfordert.

Schlüsselwörter: Langzeitforschung, natürliche Waldentwicklung, naturnahe Forstwirtschaft, Naturwaldreservate, Waldinventuren, Waldnaturschutz, Waldökologie

1 Introduction

The varying ability of trees and shrubs to create and tolerate shade has been known for centuries (Schwappach 1886, Seidensticker 1886). Drawing on earlier work by Seidensticker (1849), Heyer (1852) introduced the first hierarchical classification of tree species according to their shade tolerance, making a general distinction between light-demanding and shade-tolerant tree species. Heyer's definitions are still valid today: "The behaviours of tree species with regard to light and shade are reflected in the denser or lighter shape of tree crowns, in the ability of suppressed trunks and branches to remain alive for longer periods and in the ability of young plants to thrive in the shade of older trees." Although the assessment of most tree species has remained unchanged since the 19th century, some species remain controversial, particularly the intermediate species that fall between light-demanding and shade-tolerant trees (Fürst 1905, Ewald 2007, Bartsch and Röhrig 2016).

Light-demanding tree species are a focal topic in discussions about forest ecology and management. They play an important role in reforestation after large disturbances like storms or bark beetle infestations (Tiebel et al. 2020), in terms of appropriate thinning intensities (Niccoli et al. 2020), and in the context of biodiversity conservation (Brändle and Brandl 2001, Mölder et al. 2019). Increasing their proportion can improve light availability in mixed stands, thus promoting natural regeneration and structural diversity (Wagner and Huth 2010). However, maintaining light-demanding tree species in mixed stands with shade-tolerant tree species requires active forest management (Lüpke 1998). This is particularly true for late-successional, light-demanding tree species such as pedunculate (*Quercus robur*) and sessile oak (*Q. petraea*), which are important for the production of high-quality timber and highly valued for their rich and specialized biodiversity (Löf et al. 2016, Mölder et al. 2019). The importance of light-demanding pioneer species like birches (*Betula* sp.) or rowan (*Sorbus aucuparia*) for the reforestation of large, disturbed areas or clear-cuts is well known (Fischer and Fischer 2012, Tiebel et al. 2020). They accelerate the recovery of a humid forest microclimate and facilitate the establishment of late successional species (Tiebel 2020). In terms of adapting forest management to climate change, drought-resistant, light-demanding tree species such as *Quercus petraea* are considered important because they can tolerate more frequent and longer drought periods (Leuschner et al. 2024).

However, there has been little research on the long-term development of light-demanding tree species, both as species and on the individual tree level, in unmanaged semi-natural forests in Central Europe. Rohner et al. (2012) analysed fifty years of natural succession in Swiss strict forest reserves and found that oak mortality increased with stand basal area. This was explained by the higher light demand of oak and the lower relative competitiveness of oak compared to beech (*Fagus sylvatica*). Meyer et al. (2021) obtained similar results in their study on strict forest reserves in northwestern Germany fifty years after management was abandoned. They discovered that the mortality rate of oak and other light-demanding tree species in the canopy layer was disproportionately high, while the opposite was true for beech. A better understanding of the self-regulated dynamics of light-demanding tree species is therefore needed to support near-natural forest management.

Given the current state of research, the first step of this study was to provide an updated categorisation of light-demanding tree species through a literature review. The second step involved testing the following hypotheses using a large dataset from strict forest reserves across Germany. We expected in strict forest reserves:

- That the proportions (stem numbers and basal area) of light-demanding tree species decrease.
- Different developments of the light-demanding tree species along the nutrient and moisture gradients.
- Different developments of the light-demanding tree species regarding different forest vegetation types (beech and oak forests).

2 Materials and Methods

2.1 Light-demanding trees in the literature

A closer look at the term 'light-demanding tree species' reveals that there is no consistent definition in scientific publications. Fischer (1995) refers to "types of light wood" that require high levels of irradiation for germination and establishment. Burschel and Huss (1997) define light-demanding tree species as those whose crowns allow a high proportion of solar radiation to reach the ground and allow the establishment of a species-rich herb layer. Ellenberg (1996) emphasizes the shade-providing characteristics of different tree species. He also points to the definition of species that are particularly in need of light during the rejuvenation phase. Bartsch and Röhrig (2016) group tree species according to their shade tolerance during juvenile growth. According to the framework of the German Federal Forest Inventory, light-demanding tree species are those that appear for a limited time and space during the pioneering phases of natural forest development (Kroiher and Schmitz 2015). Ewald (2007) provides a quantitative approach by evaluating vegetation relevés from the Bavarian Mountain forest database to define shade tolerance. The author analysed the preference for light in both the tree layer and the rejuvenation. Abs et al. (2008) applied this approach to vegetation relevés from Bavarian strict forest reserves to assess the light demands of 25 tree species.

2.2 Determination of light-demanding tree species

To establish a precise definition of light-demanding tree species as a basis for further research, a comparison of various definitions for all Central European woody plants was first conducted (Ellenberg 1996, Niinemets and Valladares 2006, Abs et al. 2008, Green 2009, Schmidt et al. 2011, Bartsch and Röhrig 2016, Leuschner and Meier 2018, Bartsch et al. 2020).

It became apparent that a three-level scale (light-demanding tree species – intermediate tree species – shade tree species) was not sufficient for classification: On the one hand, some tree species behave differently in terms of light requirements when they are young compared to when they are old. On the other hand, experience also revealed clear differences between the tree species within one of the three classes in terms of their behavior and light requirement. Our group of experts, consisting of the authors therefore opted for a five-level scale, with L for light-demanding trees (including selected shrubs (Tab. 5 and Appendix A1)), HL for semi-light-demanding trees, I for intermediate trees, HS for semi-shade trees and S for shade-tolerant trees. Our final classification (Tab. 5 and Appendix A1) is based on average conditions in Central Europe. Where the literature showed no clear result, we decided together for each individual tree species into which class the species should be categorized. If the literature provided different information for rejuvenation and adult plants, we combined the values to classify shade tolerance.

2.3 Strict forest reserve data

The study sites are part of the strict forest reserve network in Germany, which includes 767 reserves covering 36,000 hectares (BLE 2024). They have been designated and maintained by the forest research institutes of the federal states since the 1960s. Most of the reserves have permanent plots to study the natural forest dynamics (Parviainen et al. 2000, Meyer 2007, Blaschke and Endres 2012).

Two different inventory designs have been established over the years. On the one hand, a regular grid of circular plots with a size between 0.05 and 0.1 ha is used, distributed over the whole reserve. On the other hand, core areas with a size of 0.5 to 2 ha have been selected, which are referred as “representative areas” for the natural forest type (Meyer et al. 2001). Data from 219 German strict forest reserves from ten federal states were available for our study. In 2017 the time since abandonment varied between 13 and 167 years. Baden-Württemberg, Hesse, Lower Saxony, Mecklenburg-Western Pomerania and Saxony-Anhalt make extensive use of the circular plot system. Core areas are used in Bavaria, Brandenburg, North Rhine-Westphalia, Rhineland-Palatinate and Schleswig-Holstein. In Lower Saxony both systems are used in parallel.

2.4 Quantitative data analysis

For our analyses, we selected permanent plots from both inventory designs. The number of plots per strict forest reserve varied from one to 108 plots with an accumulated total size ranging from 0.1 to 13.3 ha per reserve. In some reserves we could use data from both smaller circular plots and representative areas. We selected plots with at least two inventory campaigns and restricted the analysis to the first and the last inventory to maximise the time span for the analysis. The time intervals between the selected inventories ranged from 6 to 43 years with a median of 28 years. The inventories provide species determination and diameter measurements at breast height (DBH) of all living tree and shrub individuals with at least 7 cm DBH. The selected dataset contains about 400,000 tree diameter measurements from 2,644 plots with records from 1967 to 2017. It should be noted that the data set does not account for the impact of the drought period 2018 to 2022 on the forest development of the strict forest reserves under study.

We used the forest site mapping information for water balance from dry to wet and for nutrient supply from oligotrophic to eutrophic in three classes provided by the forest research institutes to characterize the site conditions and the forest type at the plot level. It should be noted that the method of forest site mapping varies between the federal states (Arbeitskreis Standortkartierung in der Arbeitsgemeinschaft Forsteinrichtung 2016). However, the information is sufficient to classify the forest type, nutrient status, and moisture conditions of the plots (Fig. 1, Tab. 2, 3).

Tab. 1: Study areas per federal state and recording system (circular plots or representative area). Some reserves comprised both circular plots and a representative area.

Tab. 1: *Verteilung der Untersuchungsgebiete auf die Bundesländer und die Erfassungssysteme (Probekreise oder repräsentative Kernflächen). Auf einige Naturwaldreservate entfallen Probekreise und Kernflächen.*

Federal state	Strict forest reserve	
	with circular plots	with representative area
Baden-Württemberg	12	
Bavaria		81
Brandenburg		1
Hesse	18	
Mecklenburg-Western Pomerania	4	
Lower Saxony	26	36
North Rhine-Westphalia		50
Rhineland-Palatinate		4
Saxony-Anhalt	1	
Schleswig-Holstein		3
total	**61**	**175**

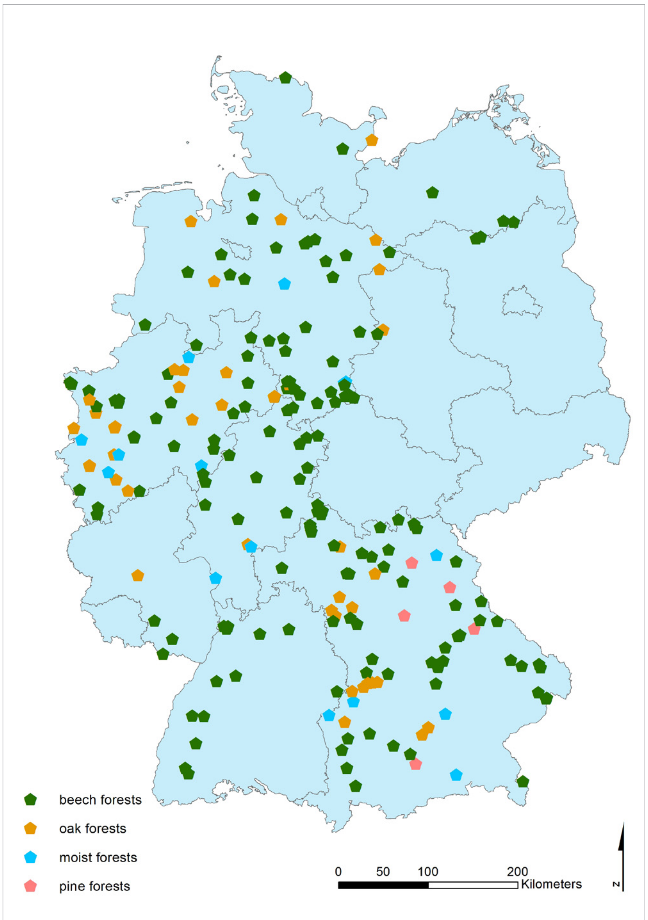

Fig. 1: Strict forest reserves included in the study and their predominant forest type.

Abb. 1: *In die Untersuchung einbezogene Naturwaldreservate und ihre Waldgesellschaften.*

For each species per plot, we calculated the net annual change rates of basal area and stem number and summarized them according to their assignment to the light species class. Rates for each site were calculated by pooling the plots within the sites. To take into account the different area of the permanent plots, we weighted the plots depending on their size. (s. Table supplement data A2)

For each species, we calculated the net annual change of the basal area as

$$netBA = ((BA_{2nd} / BA_{1nd})^{1/\Delta t} - 1)*100$$

based on the first (BA_{1nd}) and second (BA_{2nd}) inventory and Δt as the time interval between the inventories.

For each species, we calculated the net annual change of the stem number as

$$netSN = ((SN_{2nd} / SN_{1nd})^{1/\Delta t} - 1)*100$$

where SN_{1nd} is the stem number in the first and SN_{2nd} in the second inventory and Δt the time interval.

Due to their silvicultural importance, we compared the shade-tolerant beech (*Fagus sylvatica*) with the light-demanding oaks (*Quercus petraea/Q. robur*) and birches (*Betula pendula /B. pubescens*). While beech and oaks represent climax tree species, the birches are pioneer tree species. Therefore, we checked for differences in the net annual change.

We used one-way analysis of variance (ANOVA) and Scheffe's post-hoc test to determine if there were significant differences in net annual change between the light species classes. In the second step we compared the selected species beech, oaks and birches. The *p*-values were adjusted using the Benjamini-Hochberg procedure to control the false discovery rate (Benjamini and Hochberg 1995).

Data were analysed using the statistical computing environment R Version 4.1.2 (R Development Core Team 2023).

Across all tree species, data from a total of 199.633 trees and shrubs from 37 genera were available for the first survey. The dominant tree species was *Fagus sylvatica* with a share of 38.6%. Other tree species with larger proportions were*Carpinus betulus, Picea abies*, *Quercus* sp., *Pinus* sp., *Betula* sp. and *Fraxinus excelsior*. The genera *Tilia*, *Acer* and *Alnus* still achieved shares of 2–3%, while the other genera did not reach 2%.

Tab. 2: Distribution of strict forest reserves and permanent plots among forest communities.

Tab. 2: *Verteilung der Naturwaldreservate und Dauerbeobachtungsflächen auf die Waldgesellschaften.*

Forest communities		**Natura 2000 habitat**	**Number of strict forest reserves**	**Number of plots**
Beech forests	**Buchenwälder**		**181**	**2,183**
Beech forests on acidic soils	Buchenwälder bodensaurer Standorte	9110	87	1,301
Beech forests on moderately base-rich soils	Buchenwälder mäßig basenreicher Standorte	9130	5	117
Beech forests on base-rich or calcareous soils	Buchenwälder basen- bis kalkreicher Standorte	9130	79	728
Sedge beech forests on dry slopes	Orchideen-Buchenwälder kalkreicher Hangstandorte	9150	10	37
Mixed oak forests	**Eichenmischwälder**		**44**	**267**
Thermophilic mixed oak forests	Eichenmischwälder trocken-warmer, basenreicher Standorte		1	2
Moist oak-hornbeam forests	Eichen-Hainbuchenwälder frischer bis feuchter Standorte	9160	26	196
Thermophilic oak-hornbeam forests	Eichen-Hainbuchenwälder trocken-warmer Standorte	9170	17	69
Moist forests	**Feuchtwälder**		**18**	**179**
Alder swamp forests	Erlen-Sumpf- und -Bruchwälder		7	70
Alluvial forests	Erlen-Ulmen-Auen- und -Feuchtwälder	91E0	9	105
Bog forests	Moorwälder	91D0	2	4
Pine forests	**Kiefernwälder**		**5**	**5**
Pine forests on sandy soils	Sand- und Silikat-Kiefernwälder		4	4
Limestone pine forests	Kalk-Kiefernwälder		1	1
unknown			4	10

Tab. 3: Plot number per nutrient and water supply classes.

Tab. 3: Verteilung der untersuchten Dauerflächen auf die Wasser- und Nährstoffversorgung.

nutrient supply/water balance	**drier**	**favorable**	**moist/wet**
oligotrophic (low nutrient supply)	153	107	122
mesotrophic (medium nutrient supply)	154	997	382
eutrophic (high nutrient supply)	45	369	315

Tab. 4: Number and proportion of trees for each genus at the time of the first survey.

Tab. 4: *Anzahl und Anteil der Baumgattungen bei der ersten Aufnahme.*

Genus	Number of trees	Proportion in %
Fagus	77,105	38.6
Carpinus	19,459	9.7
Picea	19,342	9.7
Quercus	18,209	9.1
Pinus	17,845	8.9
Betula	9,875	4.9
Fraxinus	9,072	4.5
Alnus	5,304	2.7
Acer	5,142	2.6
Tilia	4,306	2.2
Abies	3,664	1.8
Sorbus	2,122	1.1
Ulmus	1,788	0.9
Corylus	1,353	0.7
Larix	967	0.5
Prunus	820	0.4
Crataegus	761	0.4
Rhamnus	438	0.2
Populus	418	0.2
Ilex	379	0.2
Salix	303	0.2
*Others**	961	0.5

(*for example: *Taxus, Pseudotsuga, Cornus, Sambucus, Malus*)

3 Results

3.1 Definition of light-demanding tree species

Based on the literature review and expert assessment, a list of light-demanding tree species (L) and a further list of relatively less light-demanding species (HL – semi-light-demanding tree species) were obtained (Tab. 5). As tree species are not always identified at the species level, an overall view was also included for some genera. A comprehensive overview of how tree species were evaluated and assigned to lights classes can be found in the supplements (A1).

3.2 Changes in tree species proportions

3.2.1 All study sites

Concerning all study sites, the number of stems generally slightly decreased or remained stable since the beginning of the investigations, depending on the tree species classes (Fig. 2). Considering all forest types, the highest annual decrease of about 1% occurred in the light-demanding tree species-class, where the values are significantly lower compared to all other species classes but the intermediate class. When the study sites are divided according to their nutrient supply status, no significant differences occur between the species classes within the eutrophic and the oligotrophic forest types. Within the mesotrophic forest types, the values of the light-demanding tree species class (L) are significantly lower than the shade-tolerant species class (S) (Fig. 2).

The development of the basal area of all study sites is generally positive for the shade and semi-shade tolerant species classes with an annual increase of about 1% and remained stable for the other classes. The values of the light-demanding tree species class are significantly lower as compared to all other species classes but the intermediate class. When the study sites are divided according to their nutrient supply status, no significant differences occur between the species classes (Fig. 3).

When the study sites are divided according to their water supply status, no significant differences occur between the species classes within the drier and favourable forest types. Within the moist to wet forest types, the values of the light-demanding tree species class (L) are significantly lower than those of the the semi-shade tolerant species class (HS). This applies both to the development of stem number and basal area (see supplements A3).

3.2.2 Beech forests study sites

When looking at the beech forest study sites, the general trends are very comparable to the development within all study sites, both in number of stems and basal area. This is also true when the beech forest study sites are divided with respect to nutrient (Fig. 4) and water supply (supplement A3).

3.2.3 Oak forest study sites

Considering the oak forest study sites, no significant differences between the light classes can be detected for all sites (Fig. 5). This is also true when the study sites are divided according to nutrient (Fig. 5) or water supply (supplement A3). It should be noted that the interquartile ranges of the semi-light-demanding and the intermediate tree species classes are wider at the oak forest study sites than those found on beech forest study sites and all forest study sites, showing a large dispersion of net annual percentage change. This is particularly evident for the mesotrophic and oligotrophic oak forest types (Fig. 5).

3.2.4 Dynamics of beech, oaks and birches

Concerning all study sites, the number of stems generally decreased since the beginning of the investigations for all species (Fig. 6). The highest annual decrease of about 1% occurred in the oaks. The decrease for beech is significantly lower compared to the oaks and birches. The development of the basal area is positive for beech with an annual increase of about 1% and remained stable for oaks and birches. The annual increase of beech is significantly higher when compared to the oaks and birches.

Tab. 5: List of species classified as light-demanding (L) and semi-light-demanding (HL) tree species based on literature review and the expert assessment.

Tab. 5: *Definition der Licht- (L) und Halblicht-Baumarten (HL) auf der Basis einer Literaturstudie und Expertenentscheid.*

Light value	Taxonomic name	Common English name	Common German name
L	*Aesculus hippocastanum*	Buckeye	Rosskastanie
L	*Alnus viridis*	Green alder	Grünerle
L	*Betula pendula*	Sand birch	Sandbirke
L	*Betula pubescens*	Downy birch	Moorbirke
L	*Betula sp.*	Birch	Birke
L	*Juniperus communis*	Juniper	Wacholder
L	*Larix decidua*	European larch	Europäische Lärche
L	*Larix* sp.	Larch	Lärche
L	*Pinus mugo*	Mountain pine	Bergkiefer
L	*Pinus nigra*	Black pine	Schwarzkiefer
L	*Pinus sylvestris*	Common pine	Gemeine Kiefer
L	*Quercus robur*	English oak	Stieleiche
L	*Quercus* sp.	Oak	Eiche
L	*Rosa canina*	Wild Rose	Wilde Rose
L	*Salix* sp.	Willow	Weide
HL	*Alnus incana*	White alder / grey alder	Weißerle / Grauerle
HL	*Clematis vitalba*	Clematis	Waldrebe
HL	*Cornus sanguinea*	Dogwood	Hartriegel
HL	*Crataegus* sp.	Hawthorn	Weißdorn
HL	*Malus silvestris*	Wild apple	Wildapfel
HL	*Prunus spinosa*	Blackthorn / sloe	Schwarzdorn / Schlehe
HL	*Quercus petraea*	Sessile oak	Traubeneiche
HL	*Quercus pubescens*	Downy oak	Flaumeiche
HL	*Rhamnus carthartica*	Buckthorn	Kreuzdorn
HL	*Robinia pseudoacacia*	Black locust	Robinie
HL	*Salix caprea*	Goat willow	Salweide
HL	*Salix eleagnos*	Bitter/Olive/Rosemary willow	Lavendel-/Grau-Weide
HL	*Sambucus nigra*	Black Elder	Holunder, Schwarzer
HL	*Sorbus aria*	Whitebeam	Mehlbeere
HL	*Viburnum lantana*	Woolly Snowball	Wolliger Schneeball

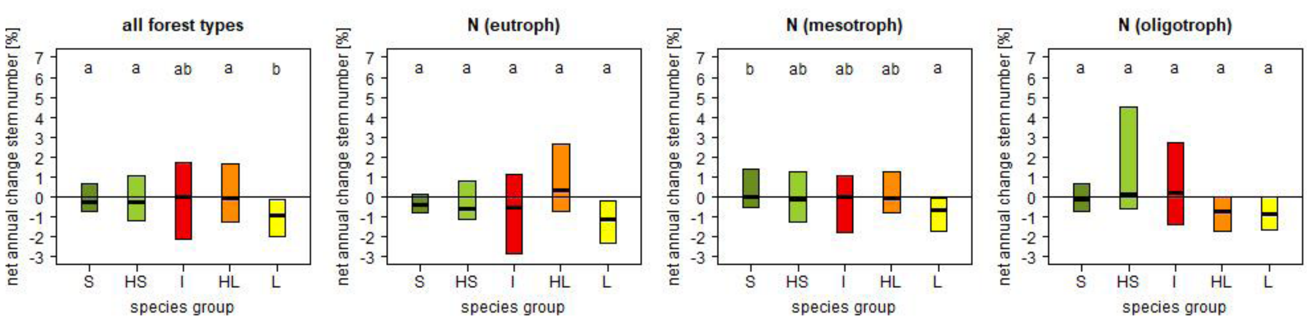

Fig. 2: Net annual percentage change of the number of stems of all light classes in all study sites. The first graph per row includes all forest types and the following are divided according to nutrient supply status. The boxes show median and interquartile range.

Abb. 2: *Jährliche prozentuale Nettoänderung der Stammzahl aller Lichtklassen in allen Untersuchungsflächen. Das erste Diagramm pro Zeile umfasst alle Waldtypen, die folgenden sind nach der Nährstoffversorgung unterteilt. Die Balken zeigen Median und Interquartilsabstand.*

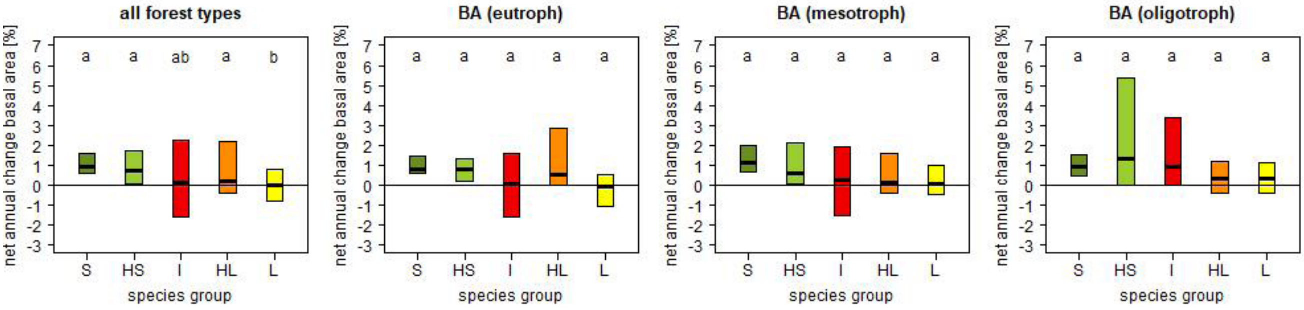

Fig. 3: Net annual percentage change of basal area of all light classes in all study sites. The first graph per row includes all forest types and the following are divided according to nutrient supply status. The boxes show median and interquartile range.

Abb. 3: *Jährliche prozentuale Netto-Änderung der Grundfläche aller Lichtklassen in allen Untersuchungsflächen. Das erste Diagramm pro Zeile umfasst alle Waldtypen, die folgenden sind nach der Nährstoffversorgung unterteilt. Die Balken zeigen Median und Interquartilsabstand.*

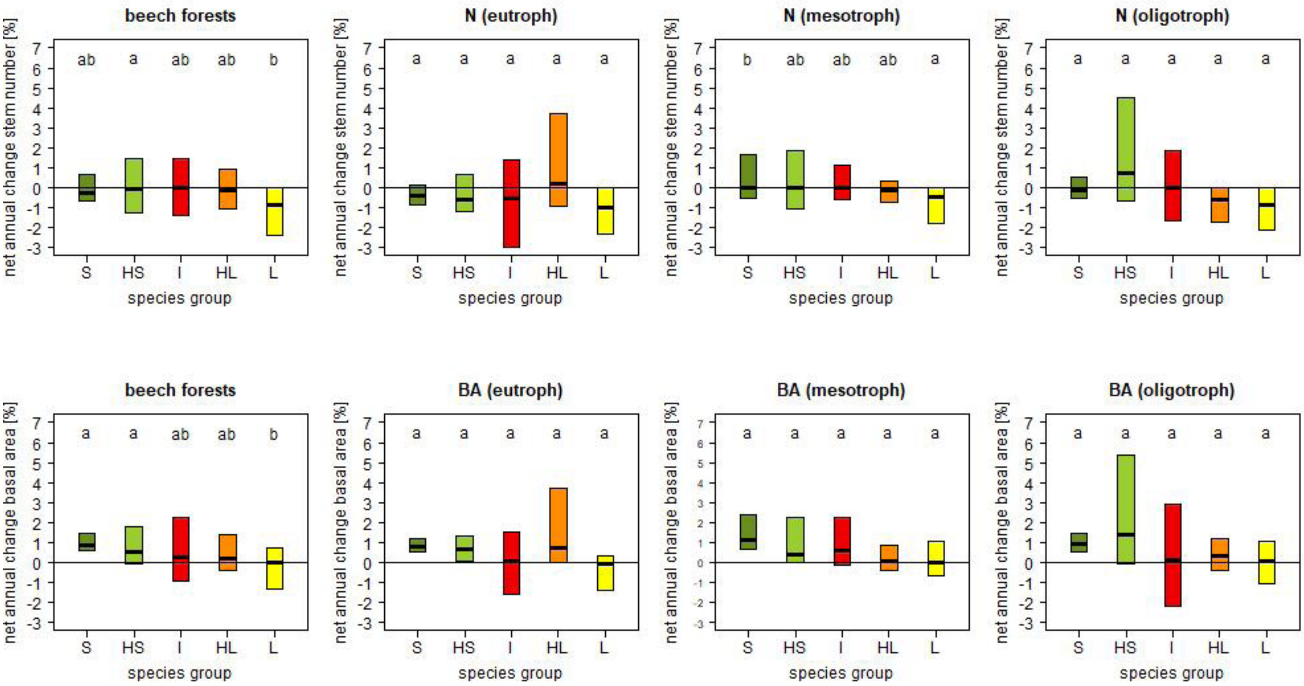

Fig. 4: Net annual percentage change of stem number (top) and basal area (below) of all light classes in the beech forests. The first graph per row includes all plots in beech forests and the following are divided according to the nutrient supply status. The boxes show median and interquartile range.

Abb. 4: *Jährliche prozentuale Nettoänderung der Stammzahl (oben) und Grundfläche (unten) aller Lichtklassen in allen Buchenwäldern. Das erste Diagramm pro Zeile umfasst alle Waldtypen, die folgenden sind nach der Nährstoffversorgung unterteilt. Die Balken zeigen Median und Interquartilsabstand.*

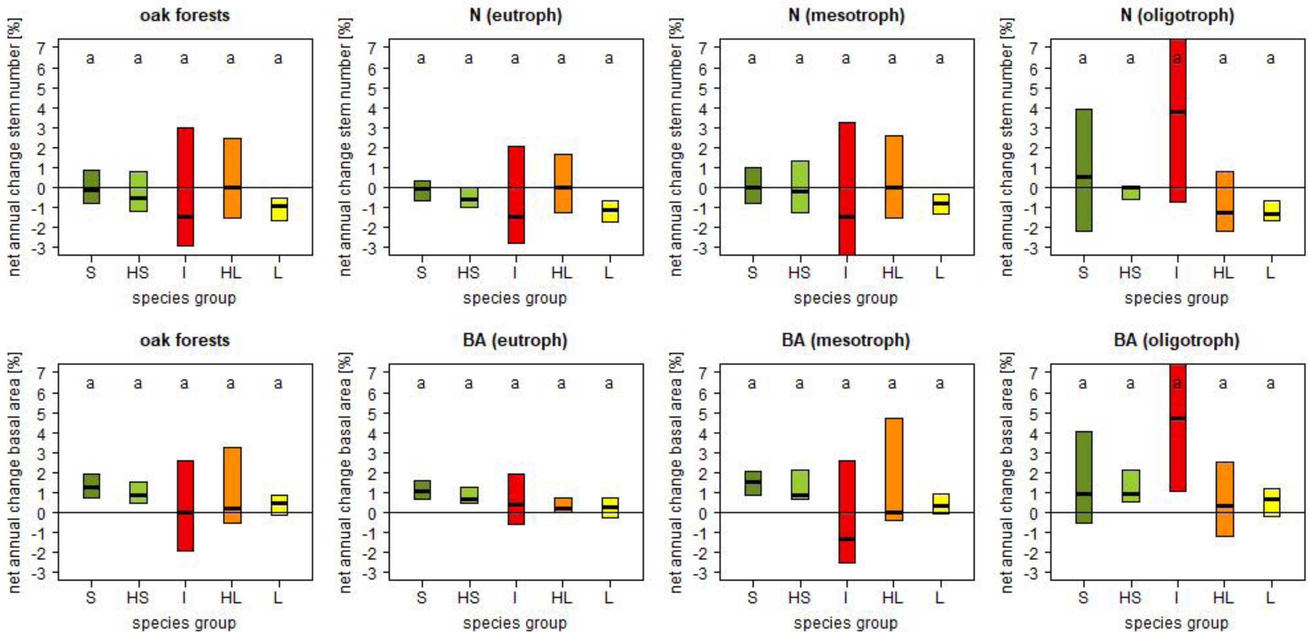

Fig. 5: Net annual percentage change of stem number (top) and basal area (below) of all light classes in the oak forests. The first graph per row includes all plots in oak forests and the following are divided according to the nutrient supply status. The boxes show median and interquartile range.

Abb. 5: *Jährliche prozentuale Nettoänderung der Stammzahl (oben) und Grundfläche (unten) aller Lichtklassen in allen Eichenwäldern. Das erste Diagramm pro Zeile umfasst alle Waldtypen, die folgenden sind nach der Nährstoffversorgung unterteilt. Die Balken zeigen Median und Interquartilsabstand.*

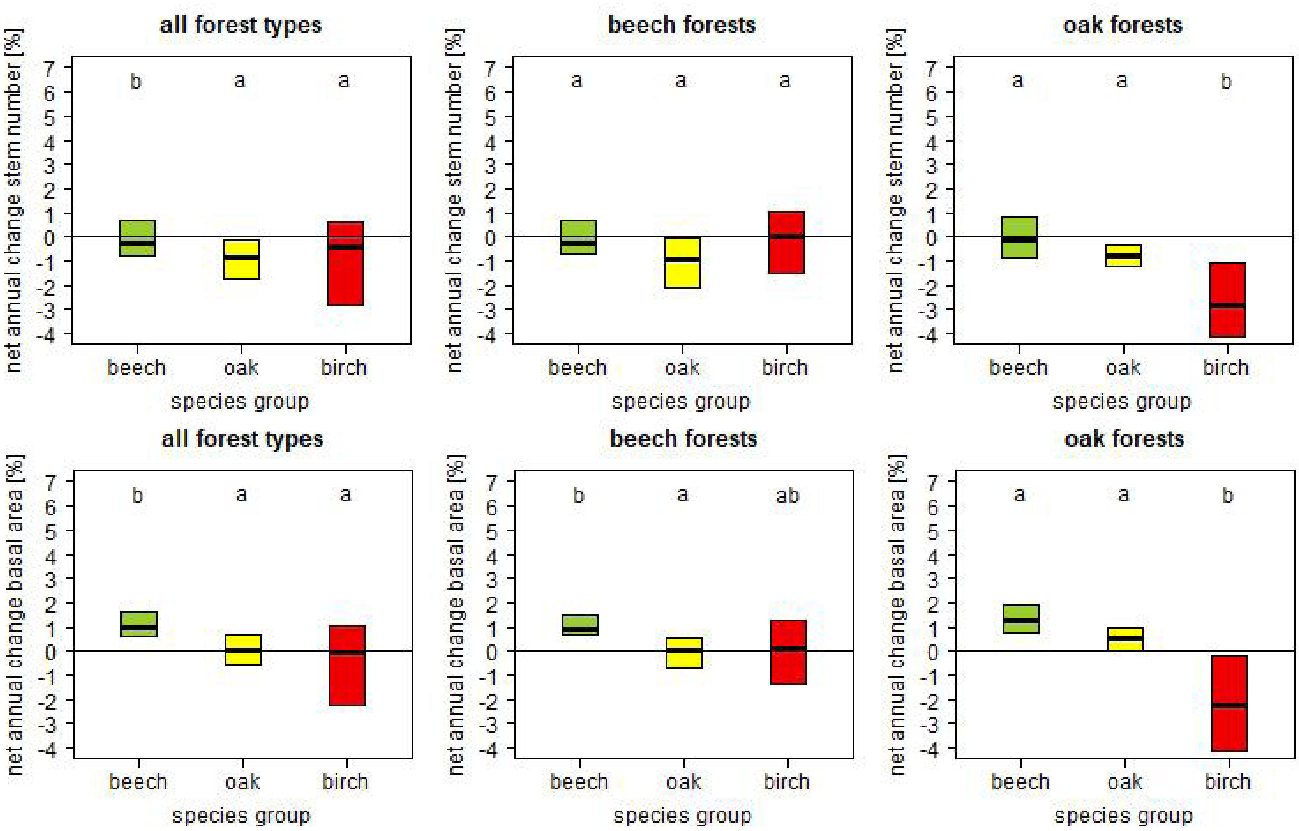

Fig. 6: Net annual percentage change of stem number (top) and the basal area (below) of *Fagus sylvatica* (beech), *Quercus* sp. (oak) and *Betula* sp. (birch) in the plots of the strict forest reserves. The boxes show median and interquartile range.

Abb. 6: *Jährliche prozentuale Nettoänderung der Stammzahl (oben) und Grundfläche (unten) von* Fagus sylvatica *(Buche),* Quercus *sp. (Eiche) und* Betula *sp. (Birke) in den Aufnahmeflächen der Naturwaldreservate. Die Balken zeigen Median und Interquartilsabstand.*

When examining the beech forests, the trends closely resemble the developments observed across all forest types, both in terms of the number of stems and the basal area. The oak forest study sites show the same general trends for beech and the oaks concerning stem numbers. The birches, however, show a remarkable annual decrease when compared to the beech forest study sites, which is significantly lower in comparison to beech and oaks. Regarding the basal area, beech and the oaks show a positive annual development, whereas the birches show a significant annual decrease of more than 2%.

4 Discussion

4.1 Classification of light-demanding tree species

It is necessary to define the light requirements of individual tree species before making statements about their development in unmanaged forests. Discussions around this definition have a long tradition in forestry literature and there are many ways in which authors have come to their conclusions.

The terms "light-demanding" and "shade-providing" have been used to describe tree species at least since the mid-19th century (Seidensticker 1849, Heyer 1852, Borggreve 1891). Heyer (1852) already gave a detailed classification of tree species and tried to take into account different aspects, from their development in old stands to aspects of thinning and regeneration. This classification is quite similar to ours. However, some species have a slightly different rating. For example, this is the case for *Picea abies*, which Heyer (1852) considered to be the most shade-tolerant of the native tree species, and which we have classified as a semi-shade tree. The discussion about the light requirements of tree species in forestry settings eventually led to an academic dispute (Fürst 1905). However, although shade tolerance has been a long-standing topic in forestry literature, authors tend to focus on species that are important for forest management and there is a lack of publications on the light requirements of other tree species.

The way in which the authors arrive at their conclusions is also quite heterogeneous. Some authors focus on seedling behaviour (Lyr et al. 1964, Leuschner and Meier 2018, Bartsch et al. 2020), while other studies consider the entire life cycle of trees (Fischer 1995, Burschel and Huss 1997). Some assessments are based on expert knowledge (Fischer 1995, Burschel and Huss 1997, Ellenberg et al. 2001, Bartsch and Röhrig 2016), while others are the result of measurements on leaves or tree growth (Lyr et al. 1964, Leuschner and Meier 2018), and still others are based on the light requirements of the surrounding vegetation (Ewald 2007, Abs et al. 2008).

Another reason for differences in classification may be that the exact specification of the tree species is not always given. Due to hybridization or overlap of the morphological characteristics, it can be difficult to assign certain trees to a specific species (Hertel and Degen 2000, Rellstab et al. 2016). This is the case with *Quercus petraea* and *Q. robur* as well as with *Tilia platyphyllos* and *T. cordata* or *Crataegus* spp. Another reason is that it is sometimes difficult to distinguish species in the field in their winter state – especially in the case of *Ulmus* spp. Therefore, during the field surveys, often only the genus or a group of species were entered into the database.

For many tree species the classification as a light-demanding or shade-tolerant tree is relatively consistent in the literature, e.g. *Abies alba* as a shade-tolerant tree, *Betula pendula* as a light-demanding tree. However, for some species (e.g. *Alnus viridis, Cornus mas,* and *Fraxinus ornus*) there are relatively few sources to classify them as light-demanding or shade-tolerant.

For all these reasons, classification may vary from study to study. In the following, we will discuss the light classes we categorised:

L – Light-demanding tree species

The classification of *Betula pendula* and *Betula pubescens* in the literature (Ellenberg 1996, Ellenberg et al. 2001, Niinemets and Valladares 2006, Bartsch et al. 2020) as light-demanding tree species is relatively uniform. However, Abs et al. (2008) state that the regeneration of *Betula pendula,* in particular, tolerates slightly more shade than *Betula pubescens*.

According to Fischer (1995), both species – *Quercus robur* and *Quercus petraea* – are light-demanding tree species. But most of the authors agree, that *Q. robur* is a typical light-demanding tree species – whereas *Q. petraea* has a lower light demand and is classified as a semi-light-demanding species (Ellenberg 1996, Ellenberg et al. 2001, Niinemets and Valladares 2006).

Of the conifer species, *Pinus sylvestris*, *P. nigra*, *Pinus mugo* s.l., *Larix decidua* and *Juniperus communis,* were classified as light-demanding tree species (Fischer 1995, Ellenberg 1996, Burschel and Huss 1997). This is confirmed by studies on *Pinus sylvestris* and *Larix decidua* (Niinemets and Valladares 2006, Abs et al. 2008).

Apart from Ellenberg (1996), there is little research on the light requirements of shrub-like woody plants. Light-demanding species include *Rosa canina*, *Juniperus communis* and *Pinus mugo* (Niinemets and Valladares 2006, Green 2009).

HL – Semi-light-demanding tree species

Quercus petraea can tolerate slightly more shade than *Quercus robur* when young (Ellenberg 1996, Ellenberg et al. 2001, Niinemets and Valladares 2006). Abs et al. (2008) even characterized both oak species as relatively shade-tolerant. Burschel and Huss (1997) suggest that *Q. petraea* has only average light requirements, but for the rejuvenation there is a general need for light. Leuschner and Meier (2018) found a different result for the photosynthesis rates of mature trees and rejuvenation of *Q. robur* and *Q. petraea*. For *Q. petraea*, photosynthesis rates corresponded more to a shade-tolerant tree species and for *Q. rob*ur it was more similar to light-demanding tree species.

Ellenberg's (1996) evaluation of *Salix caprea* as a semi-light tree species was adopted, but at the genus level *Salix* was classified as a light-demanding tree. This was confirmed by Niinemets and Valladares (2006).

Among the *Sorbus* species, *Sorbus* aria stands out. It has a low shade-tolerance when young (Ellenberg 1996). The classification as a semi-light-demanding tree species is also justified by pointer value analyses by Abs et al. (2008) and Niinemets and Valladares (2006).

Robinia pseudoacacia is listed by Ellenberg et al. (2001) with a light indicator value of 5, but is classified as a semi-shade species based on light type. On the other hand, Bartsch et al. (2020) consider the shade-tolerance of young specimens to be very low. This also applies to the results of Niinemets and Valladares (2006).

Malus sylvestris can tolerate shade as it ages (Schmidt et al. 2011), but the shade tolerance of young trees is very low (Ellenberg et al. 2001, Niinemets and Valladares 2006).

Based on the light indicator values by Ellenberg et al. (2001), typical shrub-like woody plants such as *Cornus sanguinea, Rhamnus carthartica, Viburnum opulus, Sambucus nigra, Crateagus* sp. and *Clematis vitalba* were classified as semi-light-demanding tree species.

I – Intermediate tree species

In terms of shade tolerance, these tree or shrub-like species fall between light-demanding and shade-tolerant tree species. We have classified them as „I – intermediate“.

Alnus glutinosa has the highest shade tolerance of the genus *Alnus* (Niinemets and Valladares 2006, Green 2009, Bartsch and Röhrig 2016). *Alnus incana* appears to be less shade-tolerant. The shrub-like *Alnus viridis* is described as a light-demanding tree species by Bartsch and Röhrig (2016).

Engelmann et al. (2019) observed a size class distribution in *Acer campestre* ranging from a high density of young trees to a smaller number of thicker, older trees in a riparian forest. This indicates good regeneration, even in denser parts of the forest. However, the authors expect the species to decline in unmanaged forests in the future. Holík et al. (2021) found that *Acer campestre* at the seedling stage has a relatively good chance of survival under shady conditions in flood-free sites in central Europe.

Raspé et al. (2000) describe the seedlings and young trees of *Sorbus aucuparia* as relatively shade-tolerant. Older trees have a higher demand for light in order to produce fruits. Holeksa (2000) also confirmed in his experiments in the Carpathians that *Sorbus aucuparia* can establish itself in closed stands and then grow significantly when light is available.

Sorbus domestica is classified as light-demanding tree by Paganová (2008) based on field observations. Enescu et al. (2016) also consider *Sorbus domestica* as a light-demanding species that can only survive for about five years in the shade. In contrast, Helluy et al. (2021) concluded from their studies in Southern France that *Sorbus domestica* has a certain shade tolerance and that very bright conditions tend to have a negative effect.

Ulmus minor is described by Caudullo et al. (2016) as more light-demanding than the other elms.

HS – Semi-shade tree species

This class includes, in particular, tree species of the forests of slopes, screes and ravines (Tilio-Acerion Oberdorfer 1992) like *Acer pseudoplatanus*, *A. platanoides*, *Fraxinus excelsior*, *Tilia cordata*, *T. platyphyllos*, *Ulmus glabra* and *U. laevis*. Their rejuvenation is usually considered to be shade-tolerant (Leuschner & Meier 2018, Ellenberg 1996, Niinemets and Valladares 2006), while the adult trees are often classified as intermediate (Abs et al. 2008, Ellenberg et al. 2001). They can only reach high shares where shade-tolerant tree species like beech are restricted by extreme site conditions (e.g., landslips or rockslides).

The classification may be affected by combining the values for young plants and mature trees into one value. This is the case for *Acer platanoides* and *Fraxinus excelsior*: while both are classified here as semi-shade trees, their classifications in the literature range from shade-tolerant (S) to intermediate (I).

Some plant trait databases like the USDA PLANTS Compilation (Green 2009) use a three-level classification system (‘tolerant’, ‘intermediate’, and ‘not tolerant’). Therefore, some of the tree species that we classify as semi-shade trees (HS) in the five-level scale are classified as ‘intermediate’ in the three-level classification systems.

S – Shade tree species

Abies alba, Fagus sylvatica and *Taxus baccata* are undisputed shade tree species in the literature: they tolerate shade throughout their entire life cycle. The only shrub in the group of shade trees, *Hedera helix*, is rarely mentioned in the forestry literature. This woody plant obtains light by climbing up tree trunks. Apart from Ellenberg’s light indicator values (Ellenberg et al. 2001), it is only mentioned as a shade species by Green (2009).

In addition to the shade tree species mentioned above, some authors classify *Tilia platyphyllos* as a shade tree species too, due to the high shade-tolerance of its regeneration (Ewald 2007, Abs et al. 2008). Abs et al. (2008) even categorize all slope, scree and ravine species – in addition to *Tilia platyphyllos* also *Ulmus glabra, Fraxinus excelsior* and *Acer pseudoplatanus* – in the same group as typical shade-tolerant species. They found that these species were as abundant or more abundant in the regenerating layer than in the canopy. Since we focused on the whole life cycle of trees, we gave more weight to the results of Niinemets and Valladares (2006).

4.2 Changes in tree species proportions

We studied forest development in 219 strict forest reserves throughout Germany based on inventory data of permanent plots. In agreement with our first hypothesis, that the proportions (stem numbers and basal area) of light-demanding tree species decrease with time, we find a decreasing proportion of the light-demanding tree species. We showed that the development of light-demanding tree species (L or HL) lagged behind that of shade-tolerant tree species (S or HS). The stem number of light-demanding species decreased faster than that of shade-tolerant species, and no annual increase in basal area of light-demanding species was found, whereas the basal area of shade-tolerant species increased about 1% per year. This resulted in a decreasing proportion of light-demanding tree species over time. Based on the large number of forests studied at different sites and with different tree species compositions, we interpret the increasing dominance of shade-tolerant species as a major successional trend in strict forest reserves after management cessation.

Our results are consistent with other studies in unmanaged forests. Heiri et al. (2009) observed a loss of tree-species richness over a period of almost 40 years. Most of the tree species lost were light-demanding, so the authors attributed this loss to the decreasing light availability. The light-demanding species show a bell-shaped diameter distribution, which can be indicated as a lack of regeneration. The shade-tolerant species had a more or less decreasing diameter distribution, indicating sustained regeneration. Similar trends have been described in the Białowieża forest, Poland (Bernadzki et al. 1998), in Denny Wood, England (Mountford et al. 1999), and in southern mixed hardwood forests in Texas, USA (Harcombe et al. 2002).

Contrary to our second hypothesis, that along the nutrient and moisture gradients different developments of the light-demanding tree species will be observed, we did not find clear evidence for a different development of light-demanding species along nutrient or moisture gradients. Significant differences in net annual changes of basal area or stem number between light classes were rare: Regarding nutrient supply we saw a greater annual decrease of stem number of light-demanding species than that of shade-tolerant species on mesotrophic sites, but there is no significant difference by basal area. No significant differences could be found on eutrophic or oligotrophic sites. Regarding soil moisture, only the net annual rates of stem number and basal area of light-demanding species on moist to wet sites were significantly lower than those of semi-shade species. This is in line with the results of Schmidt (2000), who showed that in the northwest German lowlands with Atlantic climate the shade-tolerant beech and hornbeam did not even avoid very wet sites with often water-saturated, poorly aerated soils.

In agreement with our third hypothesis, that regarding different forest vegetation types (beech and oak forests) different developments of the light-demanding tree species could be expected, we find a different development of light demanding species between beech and oak forests. We saw a clear trend of increasing basal area and constant stem number of shade-tolerant species in beech forests, while the basal area of light-demanding species remained constant, and the stem number was decreasing. In mixed oak forests, we found no significant differences between light-demanding species and shade-tolerant species. The decreasing proportion of light-demanding species in beech forests underlines the high competitiveness of beech due to its ability to produce and tolerate shade. Meyer et al. (2000) attributed the decrease of admixed tree species in strict forest reserves in Lower Saxony to crown competition, successful regeneration and high growth rates of beech trees.

Special attention has been given to the competition between beech and oaks which are the most common late successional native broadleaved species of European temperate forests. They often coexist in mixed stands due to human facilitation of oak (Leuschner and Ellenberg 2017, Mölder et al. 2019). We observed a 1% annual increase in basal area of beech in all forest types and in beech forests, while the annual increase of oaks was close to zero. In oak forests, both beech and oak showed an increasing basal area. Our results suggest a shift from oak to increasing beech dominance in the beech forests after cessation of management. This is consistent not only with Meyer et al. (2021), but also with Rohner et al. (2012), who described a decreasing proportion of oak relative to beech due to a higher mortality of oak over a 50-year period of natural forest development. They found that oak mortality increased with stand basal area as a plausible consequence of lower relative competitiveness and higher light demand. Saniga et al. (2014) observed oak displacement by shade-tolerant species, such as beech and hornbeam, in three Slovakian oak-dominated strict forest reserves during a forty-year period. Especially in the last decade, they noticed an increasing number of young *Fagus sylvatica* and *Carpinus betulus* trees under the canopy of old oaks. Meyer et al. (2017) found a decrease in the proportion of oak in strict forest reserves, but they couldn't attribute it solely to competition between the tree species. Therefore, several additional factors have been identified for the decline of oak after management cessation. Increasing oak mortality due to insect outbreaks (Saniga et al. 2014) or oak complex disease (Meyer 2005) has been recognized. Failures of oak regeneration due to low light availability (Strubelt et al. 2019) and browsing by ungulates (Petersson et al. 2019) were also discussed.

Strict forest reserves with large disturbance areas are hardly represented in our study. Therefore, the influence of natural disturbances on the establishment of light-demanding species couldn't be investigated separately. Light-demanding pioneer species such as birches (*Betula* sp.) benefit from large-scale disturbances (e.g., stand-replacing windthrow, snow or ice damage), which are often followed by early successional stages (Fischer and Fischer 2012, Tiebel 2020). The combination of tree species varies with site conditions and local seed supply, with birches and *Sorbus aucuparia* preferring acid and nutrient-poor soils (Ellenberg 1996). We found a strong decrease in stem numbers and basal area of more than 2% of birches in the oak forests, while the basal area of *Fagus sylvatic*a and oaks increased. The number of stems of birches also decreased considerably. This shows the pioneer character of birches with a shorter life span than late-successional species such as oaks and beech.

5 Conclusion

Our study demonstrates the potential of the German network of strict forest reserves for increasing our understanding of forest dynamics. The comprehensive dataset includes data from unmanaged forest that have been investigated for up to five decades and covers a wide range of forest types and site conditions. It provides a useful tool for future assessments, including investigations on the impact of climate change on natural forest ecosystems and their role for carbon sequestration. They form a building block in the EuFoRia Network, which was founded in 2019 to enhance visibility and exploit the potential of long-term monitoring plots in European primeval forests and forest reserves (Käber et al. 2023).

We were able to show that the development of light-demanding tree species in terms of stem numbers and basal area lags behind that of shade-tolerant tree species after management cessation. No clear evidence was found to indicate a dependency on nutrient or water supply. Surprisingly, the displacement of light-demanding tree species in mixed-species forests appears to be rather slow. However, the general trend supports the view that sustaining light-demanding tree species in mixed stands with shade-tolerant tree species requires active forest management (Lüpke 1998, Mölder et al. 2019).

Strict forest reserves with large disturbance areas are hardly represented in our study. Therefore, the influence of natural disturbances on the establishment and development of light-demanding species couldn't be investigated separately. In order to obtain more information on this crucial aspect in future, it is essential to maintain the long-term monitoring programme in strict forest reserves. This increases the likelihood of detecting the effects of major disturbances on stand development and ensures that the data set is updated regularly.

Acknowledgements

We thank the following forest research organisations for providing long-term inventory data from strictly protected forests:

- Nordwestdeutsche Forstliche Versuchs- und Forschungsanstalt (NW-FVA)
- Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg (FVA)
- Bayerische Landesanstalt für Wald und Forstwirtschaft (LWF)
- Forschungsanstalt für Waldökologie und Forstwirtschaft Rheinland-Pfalz (FAWF)
- Landesbetrieb Forst Brandenburg, Landeskompetenzzentrum Forst Eberswalde (LFE)
- Landesbetrieb Wald und Holz Nordrhein-Westfalen, Fachbereich IV – Hoheit, Schutzgebiete, Umweltbildung
- Landesforst Mecklenburg-Vorpommern, BT Forstplanung, Versuchswesen, Informationssysteme

We would like to thank Andreas Scheible for his ideas and input. He started the process for this project with us.

References

Abs, C., Ewald, J., Walentowski, H., Winter, S. (2008): Untersuchung der Schattentoleranz von Baumarten auf Grundlage der Datenbank bayerischer Naturwaldreservate. Tuexenia **28**: 23–40

Arbeitskreis Standortkartierung in der Arbeitsgemeinschaft Forsteinrichtung (2016): Forstliche Standortsaufnahme. 7. Aufl., IHW-Verlag: 400 S.

Bartsch, N., Röhrig, E. (2016): Waldökologie: Einführung für Mitteleuropa. Springer: 417 S. https://doi.org/10.1007/978-3-662-44268-5

Bartsch, N., von Lüpke, B., Röhrig, E. (2020): Waldbau auf ökologischer Grundlage. 8. Aufl.: 676 S.

Benjamini, Y., Hochberg, Y. (1995): Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society Series B: Statistical Methodology **57** (1): 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Bernadzki, E., Bolibok, L., Brzeziecki, B., Zajaczkowski, J., Zybura, H. (1998): Compositional dynamics of natural forests in the Bialowieza National Park, northeastern Poland. Journal of Vegetation Science **9**: 229–238

Blaschke, M., Endres, U. (2012): Bayerische Naturwaldreservats-Forschung auf „neue“ Füße gestellt – Zukünftig stehen 26 Schwerpunktreservate im Fokus der Wissenschaft. LWF-Aktuell **18**: 43–45.

BLE (2024): Datenbank Naturwaldreservate in Deutschland. https://fgrdeu.genres.de/naturwaldreservate

Borggreve, B. (1891): Die Holzzucht – Ein Grundriss für Unterricht und Wirthschaft. 2. Aufl., Paul Parey: 363 S.

Brändle, M., Brandl, R. (2001): Species richness of insects and mites on trees: expanding Southwood. Journal of Animal Ecology **70** (3): 491–504. https://doi.org/10.1046/j.1365-2656.2001.00506.x

Burschel, P., Huss, J. (1997): Grundriß des Waldbaus. Paul Parey: 487 S.

Caudullo, G., De Rigo, D. (2016): Ulmus – elms in Europe: distribution, habitat, usage and threats. In: Caudullo, G., De Rigo, D., Mauri, A., Houston Durrant, T., San-Miguel-Ayanz, J. (Hrsg.): Europ. Atlas of Forest Tree Species: 186–188.

Ellenberg, H. (1996): Vegetation Mitteleuropas mit den Alpen. 5. Auflage. Verlag Eugen Ulmer: 1095 S.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulissen, D. (2001): Zeigerwerte von Pflanzen in Mitteleuropa. 3. Aufl. Scripta Geobotanica, Band **18**. Erich Goltze KG: 262 S.

Enescu, C.M., De Rigo, D., Houston Durran, T., Caudullo, G. (2016): Sorbus domestica in Europe: distribution, habitat, usage and threats. In: Caudullo, G., De Rigo, D., Mauri, A., Houston Durrant, T., San-Miguel-Ayanz, J. (Hrsg.): European Atlas of Forest Tree Species: 178

Engelmann, R.A., Haack, N., Henle, K., Kasperidus, H.D., Nissen, S., Schlegel, M., Scholz, M., Seele-Dilbat, C., Wirth, C. (2019): Reiner Prozessschutz gefährdet Artenvielfalt im Leipziger Auwald. UFZ Discussion Papers **8/2019**: 1–14

Ewald, J. (2007): A phytosociological model of shade tolerance of tree species in the Bavarian Alps. Forum Geobotanicum **3**: 11–19

Fischer, A. (1995): Forstliche Vegetationskunde. Parey: 315 S.

Fischer, A., Fischer, H.S. (2012): Individual-based analysis of tree establishment and forest stand development within 25 years after wind throw. European Journal of Forest Research **131** (2): 493–501. https://doi.org/10.1007/s10342-011-0524-2

Fürst, H. von (1905): Licht- und Schattenholzarten, ein wissenschaftlich nicht begründetes Dogma? Forstwissenschaftliches Centralblatt **27** (1): 1–10. https://doi.org/10.1007/BF01864059

Green, W. (2009): USDA PLANTS Compilation. http://bricol.net/downloads/data/PLANTSdatabase/

Harcombe, P.A., Bill, C.J., Fulton, M., Glitzenstein, J.S., Marks, P.L., Elsik, I.S. (2002): Stand dynamics over 18 years in a southern mixed hardwood forest, Texas, USA. Journal of Ecology **90** (6): 947–957. https://doi.org/10.1046/j.1365-2745.2002.00735.x

Heiri, C., Wolf, A., Rohrer, L., Bugmann, H. (2009): Forty years of natural dynamics in Swiss beech forests: structure, compositon, and the influence of former management. Ecological Applications **19** (7): 1920–1934.

Helluy, M., Gavinet, J., Prévosto, B., Fernandez, C. (2021): Influence of light, water stress and shrub cover on sapling survival and height growth: the case of A. unedo, F. ornus and S. domestica under Mediterranean climate. European Journal of Forest Research **140** (3): 635–647. https://doi.org/10.1007/s10342-021-01356-1

Hertel, H., Degen, B. (2000): Unterscheidung von Stiel- und Traubeneichen (*Quercus robur* L. und *Q. petraea* [Mattuschka] Liebl.) mit Hilfe von genetischen und morphologischen Merkmalen. Forest Snow and Landscape Research **75** (1/2): 169–183.

Heyer, G. (1852): Das Verhalten der Waldbäume gegen Licht und Schatten. Enke: 88 S.

Holeksa, J. (2000): Distribution of Sorbus aucuparia (Rosaceae) regeneration in relation to trees in a subalpine spruce forest (W Carpathians, Poland). Fragmenta Floristica et Geobotanica **45** (1–2): 203–212

Holík, J., Janík, D., Adam, D. (2021): Light can modify density-dependent seedling mortality in a temperate forest. Journal of Vegetation Science **32** (1): e12992. https://doi.org/10.1111/jvs.12992

Käber, Y., Bigler, C., HilleRisLambers, J., Hobi, M., Nagel, T. A., Aakala, T., Blaschke, M., Brang, P., Brzeziecki, B., Carrer, M., Cateau, E., Frank, G., Fraver, S., Idoate-Lacasia, J., Holik, J., Kucbel, S., Leyman, A., Meyer, P., Motta, R., Samonil, P., Seebach, L., Stillhard, J., Svoboda, M., Szwagrzyk, J., Vandekerkhove, K., Vostarek, O., Zlatanov, T., Bugmann, H. (2023): Sheltered or suppressed? Tree regeneration in unmanaged European forests. Journal of Ecology **111** (10): 2281–2295. https://doi.org/10.1111/1365-2745.14181

Kroiher, F., Schmitz, F. (2015): Baumarten-Atlas zur dritten Bundeswaldinventur. Thünen Working Paper **49**: 1–43.

Leuschner, C., Ellenberg, H. (2017): Ecology of Central European Forests – Vegetation Ecology of Central Europe Volume I. Springer International Publishing: 971 S. https://doi.org/10.1007/978-3-319-43042-3

Leuschner, C., Fuchs, S., Wedde, P., Rüther, E., Schuldt, B. (2024): A multi-criteria drought resistance assessment of temperate *Acer, Carpinus, Fraxinus, Quercus,* and *Tilia* species. Perspectives in Plant Ecology, Evolution and Systematics **62**: 125777. https://doi.org/10.1016/j.ppees.2023.125777

Leuschner, C., Meier, I.C. (2018): The ecology of Central European tree species: Trait spectra, functional trade-offs, and ecological classification of adult trees. Perspectives in Plant Ecology, Evolution and Systematics **33**: 89–103. https://doi.org/10.1016/j.ppees.2018.05.003

Löf, M., Brunet, J., Filyushkina, A., Lindbladh, M., Skovsgaard, J.P., Felton, A. (2016): Management of oak forests: striking a balance between timber production, biodiversity and cultural services. International Journal of Biodiversity Science, Ecosystem Services & Management **12** (1–2): 59–73. https://doi.org/10.1080/21513732.2015.1120780

Lüpke, B. v. (1998): Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. Forest Ecology and Management **106** (1): 19–26. https://doi.org/10.1016/S0378-1127(97)00235-1

Lyr, H., Hoffmann, G., Engel, W. (1964): The influence of degrees of shading on dry matter production in young plants of some forest species. Part 2. Flora **155** (2): 305–30.

Meyer, P. (2005): Network of Strict Forest Reserves as reference system for close to nature forestry in Lower Saxony, Germany. Forest Snow and Landscape Research **79** (1/2): 33–44.

Meyer, P. (2007): Naturwaldreservate in Deutschland – Stand der Ausweisung, Methoden und Ergebnisse der Erforschung. Forstarchiv **78** (6): 179.

Meyer, P. (2020): Stubborn and adaptive – five decades of monitoring and research of self-regulated tree demography in Lower Saxony, Germany. Allg. Forst- und Jagdzeitung **190** (5/6): 120–135.

Meyer, P., Ackermann, J., Balcar, P., Boddenberg, J., Detsch, R., Förster, B., Fuchs, H., Hoffmann, B., Keitel, W., Kölbel, M., Köthke, C., Koss, H., Unkrig, W., Weber, J., Willig, J. (2001): Untersuchung der Waldstruktur und ihrer Dynamik in Naturwaldreservaten. IHW-Verlag: 107 S.

Meyer, P., Nagel, R., Feldmann, E. (2021): Limited sink but large storage: Biomass dynamics in naturally developing beech (*Fagus sylvatica*) and oak (*Quercus robur, Quercus petraea*) forests of north-western Germany. Journal of Ecology **109** (10): 3602–3616. https://doi.org/10.1111/1365-2745.13740

Meyer, P., Unkrig, W., Griese, F. (2000): Dynamik der Buche (*Fagus sylvatica* L.) in nordwestdeutschen Naturwäldern. Forst und Holz **55** (15): 470–477.

Meyer, P., Wevell von Krüger, A., Balcar, P., Blaschke, M., Braunisch, V., Schmidt, M., Schulte, U. (2017): Anpassung standortheimischer Baumarten an den Klimawandel. AFZ-DerWald **72** (16): 21–23.

Mölder, A., Meyer, P., Nagel, R.-V. (2019): Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur, Q. petraea*) forests: An overview. Forest Ecology and Management **437**: 324–339. https://doi.org/10.1016/j.foreco.2019.01.006

Mountford, E.P., Peterken, G.F., Edwards, P.J., Manners, J.G. (1999): Long-term change in growth, mortality and regeneration of trees in Denny Wood, an old-growth wood-pasture in the New Forest (UK). Perspectives in Plant Ecology, Evolution and Systematics **2** (2): 223–272. https://doi.org/10.1078/1433-8319-00072

Niccoli, F., Pelleri, F., Manetti, M.C., Sansone, D., Battipaglia, G. (2020): Effects of thinning intensity on productivity and water use efficiency of *Quercus robur* L. Forest Ecology and Management **473**: 118282. https://doi.org/10.1016/j.foreco.2020.118282

Niinemets, Ü., Valladares, F. (2006): Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecological Monographs **76** (4): 521–547.

Paganová, V. (2008): Ecology and distribution of service tree *Sorbus domestica* (L.) in Slovakia. Ekológia (Bratislava) **27** (2): 152–167.

Parviainen, J., Bucking, W., Vandekerkhove, K., Schuck, A., Paivinen, R. (2000): Strict forest reserves in Europe: efforts to enhance biodiversity and research on forest left for free development in Europe (EU-COST-Action E4). Forestry **73** (2): 107–118.

Petersson, L.K., Milberg, P., Bergstedt, J., Dahlgren, J., Felton, A.M., Götmark, F., Salk, C., Löf, M. (2019): Changing land use and increasing abundance of deer cause natural regeneration failure of oaks: Six decades of landscape-scale evidence. Forest Ecology and Management **444**: 299–307. https://doi.org/10.1016/j.foreco.2019.04.037

R Development Core Team (2023): R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Raspé, O., Findlay, C., Jacquemart, A.-L. (2000): Sorbus aucuparia L. Journal of Ecology **88** (5): 910–930. https://doi.org/10.1046/j.1365-2745.2000.00502.x

Rellstab, C., Bühler, A., Graf, R., Folly, C., Gugerli, F. (2016): Using joint multivariate analyses of leaf morphology and molecular-genetic markers for taxon identification in three hybridizing European white oak species (*Quercus* spp.). Annals of Forest Science 73 (3): 669–679. https://doi.org/10.1007/s13595-016-0552-7

Rohner, B., Bigler, C., Wunder, J., Brang, P., Bugmann, H. (2012): Fifty years of natural succession in Swiss forest reserves: changes in stand structure and mortality rates of oak and beech. Journal of Vegetation Science **23** (5): 892–905. https://doi.org/10.1111/j.1654-1103.2012.01408.x

Saniga, M., Balanda, M., Kucbel, S., Pittner, J. (2014): Four decades of forest succession in the oak-dominated forest reserves in Slovakia. iForest - Biogeosciences and Forestry **7** (5): 324–332. https://doi.org/10.3832/ifor0996-007

Schmidt, M., Ewald, J., Kriebitzsch, W.-U., Heinken, T., Schmidt, W., Abs, C., Bergmeier, E., Brand, J., Culmsee, H., Denner, M., Diekmann, M., Dierschke, H., Ebrecht, L., Ellenberg, H., Fischer, A., Friedel, A., Golisch, A., Härdtle, W., Kolb, A., Lippert, W., Peppler-Lisbach, C., Mast, R., Mayer, A., Michiels, H.-G., Oheimb v., G., Poppendieck, H.-H., Reif, A., Riedel, W., Scheuerer, M., Schmidt, P.A., Schubert, R., Seidling, W., Spangenberg, A., Storch, M., Stöcker, G., Stohr, G., Thiel, H., Urban, R., Wagner, A., Wagner, I., Weckesser, M., Westphal, C.D., Wulf, M., Zacharias, D., Zerbe, S. (2011): Waldartenlisten der Farn- und Blütenpflanzen, Moose und Flechten Deutschlands. In: Bundesamt für Naturschutz (BfN) (Hrsg.): Waldartenlisten der Farn- und Blütenpflanzen, Moose und Flechten Deutschlands. BfN-Skripten, Band **299**: 53–74.

Schmidt, W. (2000): Eiche, Hainbuche oder Rotbuche? – Zur Vegetation und Baumartenzusammensetzung von stau- und grundwasserbeeinflußten Wäldern des nordwestdeutschen Tieflandes. Ergebnisse aus den Naturwäldern Hasbruch und Pretzetzer Landwehr. Tuexenia **20**: 21–43.

Schwappach, A. (1886): Handbuch der Forst- und Jagdgeschichte Deutschlands. Julius Springer: 892 S.

Seidensticker, A. (1849): Wie verhalten sich Licht und Schatten in unseren Waldungen? Allgemeine Forst- und Jagdzeitung **15**: 90–101.

Seidensticker, A. (1886): Waldgeschichte des Alterthums. Zweiter Band. Nach Cäsar. Trowitzsch und Sohn: 460 S.

Strubelt, I., Diekmann, M., Peppler-Lisbach, C., Gerken, A., Zacharias, D. (2019): Vegetation changes in the Hasbruch forest nature reserve (NW Germany) depend on management and habitat type. Forest Ecology and Management **444**: 78–88. https://doi.org/10.1016/j.foreco.2019.04.030

Tiebel, K. (2020): The ability of pioneer tree species to mitigate the effects of site disturbance by fast and effective natural regeneration. Dissertation, Technische Universität Dresden: 187 S.

Tiebel, K., Huth, F., Frischbier, N., Wagner, S. (2020): Restrictions on natural regeneration of storm-felled spruce sites by silver birch (*Betula pendula* Roth) through limitations in fructification and seed dispersal. European Journal of Forest Research **139** (5): 731–745. https://doi.org/10.1007/s10342-020-01281-9

Wagner, S., Huth, F. (2010): Dauerwald heute – was geht, vor allem mit Blick auf die Lichtbaumarten? Eberswalder Forstliche Schriftenreihe **46**: 13–28.

Submitted: 17.12.2024
Reviewed: 07.08.2025
Accepted: 12.08.2025

Autorenanschriften:

Markus Blaschke
Bayerische Landesanstalt für Wald und Forstwirtschaft
Hans-Carl-von-Carlowitz-Platz 1
85354 Freising

E-Mail: Markus.blaschke@lwf.bayern.de

Klaus Striepen
Wald und Holz NRW
Kurt-Schumacher-Str. 50b
59759 Arnsberg

E-Mail: klaus.striepen@wald-und-holz.nrw.de

Andreas Mölder, Marcus Schmidt, Peter Meyer
Nordwestdeutsche Forstliche Versuchsanstalt
Abteilung Waldnaturschutz
Prof.-Oelkers-Str. 6
34346 Hann. Münden

Anne Wevell von Krüger
Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg
Abteilung Waldnaturschutz
Wonnhaldestraße 4
79100 Freiburg

Appendix/Anhang

Appendix 1/Anhang 1

Tab. A1: Light trait type of tree species based on average conditions in Central Europe.

Tab. A1: *Kategorisierung der Lichtbedürfnisse der mitteleuropäischen Baumarten nach Lichtklassen.*

Species name	final group light demand	forest affinity (Schmidt et al. 2011)	Ellenberg light value	shade tolerance young plants (Ellenberg 1996. S. 119)	shade casting stand (Ellenberg 1996. S. 119)	shade tolerance young plants (Bartsch et al. 2019. Tab. 2.1a)	group light demand Bartsch & Röhrig (2016. S. 30-31)	Abs et al. 2009	Ewald 2007	shade tolerance young plants (Leuschner & Meier 2018. Tab. 1)	min. light requirement shade leaves [%] (Leuschner & Meier 2018. Tab. 2)	min. light requirement saplings [%] (Leuschner & Meier 2018. Tab. 2)	shade tolerance (Niinemets & Valladares 2006)	shade tolerance (Green 2009)	shade tolerance index – (Baccara – Plant Traits of Eur. Forests. unpubl.)	shade tolerance seedlings [%] (Baccara – Plant Traits of Eur. Forests unpubl.)	shade tolerance adults – (Baccara – Plant Traits of Eur. Forests unpubl.)
Abies sp.	S	B1.1	3	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Abies alba	S	B1.1	3	5	5	5	S	3.5	S	V	1.5	4.5	4.6	na	T	0.05	1
Abies grandis	HS	na	na	na	na	4	na	na	na	na	na	na	4.01	T	na	na	na
Acer campestre	I	B2.1	5	3	3		HS	4.2	na	III	na	na	3.18	na	I-NT	0.1	5
Acer platanoides	HS	B2.1	4	4	4	4	HS	3.1	na	IV	na	na	4.2	I	T-I	0.025	4
Acer pseudoplatanus	HS	B2.1	4	4	4	4	HS	3.3	HS	IV	5	3	3.73	NT	I	0.025	4
Aesculus hippocastanum	L	B2.2	na	na	na	na	na	na	na	na	na	na	3.43	na	na	na	na
Alnus glutinosa	I	B2.1	5	3	3	1	HS	6.2	na	III	na	na	2.71	NT	NT	0.1	5
Alnus incana	HL	B2.1	6	2	3	na	HL	7.7	HS	II	na	na	2.3	I	NT	0.2	7
Alnus viridis	L	na	na	na	na	na	L	na	na	na	na	na	1.2	I-NT	na	na	na
Betula sp.	L	S2.1	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Betula pendula	L	B2.1	7	1	1	1	na	6.5	na	I	11	14	2.03	NT	NT	0.3	9
Betula pubescens	L	B2.1	7	1	1	na	na	8.7	na	I	na	na	1.85	na	NT	na	na
Carpinus betulus	HS	B1.1	4	4	5	4	HS	4.3	na	IV	2	3	3.97	na	I	0.075	3
Castanea sativa	HS	B1.1	5	3	3	na	na	na	na	III	na	na	3.15	na	na	0.1	5
Clematis vitalba	HL	S2.1	7	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Cornus mas	I	S1.2	6	na	na	na	na	na	na	na	na	na	2.68	NT	na	na	na
Cornus sanguinea	HL	S2.1	7	na	na	na	na	na	na	na	na	na	1.93	na	na	na	na
Coryllus avellana	I	S2.1	6	na	na	na	HL		na	na	na	na	3.53	na	na	0.2	6
Crateagus sp.	HL	S2.1	6/7	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Euonymus europaeus	I	S2.1	6	na	na	na	na	na	na	na	na	na	3.02	na	na	na	na
Fagus sylvatica	S	B1.1	3	5	5	5	S	3.3	S	V	1	2	4.56	na	T	0.05	1

Fraxinus excelsior	HS	B2.1	4	4	3	3	na	3.7	S	IV	10	7	2.66	na	I-NT	0.075	6
Fraxinus ornus	HS	B2.1	5	na	na	na	2	na	na	na	na	na	3.02	na	na	na	na
Fraxinus pennsylvanica	I	B2.1	na	na	na	na	2	na	na	na	na	na	3.11	T	na	na	na
Hedera helix	S	S1.1	4	na	na	na	na	na	na	na	na	na	na	T	na	na	na
Ilex aquifolium	HS	B1.1	4	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Juglans regia	I	B2.1	6	na	na	na	na	na	na	na	na	na	2.27	NT	na	na	na
Juniperus communis	L	S2.2	9	na	na	na	na	na	HL	na	na	na	1.71	NT	I	na	na
Larix sp.	L	B1.1	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Larix decidua	L	B1.1	8	1	1	1	na	7.6	I	na	na	na	1.46	NT	NT	0.4	9
Lonicera periclymenum	I	S2.1	6	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Lonicera xylosteum	HS	S1.1	5	na	na	na	na	na	na	na	na	na	3.38	na	na	na	na
Malus sylvestris	HL	B1.1	7	1	2	na	na	na	na	I	na	na	2.32	NT	I-NT	na	na
Mespilus germanica	I	S2.1	6	na	na	na	na	na	na	na	na	na	2.66	na	na	na	na
Picea abies	HS	B2.1	5	3	4	3	HS	5.2	HS	III	3	3.5	4.45	I	I	0.1	5
Pinus mugo	L	S2.2	8	na	na	na	na		HL	I	na	na	1.72	NT	na	na	na
Pinus nigra	L	B2.1	7	1	3	na	na	na	na	I	na	na	2.1	NT	na	na	na
Pinus strobus	I	B1.1	na	na	na	na	na	na	na	na	na	na	3.21	I	na	na	na
Pinus sylvestris	L	B2.1	7	1	1	2	na	8.9	HL	I	10	14	1.67	NT	NT	0.3	9
Populus balsamifera	I	B2.1	na	na	na	na	na	na	na	na	na	na	1.27	NT	na	na	na
Populus canescens	HS	B2.1	na	3	2	na	na	na	na	na	na	na	na	na	na	na	na
Populus nigra	HS	B2.1	5	3	2	na	L	na	na	III	na	na	2.46	NT	NT	0.1	5
Populus tremula	I	B2.1	6	2	2	na	L	4.8	na	II	na	na	2.22	na	NT	0.2	7
Prunus avium	HS	B2.1	4	4	3	1	na	4.3	na	IV	na	na	3.33	na	I	na	na
Prunus padus	I	B2.1	5	3	3	na	na	6.1	na	III	na	na	3.26	NT	I	na	na
Prunus serotina	I	B2.1	6	na	na	na	na	na	na	na	na	na	2.46	NT	na	na	na
Prunus spinosa	HL	S2.1	7	na	na	na	na	na	na	na	na	na	1.86	na	na	na	na
Pseudotsuga menziesii	HS	B1.1	na	na	na	3	na	na	na	na	na	na	2.78	I	na	na	na
Pyrus pyraster	I	B2.1	6	3	3	na	na	na	na	na	na	na	2.26	na	na	na	na
Quercus petraea	HL	B2.1	6	2	3	1	L	4.6	na	II	7	11	2.73	na	I	0.2	7
Quercus pubescens	HL	B1.2	7	1	2	na	L	na	na	I	na	na	2.31	na	na	0.3	7
Quercus robur	L	B2.1	7	1	2	1	L	5.5	na	I	4	11	2.45	na	I-NT	0.3	9
Quercus rubra	I	B1.1	na	na	na	2	na	na	na	na	na	na	2.75	I	na	na	na
Quercus sp.	L	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Rhamnus carthartica	HL	S2.1	7	na	na	na	na	na	na	na	na	na	1.93	na	na	na	na
Rhamnus frangula	I	S2.1	6	na	na	na	na	na	na	na	na	na	2.66	NT	na	na	na
Ribes uva-crispa	HS	S2.1	4	na	na	na	na	na	na	na	na	na	2.5	na	na	na	na

Robinia pseudoacacia	HL	B2.1	5	na	na	1	na	na	na	na	na	na	1.72	NT	na	na	na
Rosa canina	L	S2.1	8	na	na	na	na	na	na	na	na	na	1.93	na	na	na	na
Salix caprea	HL	B2.1	7	na	na	na	na	na	na	na	na	na	2.16	na	NT	na	na
Salix eleagnos	HL	na	na	na	na	na	na	na	HL	na	na	na	1.93	na	na	na	na
Salix sp.	L	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Sambucus nigra	HL	S2.1	7	na	na	na	na	na	na	na	na	na	2.29	na	na	na	na
Sambucus racemosa	I	S1.2	6	na	na	na	na	na	na	na	na	na	2.66	I	na	na	na
Sorbus aria	HL	B1.1	6	2	3	na	na	6.4	HS	II	na	na	3	na	I	0.2	7
Sorbus aucuparia	I	B2.1	6	2	2	na	na	4.7	I	II	na	na	2.73	I	T-I	0.2	7
Sorbus domestica	I	B1.2	4	na	na	na	na	na	na	IV	na	na	3.53	na	na	na	na
Sorbus torminalis	HS	B1.1	4	4	3	na	na	4.6	na	IV	na	na	3.38	na	I	na	na
Taxus baccata	S	B1.1	4	4	5	na	S	na	HS	IV	na	na	4.43	T	T	0.075	3
Tilia sp.	HS	B1.1	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Tilia cordata	HS	B1.1	5	3	4	5	HS	4.7	na	III	2	3.5	4.18	I	T-I	0.1	5
Tilia platyphyllos	HS	B1.1	4	4	4	na	S	3.6	na	IV	na	na	4	na	I	0.075	3
Ulmus glabra	HS	B1.1	4	4	4	3	HS	3.3	S	IV	na	na	3.53	na	I	0.075	3
Ulmus laevis	HS	B1.1	4	4	4	na	HS	na	na	IV	na	na	3.67	na	I	na	na
Ulmus minor	I	B2.1	5	na	na	na	L	na	na	III	na	na	3.36	na	I	na	na
Viburnum lantana	HL	S2.1	7	na	na	na	na	na	na	na	na	na	1.93	NT	na	na	na
Viburnum opulus	I	S2.1	6	na	na	na	na	na	na	na	na	na	2.66	T	na	na	na

Appendix 2/Anhang 2

Tab. A2: The total area [ha] per forest community in the analysed strict forest reserves.

Tab. A2: *Gesamtfläche (ha) nach Waldgesellschaften in den analysierten Naturwaldreservaten.*

Strict forest reserve name	Federal state	Beech forests	Mixed oak forests	Moist forests	Pine forests	unknown
Kellenhusen	Schleswig-Holstein		1.00			
Butterberg	Schleswig-Holstein	0.80				
Friedeholz	Schleswig-Holstein	1.00				
Nordahner Holz	Lower Saxony	3.00				
Franzhorn	Lower Saxony	3.85				
Herrenholz	Lower Saxony		2.00			
Tüxenfläche	Lower Saxony	1.60				
Walbecker Warte	Lower Saxony	1.20				
Großer Freeden	Lower Saxony	2.16				
Burckhardt	Lower Saxony	0.35				
Hünstollen	Lower Saxony	8.78				
Großer Staufenberg	Lower Saxony	6.44				
Stöberhai	Lower Saxony	1.80				
Bruchberg	Lower Saxony	2.00		6.00		
Landwehr	Lower Saxony	12.91	0.40			
Blütlinger Holz	Lower Saxony	0.65	0.95			
Schlenke	Lower Saxony			3.70		
Lüßberg	Lower Saxony	4.95				
Ehrhorner Dünen	Lower Saxony	7.30				
Stechpalmenwald	Lower Saxony	1.00				
Harzer Uraltfichten	Lower Saxony			1.00		
Sonnenkopf	Lower Saxony	2.85				
Vogelherd	Lower Saxony	2.00				
Friedrichshäuser Bruch	Lower Saxony	0.30	3.20			
Limker Strang	Lower Saxony	6.70				
Königsbuche	Lower Saxony	3.80				
Oderhang	Lower Saxony	1.01				
Haringer Berg	Lower Saxony	1.00				
Friedeholz	Lower Saxony	1.00				
Rieseberg	Lower Saxony	1.00				
Lohn	Lower Saxony	6.00				
Meinsberg	Lower Saxony	2.20				
Schrabstein	Lower Saxony	0.65				
Neuenburger Urwald	Lower Saxony		1.12			
Braken	Lower Saxony	5.60	5.50			
Weichel	Lower Saxony	3.00				
Meninger Holz	Lower Saxony	7.24				
Hau und Bark	Lower Saxony	4.30				
Saubrink / Oberberg	Lower Saxony	2.00				
Totenberg	Lower Saxony	1.00				
Dreyberg	Lower Saxony	1.80				
Winterlieth	Lower Saxony	10.50				
Drievorden	Lower Saxony	2.60				
Kaarßer Sandberge	Lower Saxony		5.60			
Urwald Hasbruch	Lower Saxony	2.55				
Gaim	Lower Saxony	1.10				
Dwergter Sand	Lower Saxony	1.00				
Hainholz	Lower Saxony	3.60				

Kreitzberg	North Rhine-Westphalia	3.52				
Hütterbusch	North Rhine-Westphalia	3.09				
Sandkaul	North Rhine-Westphalia	0.85				
Kerpener Bruch	North Rhine-Westphalia			2.00		
Am Sandweg	North Rhine-Westphalia		2.00			
Hinkesforst	North Rhine-Westphalia		1.00			
Littard	North Rhine-Westphalia		2.00			
Hochwald I	North Rhine-Westphalia	2.00				
Rehsol	North Rhine-Westphalia	2.00				
Geldenberg	North Rhine-Westphalia	2.00				
Steinsieperhöh	North Rhine-Westphalia	1.00				
Meersiepenkopf	North Rhine-Westphalia	1.50				
Herbremen	North Rhine-Westphalia		1.00			
Schiefe Wand	North Rhine-Westphalia	4.00				
Teppes Viertel	North Rhine-Westphalia		2.00			
Wartenhorster Sundern	North Rhine-Westphalia		2.00			
Nammer Berg	North Rhine-Westphalia	2.00				
Am Weißen Spring	North Rhine-Westphalia	2.00				
Kurzer Grund	North Rhine-Westphalia	4.00				
Am Karlsbrunn	North Rhine-Westphalia	2.00				
Eichenberg	North Rhine-Westphalia	0.75	0.50			
Süstertal	North Rhine-Westphalia	1.55	1.50			
Im Hirschbruch	North Rhine-Westphalia	1.25		0.25		
Schorn	North Rhine-Westphalia		2.00			
Hunau	North Rhine-Westphalia	1.75				
Worringer Bruch	North Rhine-Westphalia			1.00		
Niederkamp	North Rhine-Westphalia	2.50				
Hiesfelder Wald	North Rhine-Westphalia	1.00				
Krummbeck	North Rhine-Westphalia	2.00				
Altwald Ville	North Rhine-Westphalia		2.00			
Amelsbüren	North Rhine-Westphalia	4.00				
Schwalmtal	North Rhine-Westphalia			3.00		
Vinnenberg	North Rhine-Westphalia			0.20		
Netphener Hauberg	North Rhine-Westphalia	2.20				
Eichenwälder Bruch	North Rhine-Westphalia			1.00		
Lindenberger Wald I	North Rhine-Westphalia		1.50			
Lindenberger Wald II	North Rhine-Westphalia		1.50			
Probstforst	North Rhine-Westphalia		2.00			
Kirchheller Heide	North Rhine-Westphalia	1.50				
Überanger Mark	North Rhine-Westphalia		1.50			
Am Rintelner Weg	North Rhine-Westphalia	2.00				
Nonnenstromberg	North Rhine-Westphalia	1.00				
Ochsenberg	North Rhine-Westphalia	1.00				
Winkel'scher Busch	North Rhine-Westphalia		3.40			
Brachter Wald	North Rhine-Westphalia		1.00			
Hengsteysee	North Rhine-Westphalia	0.80				
Hochwald II	North Rhine-Westphalia	2.00				
Heerener Holz	North Rhine-Westphalia	3.60				
Holter Wald	North Rhine-Westphalia		1.50			
Laendern	North Rhine-Westphalia		1.50			
Goldbachs- und Ziebachsrück	Hesse	2.45				
Schönbuche	Hesse	2.60				
Wattenberg u. Hundsberg	Hesse	3.60				
Meißner	Hesse	3.60				0.20
Ruine Reichenbach	Hesse	2.10				0.05

Hohestein	Hesse	1.50				
Hasenblick	Hesse	4.50				
Waldgebiet östl. Oppershofen	Hesse	1.90				
Kreuzberg	Hesse	2.75				0.50
Zackenbruch	Hesse	1.70				
Karlswörth	Hesse			4.05		
Bruchköbel	Hesse		0.55			
Eichberg	Hesse	1.00				
Kinzigaue	Hesse			1.55		
Hundsrück	Hesse	2.00				
Weserhänge	Hesse	1.15				
Stirnberg	Hesse	4.70				
Langenstüttig	Hesse	2.25				
Adelsberg-Lutzelhardt	Rhineland-Palatinate	1.38				
Wildensteinertal	Rhineland-Palatinate		0.52			
Rotenberghang	Rhineland-Palatinate	2.94				
Pfaffenberg	Rhineland-Palatinate	2.83				
Schlierbach	Baden-Württemberg	6.30				
Hofstatt	Baden-Württemberg	3.30				
Scheibenfelsen	Baden-Württemberg	1.95				
Zimmeracker	Baden-Württemberg	1.60				
Feldseewald	Baden-Württemberg	3.50		0.05		0.10
Schnepfenmoos	Baden-Württemberg	0.80		0.30		
Maienberg	Baden-Württemberg	1.50				
Riedis	Baden-Württemberg	3.95				
Siedigkopf	Baden-Württemberg	5.90				
Schwetzinger Hardt: Kartoffelacker	Baden-Württemberg	3.05				
Schwetzinger Hardt: Franzosenbusch	Baden-Württemberg	3.70				
Schwetzinger Hardt: Saubusch	Baden-Württemberg	7.45	0.20			
Höllgraben	Bavaria	1.05				
Schelm	Bavaria	1.02				
Heilige Hallen	Bavaria		1.00			
Fuchsberg	Bavaria		0.57			
Eschenschlag	Bavaria		1.00			
Schweinsdorfer Rangen	Bavaria	1.07				
Göppelt	Bavaria	1.06				
Wolfsee	Bavaria		2.04			
Mitteleich	Bavaria		0.98			
Karolinenwörth	Bavaria			1.01		
Deutschordensbrand	Bavaria	1.14				
Falken	Bavaria		1.00			
Sulz	Bavaria		1.01			
Dumler	Bavaria		0.98			
Brunnschlag	Bavaria		0.98			
Rohrhalde	Bavaria	1.08				
Wertachhalde	Bavaria	0.92				
Halde	Bavaria	1.76				
Seeben	Bavaria		0.48			
Schneetal	Bavaria	0.96				
Krebswiese - Langerjergen	Bavaria	1.01				
Dreiangel	Bavaria			0.46		
Wolfsruhe	Bavaria		0.99			

Hofwiese	Bavaria	0.99				
Wasserberg	Bavaria	1.00				
Fichtelseemoor	Bavaria			1.00		
Kitschentalrangen	Bavaria	0.95				
Schwengbrunn	Bavaria	0.11				
Rainersgrund	Bavaria	1.00				
Schmidtsberg	Bavaria	1.00				
Ramschleite	Bavaria	1.00				
Lohntal	Bavaria	0.99				
Hammerleite	Bavaria	0.94				
Kienberg	Bavaria	0.49				
Groppenhofer Leite	Bavaria	0.90				
Echinger Lohe	Bavaria		1.01			
Isarau	Bavaria			0.71		
Schönwald	Bavaria	1.01				
Fasanerie	Bavaria		1.03			
Neukreut	Bavaria			1.00		
Weiherbuchet	Bavaria	1.02				
Pupplinger Au	Bavaria				1.00	
Gailenberg	Bavaria	0.93				
Teufelsgesperr	Bavaria	0.92				
Krakel	Bavaria	1.01				
Rusler Wald	Bavaria	0.97				
Frauenberg	Bavaria	0.20				
Rehberg	Bavaria	0.91				
Habichtsbaum	Bavaria	1.00				
Hecke	Bavaria	0.57				
Leitenwies	Bavaria	1.01				
Platte	Bavaria	1.05				
Donauhänge	Bavaria	0.44				
Bruckschlägelleite	Bavaria	0.86				
Hammerleite	Bavaria	0.88				
Knittelschlag	Bavaria	0.99				
Gitschger	Bavaria	1.11				
Schwarzwihrberg	Bavaria	0.89				
Osta	Bavaria	0.50				
Naabrangen	Bavaria	0.39				
Klamm	Bavaria	0.28				
Stückberg	Bavaria	1.03				
Lösershag	Bavaria	1.03				
Kalkberg	Bavaria	0.98				
Stachel	Bavaria	0.98				
Waldhaus	Bavaria	0.99				
Brunnstube	Bavaria	0.96				
Platzer Kuppe	Bavaria	1.05				
Schloßberg_alt	Bavaria	2.05				
Elsbach	Bavaria	1.04				
Eisgraben	Bavaria	0.70				
Hoher Knuck	Bavaria	1.04				
Deutschholz	Bavaria		0.99			
Wildacker	Bavaria	0.99				
Dürrenberg	Bavaria				0.99	
Sauhübel	Bavaria				0.24	
Turmkopf	Bavaria	1.00				
Geissmann	Bavaria				0.49	

Hüttenhänge	Bavaria	0.98				
Damm	Bavaria	1.02				
Grenzweg	Bavaria				0.25	
Naturwald Buchheide Zechlin	Brandenburg	0.30				
Stephansberg	Mecklenburg-Western Pomerania	1.50				
Heilige Hallen	Mecklenburg-Western Pomerania	3.70				
Wummsee	Mecklenburg-Western Pomerania	2.50				
Serrahner Berge	Mecklenburg-Western Pomerania	3.90				
Nievoldhagen	Saxony-Anhalt		4.60			
	Total	346.5	69.6	28.2	2.9	0.8

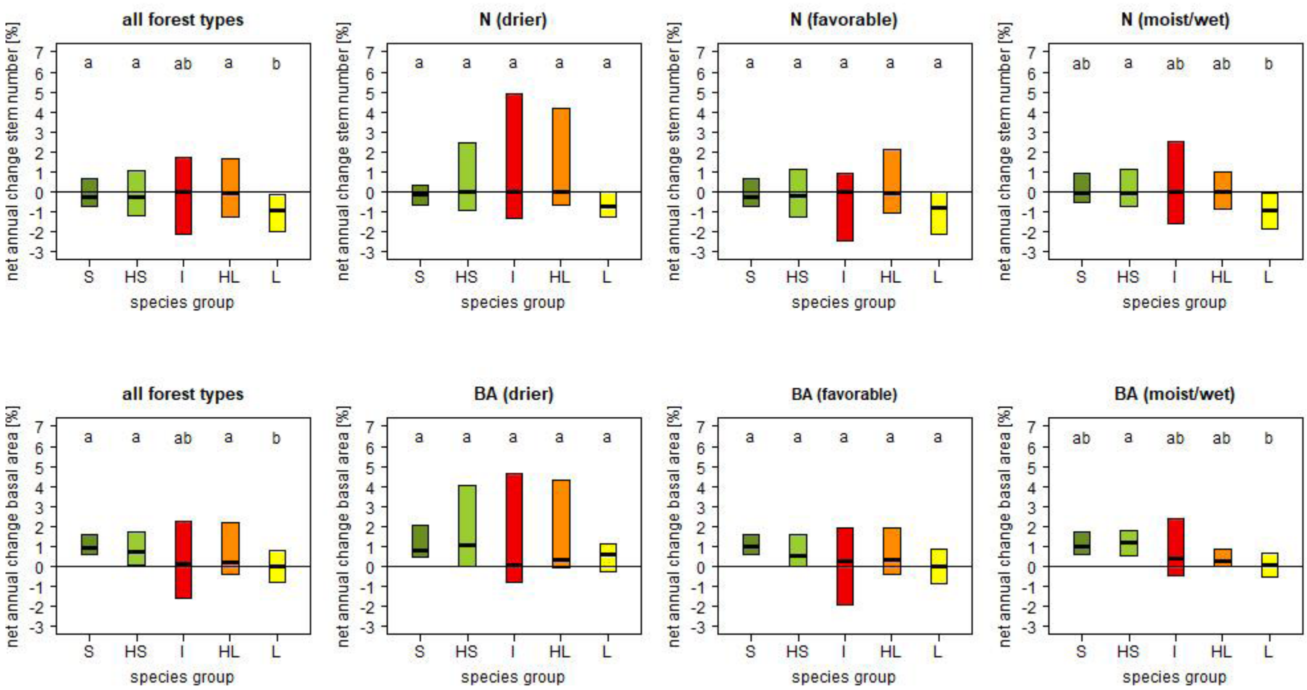

Fig. A1: Net annual percentage change of stem number (top) and basal area (below) of all light classes in all study sites. The first graph per row includes all forest types and the following are divided according to water supply status. The boxes show median and interquartile range.

Abb. A1: *Jährliche prozentuale Nettoänderung der Stammzahl (oben) und Grundfläche (unten) aller Lichtklassen in allen Naturwaldreservaten. Das erste Diagramm pro Zeile umfasst alle Waldtypen, die folgenden sind nach der Wasserversorgung unterteilt. Die Balken zeigen Median und Interquartilsabstand.*

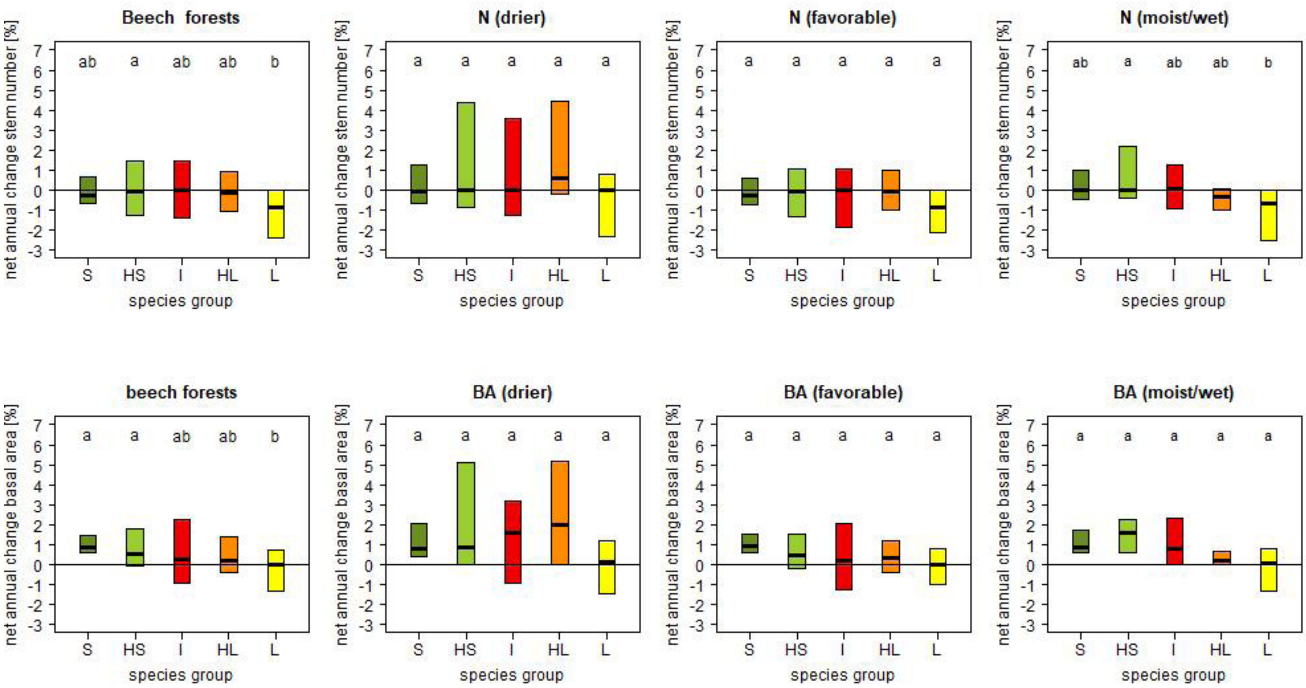

Fig. A2: Net annual percentage change of stem number (top) and basal area (below) of all light classes in the beech forests. The first graph per row includes all plots in beech forests and the following are divided according to the water supply status. The boxes show median and interquartile range.

Abb. A2: *Jährliche prozentuale Nettoänderung der Stammzahl (oben) und Grundfläche (unten) aller Lichtklassen in allen Buchenwäldern. Das erste Diagramm pro Zeile umfasst alle Waldtypen, die folgenden sind nach der Wasserversorgung unterteilt. Die Balken zeigen Median und Interquartilsabstand.*

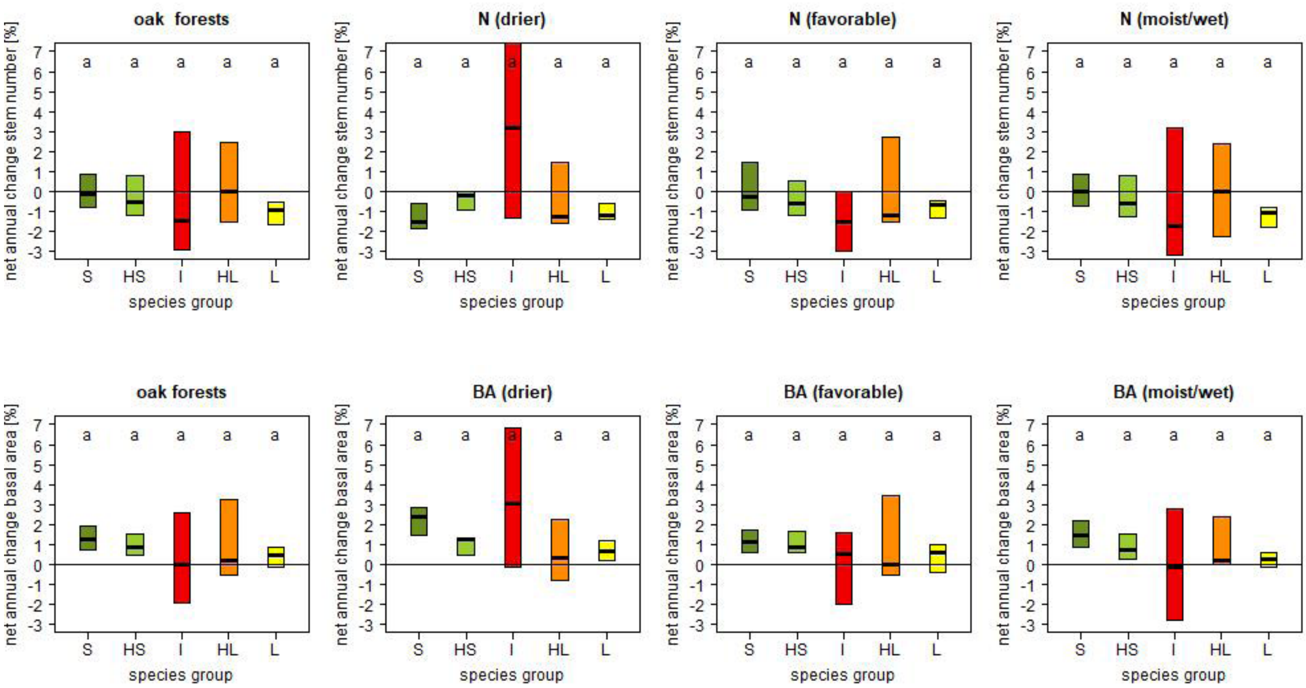

Fig. A3: Net annual percentage change of stem number (top) and basal area (below) of all light classes in the oak forests. The first graph per row includes all plots in beech forests and the following are divided according to the water supply status. The boxes show median and interquartile range.

Abb. A3: *Jährliche prozentuale Nettoänderung der Stammzahl (oben) und Grundfläche (unten) aller Lichtklassen in allen Buchenwäldern. Das erste Diagramm pro Zeile umfasst alle Waldtypen, die folgenden sind nach der Wasserversorgung unterteilt. Die Balken zeigen Median und Interquartilsabstand.*