ONTOGENETIC SCALES OF RELATION OF TREES TO LIGHT (ON THE EXAMPLE OF EASTERN EUROPEAN FORESTS)

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ОНТОГЕНЕТИЧЕСКИЕ ШКАЛЫ ОТНОШЕНИЯ ДЕРЕВЬЕВ К СВЕТУ (НА ПРИМЕРЕ ВОСТОЧНОЕВРОПЕЙСКИХ ЛЕСОВ)

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Abstract. Scales of shade tolerance, light demand and ranges of light possibilities for 13 tree species of the Eastern European forests have been developed. The variability of these plant properties in ontogeny is shown. Shade tolerance is the lower limit of the light and production potential of plants. The light minimum of the undergrowth is based on the ontogenetic scales of shade tolerance. The light minimum was determined with the help of individuals with extremely low vitality and which grew under a dense forest canopy under the conditions of light deficiency. The light demand is the upper limit of the light and production capabilities of plants. The basis of the ontogenetic scale of light demand is the production (average annual increment of biomass) of individuals that have grown in conditions of free growth at high irradiance levels. The range of light possibilities is the irradiance limit where the production process of plants can be carried out. Ontogenetic scales of ranges of light possibilities of trees are constructed on the basis of a comparing the position of species in the scales of light demand and shade tolerance.

Key words: shade tolerance of trees, light demand of trees, ranges of light possibilities of trees, light minimum of undergrowth, ontogeny of a tree, Eastern European forests.

Аннотация. Разработаны шкалы теневыносливости, светолюбия и диапазонов световых возможностей для 13 видов деревьев Восточноевропейских лесов. Показана изменчивость этих свойств растений в онтогенезе. Теневыносливость – это нижний предел световых и продукционных возможностей растений. В основу онтогенетических шкал теневыносливости положен световой минимум подроста. Его определяли над особями крайне низкой жизненности, которые выросли под пологом леса в условиях светового дефицита. Светолюбие – это верхний предел световых и продукционных возможностей растений. В основу онтогенетических шкал светолюбия положена продукция (среднегодовой прирост биомассы) особей, которые выросли в условиях сводного роста на полном свету. Диапазон световых возможностей – это пределы освещенности, в которых может осуществляться продукционный процесс растений. Онтогенетические шкалы диапазонов световых возможностей деревьев построены на основе сравнения положения видов в шкалах светолюбия и теневыносливости.

Ключевые слова: теневыносливость деревьев, светолюбие деревьев, диапазон световых возможностей деревьев, световой минимум подроста, онтогенез дерева, Восточноевропейские леса.

Introduction

The organisation of forest communities is largely determined by the specific nature of the relation of trees to light. This plant property has been the centre of attention of forest science from the moment of its origin to the present time [1–5]. The results of more than a century of experience in studying the relation of plants to light can be reduced to three propositions:

1. Hierarchy of the photosynthetic apparatus structure. For researchers who determine the light capabilities of plants, an important object of study should be their photosynthetic apparatus. A distinctive feature of this apparatus is the hierarchical organisation of the structure [6]. The conception of

hierarchy, on the one hand, makes it possible to explain the contradictory positions of species in the scales of different authors, while on the other hand, it enables us to find an integral indicator of the relation of plants to light. Analysis of the light requirements scales of trees showed that the traits underlying their creation belong to different structural levels: to the leaf [1, 5, 7–11], to the branch [2, 12] and to the individual as a whole [9, 13–16]. In these scales, the same species are characterised by slightly different relations to light. Objectively, this contradiction arises because traits that reflect the work of the photosynthetic apparatus at different levels of its organisation are analysed and because of different aspects of the relation of plants to light. Undoubtedly, when studying the light capabilities of trees, one must take into account the features of the functioning of the photosynthetic apparatus at different levels of the organisation. However, the traits of the organismal level should come first in ecological and forestry research.

2. Separate assessment of shade tolerance, light demand, ranges of light possibilities of trees species. The approach is adequate because the basis for the existence of trees within the community is a production process that is characterised by a certain range. The lower limit of this range, determined in conditions of light deficiency, reflects the shade tolerance of plants, while the upper limit, revealed in the open space at full irradiance, reflects the light demand [17, 18]. The need to separate the listed properties of plants has been shown by physiologists and forest ecologists [4, 5, 7, 19].

The main characteristics of the photosynthesis-irradiance (*PI*) curve can be considered as the criteria of shade tolerance, light demands and range of light possibilities of tree species at the level of the leaf and the light curve of productivity at the level of the organism. The most important indicators of these *PI* curves are the compensation point (*CP*) and the saturation point (*SP*). The *CP* characterises the value of solar irradiance on the *PI* curve when photosynthesis (or production) equals respiration, while the *SP* determines the solar irradiance above which light does not increase the intensity of photosynthesis (or the quantity of biomass production). The light range of the plant's production capacity lies between the *CP* and the *SP*. A comparison of the *PI* curves of the leaf and the light curves of the productivity of the whole organism shows that the *CP* and the *SP* of the leaf lie in a lower light intensity range than the *CP* and the *SP* of the whole organism [5, 20].

3. Ontogenetic variability of a plant's relation to light. The assessment of light demand should be carried out separately for individuals of different ages, since this feature varies significantly with on-togeny [4, 21–23]. Physiologists have shown that the thickness of the leaves and the height of the palisade cells of deciduous trees rapidly increase to a certain age (for example, in oak up to 25 years), with a subsequent decrease. The maximum measured values were observed in 50–80-year-old trees. The intensity of photosynthesis increases in proportion to the thickness of the leaf [24–26]. The mass, volume, surface and expenses of the organism for maintaining vital activity increase with age, and the growing crown shades a part of the leaves. With age, the ratio between photosynthetic and non-photosynthetic plant parts changes towards an increase of respiratory organs [4]. The decrease in shade-tolerance of trees with age is established empirically [15, 27, 28], but has been proved experimentally only for certain species [4, 16, 29]. Thus, the ontogenetic variability of the relation of plants to light must be taken into account in studies of forest communities in which the organisation is largely determined by the light regime.

In this context, the objective of this study is to develop ontogenetic scales of shade tolerance, light demand and the range of productive capacities of the trees of the Eastern European forests.

Objects, area and methods of research

Objects of research. Thirteen species of broadleaf and coniferous-broadleaf forests of Eastern Europe were selected: silver birch (*Betula pendula* Roth), Scotch elm (*Ulmus glabra* Huds.), European hornbeam (*Carpinus betulus* L.), pedunculate oak (*Quercus robur* L.), Norway spruce (*Picea abies* (L.) Karst.), goat willow (*Salix caprea* L.), Norway maple (*Acer platanoides* L.), field maple (*A. campestre* L.), Tatar maple (*A. tataricum* L.), small-leaved linden (*Tilia cordata* Mill.), common aspen (*Populus tremula* L.), Scots pine (*Pinus sylvestris* L.) and European ash (*Fraxinus excelsior* L.).

Research area. The main studies were carried out in the hornbeam forests of the Kanevsky Nature Reserve of the Cherkasy Oblast (Ukraine). In botanical-geographical terms, the territory belongs to the Middle Dnepr subprovince of the Eastern European forest-steppe province [30]. The choice of hornbeam forests as the main object of research is not accidental; in these communities, the irradiance at the level of the undergrowth averages 1 % of the above-canopy light due to the low light transparency of hornbeam crowns [21, 31]. Analysis of experimental works in forests with a similar light regime clearly revealed two circumstances: 1) isolation of the root system of adult trees does not improve the life state of the undergrowth; 2) mobile forms of mineral elements are underused by depressed plants [32–34]. In other

words, the survival of the undergrowth in dark hornbeam forests depends on the adaptation of plants to low irradiance.

Additional research was conducted in the spruce-broadleaf and pine forests of the State Nature Biosphere Reserve "Bryanskii Les" (Russian Federation). The territory is located at the belt of the Northern broadleaf forests (with a small admixture of spruce), which belongs to the Polesie subprovince of the Eastern European Province of the European broadleaf forest [30].

Methods of research. Based on centuries-old experience, the traits of the organism level were chosen as integral indicators of the light requirements of trees: 1) the average annual increment of biomass (or production) and 2) the light minimum of undergrowth. The production of the individuals (P) was calculated formulas follows:

$$P = \frac{Wp}{A} + Wl,$$

where Wp is the mass of the perennial plant parts (stems, roots), Wl is the mass of the leaves, A is the age of the plant in years. The product is the result of the work of all levels of the photosynthetic apparatus. In this regard, additional indicators on which the production of plants depends were used in the study: leaf area of the whole organism (LA) and the specific density of the leaf (SDL). The SDL is leaf dry mass per unit area and closely related to the intensity of photosynthesis [5]. All mass parameters were determined in an air-dry state. At the same time, we studied two groups of individuals, which grew in contrasting conditions in terms of irradiance: 1) under the dense forest canopy under extreme conditions of light oppression; 2) in full light in the nursery. The signs of individuals of the first group were used to analyse the shade tolerance of plants, and the indices of individuals of the second group were used to study the light demands.

Previous studies have shown that the average annual increment in biomass, determined in individuals under the extreme conditions of light oppression, makes it possible to identify only groups of species that have a similar shade tolerance and a similar mechanism for its development [18, 35]. In this regard, a light minimum of the undergrowth was used for a more delicate diagnosis of shade tolerance. It reflects the level of irradiance at which a positive balance of the plant between the formation of organic matter in photosynthesis and its expenditure on respiration is still possible [4]. It is understood that a small positive balance ensures the survival of the undergrowth vegetation. We determined the light minimum with the help of an LX1010BS luxmetre in the middle of summer. Measurements were carried out under individuals of extremely low vitality every hour from 9 am to 6 pm during several sunny days. Simultaneously, full irradiance in the open space was measured, and the values of the irradiance over the individuals were expressed as a percentage of full light. Undergrowth vegetation was selected in the most shaded areas of the forest under optimal moisture and nutrient conditions, using the ecological scales proposed by Tsyganov [36]. Shoot and root systems did not overlap. The most suitable conditions for undergrowth of linden, ash and elm were provided by hornbeam forests with domination of *Aegopodium podagraria* L. in the field layer, while for Norway maple and field maple, they were provided by hornbeam forests with domination of *Carex pilosa* Scop. and *Aegopodium podagraria* L. For hornbeam and Tatar maple, forests dominated by *Poa nemoralis* L. and *Carex pilosa* Scop. were most suitable. For birch, spruce, willow and aspen, treefall gaps of different sizes, with decaying trunks, provided suitable conditions. In the case of oak and pine, such conditions were provided by green moss pine forests.

As mentioned before, the ecological properties of plants vary with age. In this regard, the scale of the ratio of trees to light is developed for different ontogenetic stages (Fig. 1). The periodisation of ontogenesis for tree species has been used in previous studies [37, 38]. In this study, the different ontogenetic stages are designated by the following indices: p – seedling, j – juvenile, im_1 – immature of the first subgroup, im_2 – immature of the second subgroup, v_1 – virginile of the first subgroup, v_2 – virginile of the second subgroup, g_1 – young generative, g_2 – mature generative, g_3 – old generative, s – senile. The choice of ontogenetic stages (biological age) as an object of investigation is not accidental: different species and even different individuals of the same species reach the same ontogenetic state during different time intervals [39–43], which means that it is more logical to assess the impact of trees on the environment not in terms of calendar age, but on the basis of the level of their ontogenetic development.

Statistical processing. The light minimum of the undergrowth for each species in all ontogenetic states (j, im_1, im_2, v_2) was measured in 32–181 replicates. The average annual increment of biomass (production), leaf area and SDL for each species in all ontogenetic states (j, im_1, im_2, v_1, v_2, g_1) and in all conditions was determined 4–49 times. The following statistical parameters were determined: arithmetic mean (M), mean error (m) and standard deviation (σ). Normality of the data distribution

was estimated using the χ^2 test. For a pairwise comparison of disjoint, normally distributed samples, the Student test was used. For pairwise comparison of disjoint samples of small values, the non-parametric Mann-Whitney criterion was applied [44]. Details of the statistical processing of the material are provided in the previous publication [35].

Fig. 1. Ontogenetic stages of *Quercus robur* L.: *p* – seedling, *j* – juvenile, *im₁* – immature of the first subgroup, *im₂* – immature of the second subgroup, *v₁* – virginile of the first subgroup, *v₂* – virginile of the second subgroup, *g₁* – young generative, *g₂* – mature generative, *g₃* – old generative, *s* – senile. Pictures by N. V. Korotkova

Results of the study

Ontogenetic scales of shade tolerance of trees

Shade tolerance is the lower limit of the light and the productive potential of plants [17, 18]. The light minimum as the level of irradiance at which a positive balance between the formation of organic matter and its expenditure on respiration are still possible is represented by the integral in-dex of shade-tolerance [4]. In this study, it was determined over individuals of extremely low vitality, which grew under a dense forest canopy (Fig. 2). In terms of its indicators, the light minimum is close to the compensation point on the light curve of the organism's productivity [5]. Based on the values of the light minimum in the habitats of sub-lethal individuals (Table 1), series of species were obtained with reduced shade tolerance at different ontogenetic stages (Table 2).
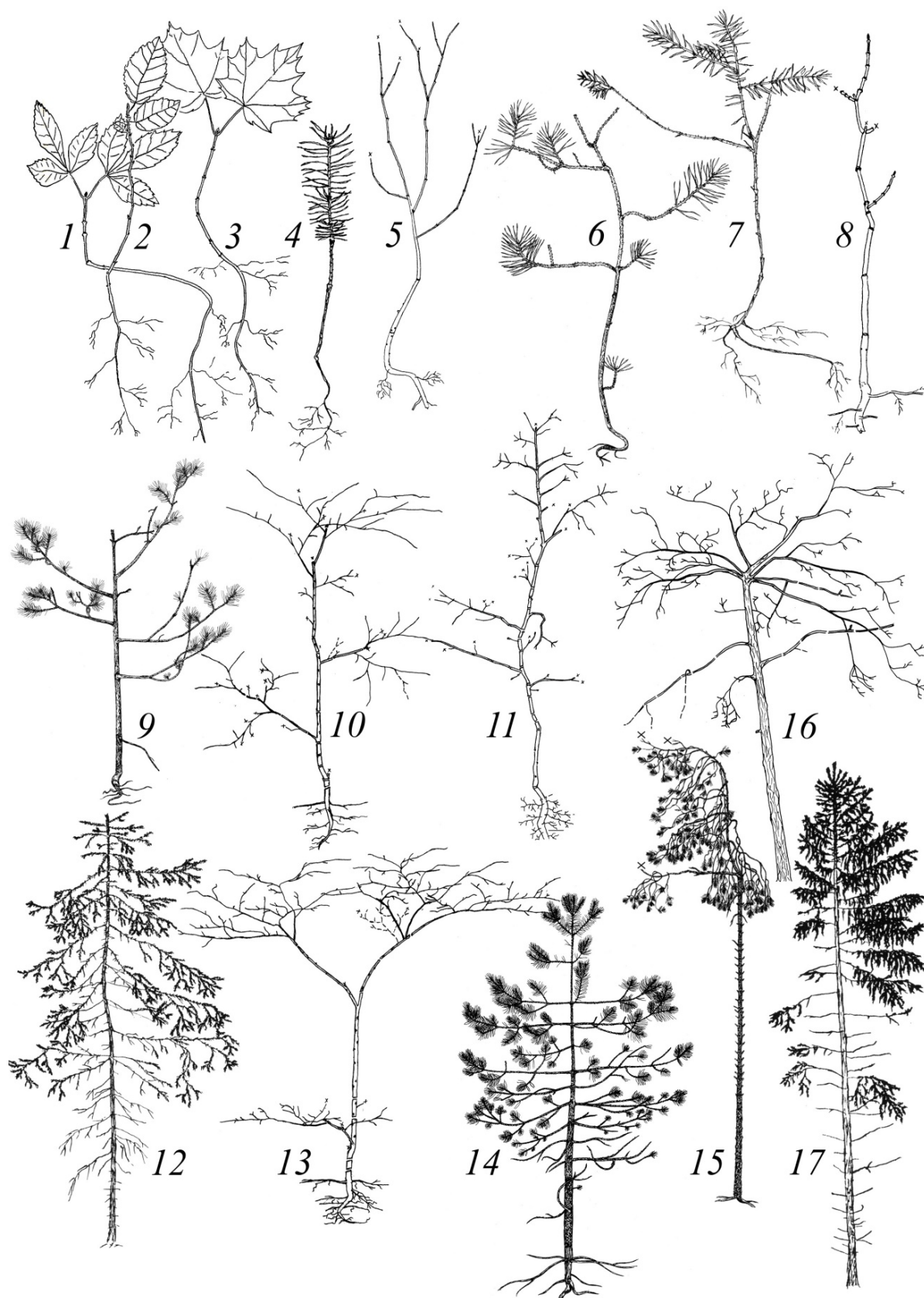
Fig. 2. Appearance of the undergrowth of extremely low vitality which grew at minimum light under dense forest canopy. Juvenile individuals (height of aboveground part up to 10 cm): 1 – *Fraxinus excelsior,* 2 – *Carpinus betulus,* 3 – *Acer platanoides,* 4 – *Picea abies.* Immature plants of the first subgroup (height 0.8 m): 5 – *Ulmus glabra,* 6 – *Pinus sylvestris,* 7 – *Picea abies,* 8 – *Fraxinus excelsior.* Immature plants of the second subgroup (height 2.0 m): 9 – *Pinus sylvestris,* 10 – *Ulmus glabra,* 11 – *Quercus robur.* Virginile plants of the first subgroup (height 2.0–4.0 m): 12 – *Picea abies,* 13 – *Ulmus glabra,* 14 – *Pinus sylvestris.* Virginile plants of the second subgroup (height 6.0 m): 15 – *Pinus sylvestris,* 16 – *Quercus robur,* 17 – *Picea abies.* Source of images – [38]

Table 1

Light minimum of tree undergrowth in different ontogenetic stages (% of full light in the open place)

Tree species	Ontogenetic stages							
	j		im_1		im_2		v_2	
	$M \pm m$	σ	$M \pm m$	σ	$M \pm m$	σ	$M \pm m$	σ
Acer campestre	0.42 ± 0.014	0.131	0.48 ± 0.011	0.116	0.58 ± 0.014	0.153	0.96 ± 0.029	0.189
Acer platanoides	0.28 ± 0.017	0.129	0.36 ± 0.008	0.057	0.45 ± 0.011	0.099	0.78 ± 0.021	0.231
Acer tataricum	0.55 ± 0.011	0.135	0.85 ± 0.027	0.329	1.49 ± 0.039	0.389	3.15 ± 0.122	1.174
Betula pendula	3.09 ± 0.081	0.642	4.51 ± 0.192	1.720	9.62 ± 0.198	1.428	22.98 ± 1.264	9.710
Carpinus betulus	0.71 ± 0.019	0.176	1.47 ± 0.083	0.594	1.50 ± 0.021	0.144	1.84 ± 0.104	0.770
Fraxinus excelsior	0.38 ± 0.008	0.089	0.50 ± 0.012	0.112	0.88 ± 0.020	0.244	4.19 ± 0.202	1.264
Picea abies	1.04 ± 0.029	0.253	1.06 ± 0.030	0.338	1.17 ± 0.019	0.181	1.33 ± 0.032	0.383
Pinus sylvestris	6.01 ± 0.139	1.356	11.00 ± 0.358	4.817	13.89 ± 0.359	2.280	34.27 ± 2.720	16.545
Populus tremula	2.67 ± 0.055	0.366	4.27 ± 0.278	1.822	6.60 ± 0.385	2.342	17.85 ± 1.901	10.756
Quercus robur	1.21 ± 0.083	0.523	2.60 ± 0.238	1.484	4.47 ± 0.186	1.231	10.36 ± 0.314	0.631
Salix caprea	1.50 ± 0.100	0.820	2.75 ± 0.180	1.414	6.40 ± 0.287	2.527	13.87 ± 1.312	8.400
Tilia cordata	0.60 ± 0.018	0.178	0.71 ± 0.022	0.196	0.81 ± 0.027	0.261	0.98 ± 0.037	0.305
Ulmus glabra	0.48 ± 0.023	0.200	0.58 ± 0.019	0.176	0.66 ± 0.019	0.225	1.08 ± 0.073	0.518

Note: M – arithmetic mean, *m* – average error, *σ* – mean of square deviation.

Table 2

Shade tolerance scales of East European tree species at different ontogenetic stages.
The scales are compiled on the basis of the light minimum of the undergrowth (Table 1).
The most shade-tolerant species are at the beginning and the least shade-intolerant species are at the end of the list. Note: * – based on comparison of the scales of shade tolerance in the ontogenetic stages im_2 and in v_2. The number prior to the name of the species represents the score of shade tolerance

Ontogenetic stages				
Juvenile (j)	Immature of the first subgroup (im_1)	Immature of the second subgroup (im_2)	Virginile of the first subgroup (v_1)*	Virginile of the second subgroup (v_2)
13. *Acer platanoides*	13. *Acer platanoides*	13. *Acer platanoides*	13. *Acer platanoides*	13. *Acer platanoides*
12. *Fraxinus excelsior*	12. *Acer campestre*	12. *Acer campestre*	12. *Acer campestre*	12. *Acer campestre*
11. *Acer campestre*	11. *Fraxinus excelsior*	11. *Ulmus glabra*	11. *Ulmus glabra*	11. *Tilia cordata*
10. *Ulmus glabra*	10. *Ulmus glabra*	10. *Tilia cordata*	10. *Tilia cordata*	10. *Ulmus glabra*
09. *Acer tataricum*	09. *Tilia cordata*	09. *Fraxinus excelsior*	09. *Picea abies*	09. *Picea abies*
08. *Tilia cordata*	08. *Acer tataricum*	08. *Picea abies*	08. *Acer tataricum*	08. *Carpinus betulus*
07. *Carpinus betulus*	07. *Picea abies*	07. *Acer tataricum*	07. *Fraxinus excelsior*	07. *Acer tataricum*
06. *Picea abies*	06. *Carpinus betulus*	06. *Carpinus betulus*	06. *Carpinus betulus*	06. *Fraxinus excelsior*
05. *Quercus robur*	05. *Quercus robur*	05. *Quercus robur*	05. *Quercus robur*	05. *Quercus robur*
04. *Salix caprea*	04. *Salix caprea*	04. *Salix caprea*	04. *Salix caprea*	04. *Salix caprea*
03. *Populus tremula*	03. *Populus tremula*	03. *Populus tremula*	03. *Populus tremula*	03. *Populus tremula*
02. *Betula pendula*	02. *Betula pendula*	02. *Betula pendula*	02. *Betula pendula*	02. *Betula pendula*
01. *Pinus sylvestris*	01. *Pinus sylvestris*	01. *Pinus sylvestris*	01. *Pinus sylvestris*	01. *Pinus sylvestris*

Measurement of the light minimum showed that for each tree species, there was a limit of tolerance to low irradiance, which does not remain constant throughout its life, but rather increases as the individual grows. This is consistent with the views of forest ecologists in terms of a reduced shade tolerance of undergrowth with age. This is associated with an increase of the proportion of non-photosynthetic parts of the plant, such as roots, stems and the trunk [4]. Our studies of the ratio of the mass of leaves and non-photosynthesising parts showed that in all species, the percentage of leaves in the total mass of the individual decreased with age (Fig. 3). In other words, with increasing age, the undergrowth requires more light for growth and development.
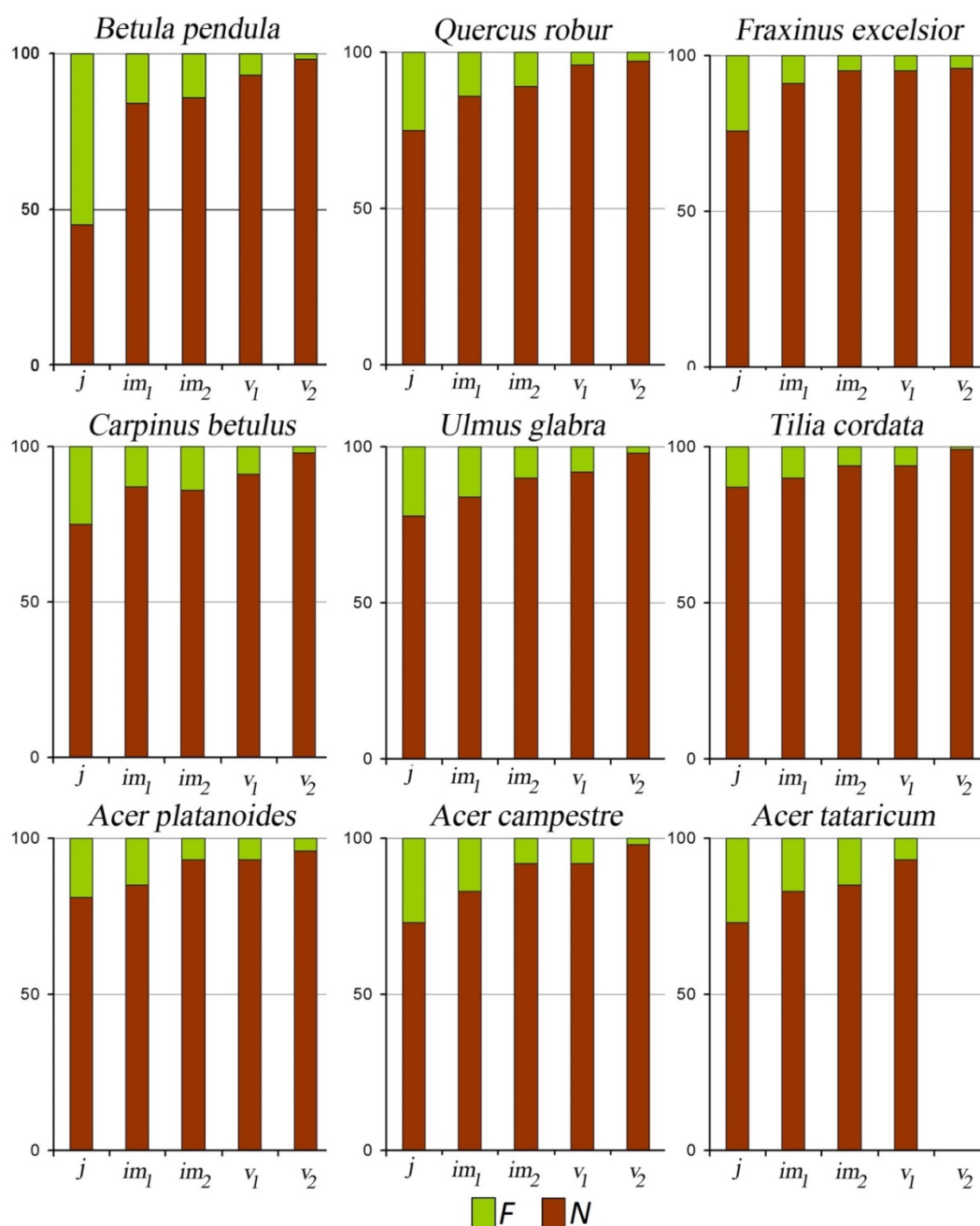
Fig. 3. Change in the ratio of the mass of photosynthetic (*F*) and non-photosynthetic (*N*) parts in tree ontogeny under minimum light below the forest canopy. The x-axis represents the ontogenetic stages, while the y-axis represents the percentages. Ontogenetic stages: *j* – juvenile, *im*$_1$ – immature of the first subgroup, *im*$_2$ – immature of the second subgroup, *v*$_1$ – virginile of the first subgroup, *v*$_2$ – virginile of the second subgroup

A comparison of the scales of shade-tolerance allows us to distinguish several species groups that have a similar shade-tolerance and a similar development mechanism. The first group includes pine, birch, aspen, willow and oak; in all ontogenetic states, they showed the highest light demand (Table 2), based on the highest values of the light minimum of the undergrowth (Table 1). The low shade tolerance of pine, birch, aspen, willow and oak has already been reported in the experimental works of the classics of forest science [1, 12, 14, 15] and is most likely related to the high respiration rate of these trees [5, 45–47]. At this level of "consump-

tion", the existence of individuals in forest communities is only possible at a high production (Table 3), which can only be guaranteed in habitats with high light conditions. The light availability corresponding to the lower limit of tolerance of these species only occurs in communities in tree gaps [48] as well as in park-type forests with a sparse tree layer. The undergrowth of these species is completely absent under the dense canopy of shade forests. This is also associated with the low lability of their photosynthetic apparatus and with the fact that the compensation point on their photosynthesis light curves lies in the high light densities [11, 19, 49].

The second group is represented by Norway maple, field maple and elm; their undergrowth has the highest shade tolerance in all ontogenetic states (Table 2), which is manifested in the lowest values of the light minimum (Table 1). In contrast to the previous group, elm, Norway maple and field maple are characterised by an insignificant increase of biomass under conditions of "light hunger" (Table 3), and the undergrowth of these species is characterised by a relatively low level of breathing under limited irradiance [5, 45–47, 49–51]. An insignificant level of "consumption" allows them to exist in the darkest sites of the forests, albeit with a relatively low productivity, also because the compensation point on the photosynthesis-irradiance curve lies in the low light densities [8, 11, 19, 49]. The high tolerance of elm, Norway maple and field maple to light deficit is confirmed by some previously developed scales of shade tolerance [1, 12, 14, 15].

Table 3

Average annual biomass increases (g·year⁻¹) of the undergrowth
under a dense forest canopy at light minimum in different ontogenetic stages

Species	Ontogenetic stages					
	j		im_1		im_2	
	$M \pm m$	N	$M \pm m$	N	$M \pm m$	N
Acer campestre	0.12 ± 0.013	23	1.47 ± 0.094	39	6.7 ± 0.71	27
Acer platanoides	0.06 ± 0.003	40	1.19 ± 0.110	26	6.8 ± 0.41	34
Acer tataricum	0.13 ± 0.014	16	1.69 ± 0.129	49	8.6 ± 0.92	11
Betula pendula	0.79 ± 0.190	4	4.50 ± 0.956	9	36.1 ± 4.33	17
Carpinus betulus	0.06 ± 0.003	40	1.52 ± 0.160	34	12.2 ± 0.84	38
Fraxinus excelsior	0.05 ± 0.004	40	0.85 ± 0.067	28	9.2 ± 0.68	40
Picea abies	0.10 ± 0.015	8	1.18 ± 0.107	10	9.6 ± 0.35	10
Pinus sylvestris	0.26 ± 0.034	16	2.37 ± 0.102	10	44.7 ± 2.24	10
Populus tremula	0.82 ± 0.030	9	3.90 ± 0.135	10	40.2 ± 4.13	11
Quercus robur	0.86 ± 0.129	19	2.65 ± 0.334	17	47.3 ± 6.05	15
Salix caprea	1.52 ± 0.104	4	3.52 ± 0.165	10	35.3 ± 3.43	13
Tilia cordata	0.15 ± 0.014	24	1.72 ± 0.145	43	8.5 ± 0.61	31
Ulmus glabra	0.04 ± 0.004	25	0.91 ± 0.098	18	11.4 ± 0.73	26
Note: M – arithmetic mean, *m* – average error, *N* – sample size						

The third group is formed by hornbeam, Tatar maple and spruce, which occupy an intermediate position according to the values of the light minimum and the average annual biomass increase. Their positions change in the ontogenetic scales of shade tolerance: Tatar maple is most shade-tolerant in the stages j–im_1, while hornbeam and spruce are most shade-tolerant in the stage v_2 (Table 2). Undergrowth of these species is more common in habits with high light conditions: for example, Tatar maple and hornbeam reproduced mainly on the southern light slopes in hornbeam forests, while spruce undergrowth was located in treefall gaps of coniferous-broadleaf forests. Note that in some scales, hornbeam and spruce are among the most shade-tolerant species [2, 12, 15]. However, according to the light minimum, their undergrowth is close to the shade-intolerant oak (Table 1); this contradiction can be explained as follows: forest scientists have adopted the crown characteristics of adult trees as the leading criterion of shade tolerance, and the dense crowns of hornbeam and spruce form a strong twilight under the forest canopy, even on bright, sunny days.

A separate position in the scales is occupied by ash and linden, which are characterised by distinct changes in shade tolerance over time. Ash is extremely shade-tolerant, comparable to Norway maple in the j stage. However, in the subsequent stages of ontogeny, its light requirements sharply increase, and in the v_2 stage, the shade tolerance of ash is as low as that of oak (Table 2). The age variability of the light requirement of ash has been described previously [15, 27]. The relative shade tolerance of linden varies in the opposite way. Linden is comparable to spruce and hornbeam in the j stage, according the value of the light minimum. However, the comparative shade tolerance of the linden increases and is similar to that of maple and Norway maple in the v_2 stage.

The study of the ontogenetic variability of shade tolerance allows us to predict the minimum size of treefall gaps in the forest canopy in which individuals of different tree species can develop normally and undergo complete ontogeny. The smallest areas of the treefall gaps are characteristic for shade-tolerant species, while the largest are suitable for shade-intolerant species. There is a general trend in the formation of the younger generation: the regular growth of the undergrowth when the gap size increases [48, 52]; this goes in parallel with the increase in the light requirement of the individuals in ontogenesis. Due to the spe-

cies and ontogenetic variability of tree shade-tolerance within a community, a variety of light conditions can be used: from small clearances in the upper layer of the forest to large gaps caused by the uprooting of several trees.

Ontogenetic scales of light demands of trees

The light demand represents the upper limit of light and production capabilities of plants [17, 18]. The average annual biomass increase (productivity) of individuals that grew under conditions of free growth in the nursery under full light was used as an indicator for the development of scales of light de-

mand (Fig. 4) and is close to the point of saturation on the light curve of the productivity of the organism. Ontogenetic scales of light demands for individuals from the stages j to g_1 were constructed on the basis of the mean annual biomass growth, and the scale was constructed using the current net growth ($m^3 \cdot ha^{-1} \cdot year^{-1}$) of pure stands for trees in the stage g_2 (Table 4, Table 5). The average annual biomass growth and the current net growth characterise the upper limit of the production capacity of plants, which is realised at full light. Several groups of species are distinguished along these scales, according to the nature of the use of full light at different ontogenetic stages.

Fig. 4. Appearance of the undergrowth which grew at full light in open space. Juvenile individuals (height of aboveground part up to 15 cm): 1 – *Picea abies*, 2 – *Pinus sylvestris*, 3 – *Quercus robur*, 4 – *Betula pendula*. Immature plants of the first subgroup (height 0.8 m): 5 – *Acer campestre*, 6 – *Picea abies*, 7 – *Fraxinus excelsior*. Immature plants of the second subgroup (height 2.0 m): 8 – *Populus tremula*, 9 – *Quercus robur*, 10 – *Picea abies*, 11 – *Pinus sylvestris*. Virginile plants of the first subgroup (height 3.0 m): 12 – *Tilia cordata*, 13 – *Pinus sylvestris*, 14 – *Quercus robur*. Virginile plants of the second subgroup (height 6.0 m): 15 – *Pinus sylvestris*, 16 – *Picea abies*, 17 – *Quercus robur*. Source of images – [38]

Table 4

Average annual biomass growth of trees at different ontogenetic stages (in the nursery in full light)

Species	Ontogenetic stages and units										
	j (g·year^{-1})		im_1 (g·year^{-1})		im_2 (g·year^{-1})		v_1 (10^3 g·year^{-1})		g_1 (10^3 g·year^{-1})		g_2 (m^3·ha^{-1}·year^{-1})*
	$M \pm m$	N	$M \pm m$	N	$M \pm m$	N	$M \pm m$	N	$M \pm m$	N	
Acer campestre	4.7 ± 0.52	7	38 ± 6	16	529 ± 74	4	1.7 ± 0.1	7	7.4 ± 0.45	5	5.0
Acer platanoides	18.2 ±1.72	8	342 ± 54	10	1780 ± 250	11	4.8 ± 0.22	7	7.8 ± 0.56	5	6.4
Acer tataricum	8.1 ± 0.58	8	15 ± 2	12	106 ± 20	6	0.8 ± 0.13	7	2.3 ± 0.38	5	0.8
Betula pendula	1.1 ± 0.08	11	155 ± 16	22	2868 ± 937	7	10.1 ± 0.68	7	23.9 ± 2.10	5	12.8
Carpinus betulus	1.3 ± 0.18	8	62 ± 8	23	851 ± 153	6	3.9 ± 0.30	7	8.3 ± 0.76	5	8.6
Fraxinus excelsior	14.2 ± 0.83	9	245 ± 31	19	1380 ± 101	7	6.5 ± 0.38	7	10.8 ± 0.75	5	12.2
Picea abies	7.1 ± 0.44	11	121 ± 4	11	4810 ± 162	5	19.5 ± 0.95	7	30.0 ± 1.79	5	25.0
Pinus sylvestris	6.0 ± 0.48	11	126 ± 4	11	4950 ± 269	11	18.1 ± 1.01	7	43.6 ± 1.94	5	19.7
Populus tremula	0.4 ± 0.05	11	54 ± 4	11	4380 ± 174	5	23.3 ± 1.20	7	39.9 ± 2.06	5	11.5
Quercus robur	14.2 ± 1.53	8	130 ± 14	21	2027 ± 234	5	7.8 ± 0.45	7	11.9 ± 0.92	5	17.1
Salix caprea	0.8 ± 0.08	11	118 ± 4	11	5817 ± 245	11	17.8 ± 1.31	7	14.0 ± 1.30	5	4.0
Tilia cordata	8.4 ± 0.84	10	71 ± 7	17	1318 ± 250	7	2.0 ± 0.14	7	9.8 ± 0.59	5	9.3
Ulmus glabra	11.1 ± 1.87	8	1113 ± 122	5	4570 ± 825	11	20.6 ± 1.11	7	16.1 ± 1.08	5	7.4

*Note: M – arithmetic mean, m – average error, N – sample size. * – Maximum basic growth of middle-aged pure tree stands [53–60]*

Table 5

Light demand scales of East European tree species at different ontogenetic stages.
The most heliophilous species are at the beginning and the less heliophilous species at the end of the list. The scales for the ontogenetic stages j–g_1 were compiled on the basis of biomass growth of the undergrowth which grew in the nursery under full light. The scales for stage g_2 were compiled on the basis of the maximum basic growth of middle-aged pure tree stands (Table 4).
The number prior to the name of the species represents the score of light demand

		Ontogenetic stages			
Juvenile (j)	Immature of the first subgroup (im_1)	Immature of the second subgroup (im_2)	Virginile of the first subgroup (v_1)	Young generative (g_1)	Mature generative (g_2)
13. Acer platanoides	13. Ulmus glabra	13. Salix caprea	13. Populus tremula	13. Pinus sylvestris	13. Picea abies
12. Fraxinus excelsior	12. Acer platanoides	12. Pinus sylvestris	12. Ulmus glabra	12. Populus tremula	12. Pinus sylvestris
11. Quercus robur	11. Fraxinus excelsior	11. Picea abies	11. Picea abies	11. Picea abies	11. Quercus robur
10. Ulmus glabra	10. Betula pendula	10. Ulmus glabra	10. Pinus sylvestris	10. Betula pendula	10. Betula pendula
09. Tilia cordata	09. Quercus robur	09. Populus tremula	09. Salix caprea	09. Ulmus glabra	09. Fraxinus excelsior
08. Acer tataricum	08. Pinus sylvestris	08. Betula pendula	08. Betula pendula	08. Salix caprea	08. Populus tremula
07. Picea abies	07. Picea abies	07. Quercus robur	07. Quercus robur	07. Quercus robur	07. Tilia cordata
06. Pinus sylvestris	06. Salix caprea	06. Acer platanoides	06. Fraxinus excelsior	06. Fraxinus excelsior	06. Carpinus betulus
05. Acer campestre	05. Tilia cordata	05. Fraxinus excelsior	05. Acer platanoides	05. Tilia cordata	05. Ulmus glabra
04. Carpinus betulus	04. Carpinus betulus	04. Tilia cordata	04. Carpinus betulus	04. Carpinus betulus	04. Acer platanoides
03. Betula pendula	03. Populus tremula	03. Carpinus betulus	03. Tilia cordata	03. Acer platanoides	03. Acer campestre
02. Salix caprea	02. Acer campestre	02. Acer campestre	02. Acer campestre	02. Acer campestre	02. Salix caprea
01. Populus tremula	01. Acer tataricum	01. Acer tataricum	01. Acer tataricum	01. Acer tataricum	01. Acer tataricum

Acer platanoides. The maple is characterised by the greatest light demand in the stages *j* and *im₁* (Table 5), based on the high values of average annual biomass growth (Table 4). This is facilitated by a large area of leaves (Table 6). A significant light-absorbing surface compensates for the relatively low intensity of the photosynthetic apparatus at the sub-organism level: according to the values of *SDL* and, accordingly, the intensity of photosynthesis, the maple occupies an average position among the trees. The high light demand of the maple at a young age is also due to the early germination of its seeds: seedlings appear in the spring 2–3 months earlier than those of other species, which allows the formation of a fairly developed root system, and the tree directs the main effort to the formation of leaves by the beginning of the summer (relatively dry) season. From the stage *im₂* onwards, the relative light demand of the maple decreases. At first the maple gradually gives way to willow, pine, spruce, elm, aspen, birch and oak, and then – to ash, linden and hornbeam. As a result, this species moves to one of the last places in the scale of light demand. The reasons for the relatively low light demand of the maple in states *g₁* and *g₂* are the comparatively small area of leaves and the small value of *SDL* (Table 6).

Ulmus glabra. In the stage *j*, elm has lower light demand than maple, ash and oak (Table 4, Table 5), which might be associated with a small supply of plastic substances in the seed. However, the high rate of biomass accumulation allows the species to rank first on the light demand scale in the stages *im-v*. Thus, the mass of *im₁* individuals of elm exceeds the mass of *j* plants by 200 times, while this factor is only 40 for maple and ash and 20 for oak. This high biomass accumulation rate is a result of two biological features of elm. First, the leaf surface grows rapidly, because in the stage *j*, an essential part of assimilates is directed to the creation of photosynthetically active tissue (Fig. 5). Second, elm individuals in the stages *im-v* differed in terms of leaf area and *SDL* values and, subsequently, in the intensity of photosynthesis (Table 6). At the beginning of stage *g₁*, elm has lower light demand than pine, aspen, spruce, birch; in the stage *g₂*, elm has lower light demand than oak, ash, linden and hornbeam (Table 5).
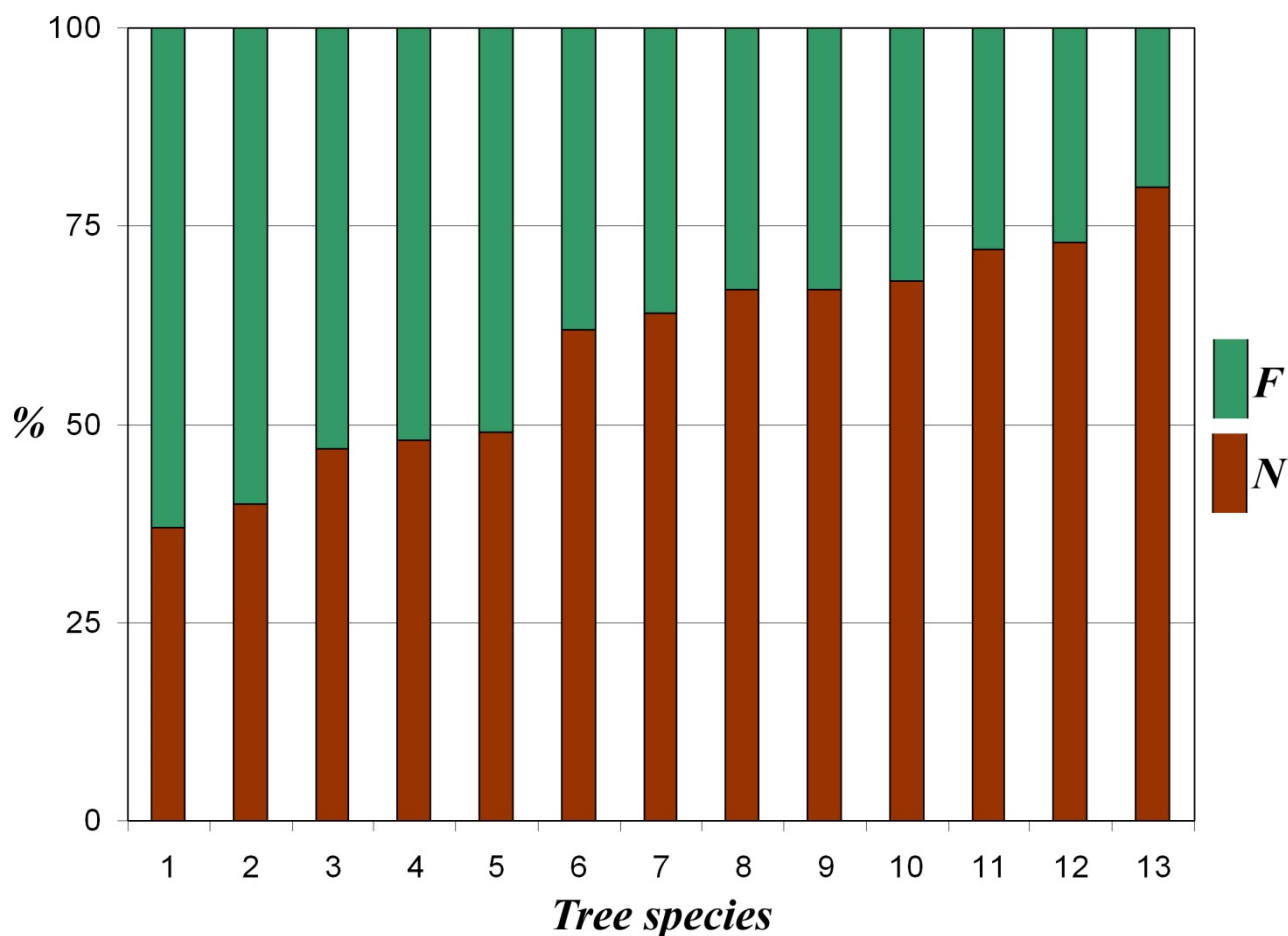

Fig. 5. Ratio of the mass of photosynthetic (*F*) and non-photosynthetic (*N*) parts of juvenile plants of the first year grown in the nursery. Tree species: 1 – *Salix caprea*, 2 – *Populus tremula*, 3 – *Picea abies*, 4 – *Betula pendula*, 5 – *Pinus sylvestris*, 6 – *Ulmus glabra*, 7 – *Acer campestre*, 8 – *Acer platanoides*, 9 – *Carpinus betulus*, 10 – *Tilia cordata*, 11 – *Fraxinus excelsior*, 12 – *Acer tataricum*, 13 – *Quercus robur*

Betula pendula, Populus tremula, Salix caprea and Pinus sylvestris. This group of species, according to the ontogenetic variability of light demand, was similar to the elm. In the first years of life, these plants develop a relatively small photosynthetic apparatus because of the small amount of plastic substances in the seed: according to the leaf area and the *SDL* value, their *j* individuals were inferior to those of other tree species and are distinguished by the least light demand (Table 4, Table 5). However, as early as in phase *j*, they directed the main flow of assimilates into the leaves (Fig. 5). This circumstance is extremely important for fast-growing species, as it ensures a rapid accumulation of biomass. In stage im_2, the assimilating surface area was relatively large, along with a high *SDL* value (Table 6), resulting in significant advantages in light use to accumulate biomass (Table 4). In the stages im_2–*v*, willow, birch, aspen and pine had the highest light demand, which, however, decreased in willow after stage g_1 (Table 5).

Quercus robur. In the stage *j*, oak only had a lower light demand than maple and ash. The relatively high light demand of this species is deter-mined by a significant amount of plastic substances in the seed, which allows *j*–individuals to develop numerous leaves (Fig. 5). However, elm and birch, followed by willow, pine, spruce and aspen, showed higher light demands than oak from the stage *im* onwards, with a significantly increased leaf area. However, in stage g_2, the light demand of oak was again higher than that of birch, willow, elm and aspen (Table 5). The high light demand of oak in all ontogenetic stages in comparison with other broadleaf trees (maples, linden and hornbeam) is a result of the high intensity of photosynthesis, based on the significant *SDL* value (Table 6).

Fraxinus excelsior. The ontogenetic variability of light demand of this species is analogous to that of oak. In the early years, ash and oak only have a lower light demand than Norway maple. The light demand of ash increases in stage g_2, similar to that of oak (Table 5); both species use full light, and their significant productivity is a result of high photosynthesis rates (Table 6). In contrast, in the case of Norway maple and elm, the high productivity in stages *j* and im_1 is a result of the increased leaf area.

Table 6

Leaf area (*LA*) and specific density of the leaf (*SDL*) of trees in different ontogenetic stages in the nursery under full light

Species	Ontogenetic stages									
	j		im_1		im_2		v_1		g_1	
	LA, sm^2 $M \pm m$	SDL, mg·dm^{-2} $M \pm m$	LA, m^2 $M \pm m$	SDL, mg·dm^{-2} $M \pm m$	LA, m^2 $M \pm m$	SDL, mg·dm^{-2} $M \pm m$	LA, m^2	SDL, mg·dm^{-2} $M \pm m$	LA, m^2 $M \pm m$	SDL, mg·dm^{-2} $M \pm m$
Acer campestre	257 ± 40	666 ± 23	0.28 ± 0.05	663 ± 20	3.7 ±0.65	671 ± 6	16	696 ± 17	82 ± 7	763 ± 47
Acer platanoides	922 ± 196	654 ± 24	2.61 ± 0.42	664 ± 18	14.3 ±0.30	747 ± 17	36	774 ± 22	90 ± 5	714 ± 13
Acer tataricum	324 ± 54	712 ± 24	0.10 ± 0.01	656 ± 20	1.2 ± 0.22	616 ± 8	8	671 ± 44	17 ± 1	709 ± 33
Betula pendula	71 ± 17	569 ± 32	1.24 ± 0.14	691 ± 18	18.8 ± 5.05	833 ± 28	81	871 ± 9	230 ± 27	947 ± 17
Carpinus betulus	74 ± 11	650 ± 14	0.47 ± 0.07	768 ± 14	6.6 ± 0.99	749 ± 30	27	850 ± 32	51 ± 3	870 ± 20
Fraxinus excelsior	406 ± 61	975 ± 26	1.85 ± 0.24	799 ± 20	7.9 ± 1.74	793 ± 27	50	855 ± 23	72 ± 3	985 ± 18
Picea abies	929 ± 39	405 ± 8	2.02 ± 0.09	401 ± 22	88.3 ± 2.94	458 ± 30	271	605 ± 30	378 ± 33	666 ± 26
Pinus sylvestris	432 ± 35	708 ± 9	0.96 ± 0.02	850 ± 30	40.7 ± 1.63	987 ± 22	159	913 ± 27	321 ± 30	989 ± 32
Populus tremula	45 ± 7	492 ± 49	0.42 ± 0.09	683 ± 14	24.3 ± 2.02	976 ± 14	84	950 ± 19	125 ± 30	1,019 ± 21
Quercus robur	392 ± 52	750 ± 19	0.70 ± 0.08	858 ± 13	10.2 ± 1.89	1,148 ± 122	41	939 ± 11	110 ± 4	1,022 ± 27
Salix caprea	115 ± 15	440 ± 6	0.89 ± 0.15	791 ± 34	49.9 ± 6.33	917 ± 20	141	1,078 ± 8	103 ± 13	1,039 ± 22
Tilia cordata	515 ± 125	507 ± 24	0.53 ± 0.06	576 ± 24	11.5 ± 0.31	620 ± 24	25	892 ± 15	99 ± 4	765 ± 17
Ulmus glabra	581 ± 100	707 ± 20	5.82 ± 0.78	848 ± 50	33.6 ± 6.00	888 ± 89	159	882 ± 21	144 ± 14	1,017 ± 35
Note: M – arithmetic mean, *m* – average error										

Picea abies. In the stage *j*, spruce had an intermediate light demand. Because of its relatively large photosynthetic surface, juvenile specimens had a higher light demand than birch, pine, hornbeam and *Acer campestre*. However, because of the unusually low *SDL* value, juvenile spruce specimens had a lower light demand than maple, oak, elm and linden (Table 4, Table 5). Nevertheless, because of its relatively high needle surface, the light demand of spruce gradually increased and reached the highest values of all species in the stage g_2. Therefore, aspen, birch and pine have priority in the use of full light for biomass production due to their relatively large leaf area and *SDL* values, while spruce only has a relatively large photosynthetic surface (Table 6). In other words, the highest productivity of spruce is a result of a highly efficient way of using light.

Tilia cordata, Carpinus betulus, Acer campestre and *Acer tataricum*. These species are characterised by low productivity and relatively weak light demands in all ontogenetic stages (Table 4, Table 5). The general properties of this group are the small values of *SDL* and leaf area (Table 6). The location of these species in the scales of light demands is constantly changing. Tatar maple in the *j* stage has a greater light demand than field maple and hornbeam. However, in subsequent ontogenetic stages, Tatar maple has a minimal light demand than all other species. Hornbeam, in most scales, is placed just behind the linden, which has some advantages in using full light. Linden has a larger leaf surface than hornbeam and maples, which is the reason why in the g_2 stage, it has similar light demands than aspen and ash (Table 5).

The developed scales of light demands can be used to predict the behaviour of tree species when they grow together in treefall gaps. Thus, long-term observations on group treefalls in broadleaf forests have revealed a correspondence between the succession dynamics of the undergrowth vegetation and the ontogenetic variability of the light demands of tree species. In the first years after the treefall gap formation, the species most photophilous in the first ontogenetic stages (maple, ash and elm) develop. In the virginile stages, willow, aspen and birch take over, as they are more effective than other tree species in terms of light use. Tree species with low light demands in all stages of ontogenesis occupy a subordinate position at all stages of treefall gap overgrowing.

Ontogenetic scales of ranges of light possibilities of trees

The range of light possibilities (*RLP*) is the limit of irradiance within which the production process can be carried out. The lower limit of this range is determined by the level of irradiance (light minimum) at which the positive growth of tree biomass is still possible. This limit differs between tree species and determines the survival of the undergrowth vegetation. The upper limit of the range is determined by the maximum value of biomass production which is achieved under conditions of free growth in full light. Previously, it was shown that different tree species differ significantly in the possibilities of using full light for biomass production.

The sum of points of shade tolerance and light demands was used to construct ontogenetic scales of *RLP* of tree species (Table 2, Table 5, Fig. 6). The maximum score of shade tolerance (13) was given to tree species with the greatest degree of tolerance to a lack of light, while the minimum score (1) was given to shade-intolerant species. A score of light demands was calculated in a similar way.

An analysis of the position of tree species in the scales showed no pronounced relationship between shade tolerance and light demands, and different combinations of these properties are possible for tree species (Fig. 6). First, tree species with a wide *RLP* are distinguished; these species (for example, maple, elm and spruce in j–v_2 ontogenetic stages) are characterised by a considerable shade tolerance and a high light demand. Such species demonstrate that the gain in productivity in full light is not always accompanied by a loss of shade tolerance. Secondly, tree species with a narrow *RLP* are highlighted. The *RLP* of willow, aspen, birch and pine in im_2–v_2 stages shifted towards high irradiance, as these species are characterised by a high light demand and low shade tolerance. The *RLP* values of Norway maple, field maple, Tatar maple, linden and hornbeam in j–v_2 stages were located in the low-light range due to the high shade tolerance and low light demand of these species.

Relative *RLP* changes in ontogenesis; for example, willow, aspen, birch and pine in the *j* stage showed an extremely narrow *RLP*, which, however, increased with age due to a significant increase in light demand. On the contrary, ash in the *j* stage had a relatively wide *RLP*, which narrowed down with age due to a decrease in shade-tolerance and light demand. On the contrary, the *RLP* of spruce slightly increased with age due to some increase in shade tolerance and light demand (Fig. 6).

The *RLP* scales can be used to predict a set of habitats with different irradiance levels, thereby allowing the prediction of the survival and development of different tree species. Species with a broad *RLP* are actively developing different habitats: from small openings in the crowns of adult trees to large treefall gaps. Species with a narrow *RLP*, which lies in high light densities, gain an advantage in large treefall gaps. Tree species with a

narrow *RLP*, in low light densities, develop successfully in small-sized treefall gaps; these species are also able to survive under the forest canopy in

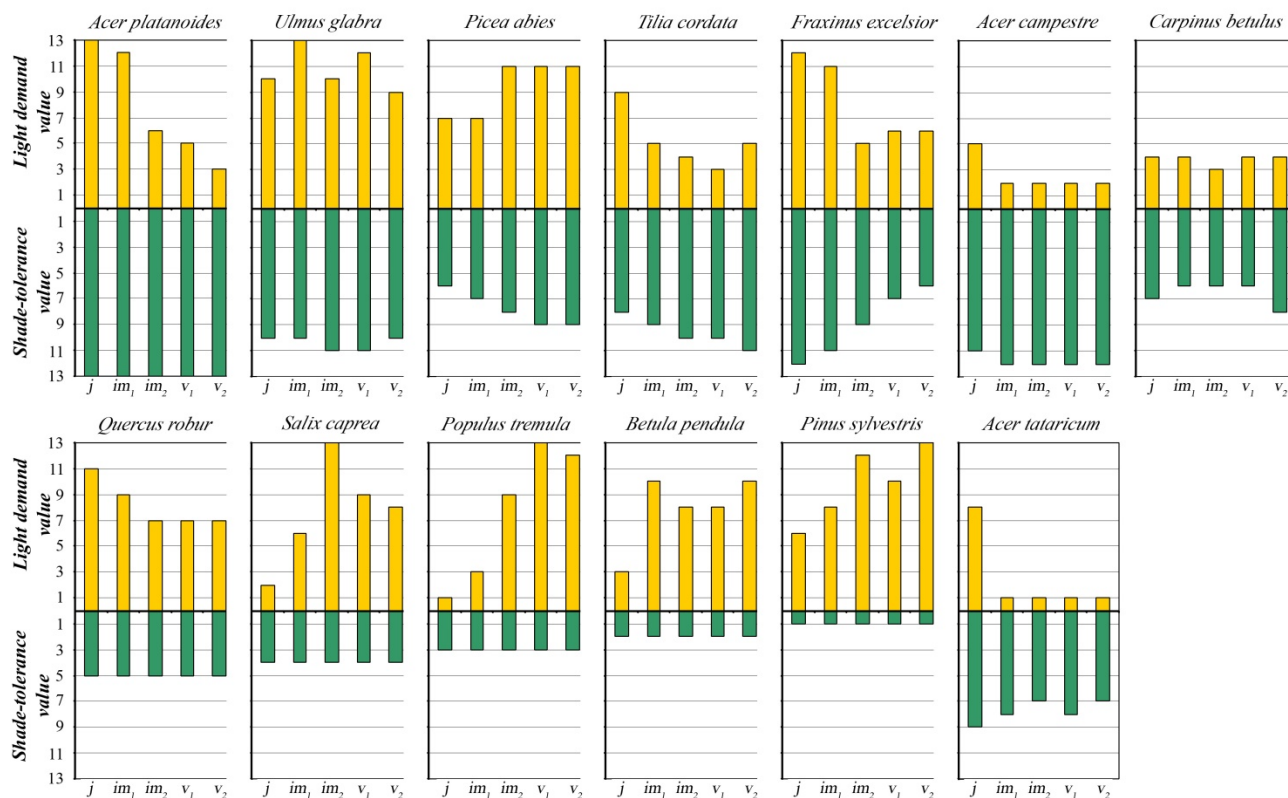anticipation of suitable conditions for development.

Fig. 6. Relative scales of ranges of light possibilities of tree species of the Eastern European forests, depending on the ontogenetic stages: *j* – juvenile, *im₁* – immature of the first subgroup, *im₂* – immature of the second subgroup, *v₁* – virginile of the first subgroup, *v₂* – virginile of the second subgroup

Conclusion

For a more complete understanding of the mechanisms of maintaining tree populations in the forest community, it is necessary to distinguish shade tolerance, light demand and the range of light possibilities among different reactions to light as well as to take into account the hierarchy of the structure of the photosynthetic apparatus and the ontogenetic variability of tree species in relation to light. The idea of the hierarchical organisation of the photosynthetic apparatus of plants made it possible to single out the integral indices of the ratio of plants to light: light minimum of undergrowth and average annual increment of biomass. These indicators of plants do not remain constant throughout life.

Shade tolerance characterises the lower limit of light and production capabilities of plants. Analysis of the species and ontogenetic variability of

shade tolerance allows us to predict the minimum size of treefall gaps in which individuals can normally develop and undergo complete ontogeny. Light demand reflects the upper limit of the light and production capabilities of plants. The developed scales of light demands can be used to predict the behaviour of tree species when they grow together in treefall gaps. The range of light possibilities of the species characterises the limits in which the production process can be carried out. The developed scales of the light possibilities of species can be used to predict a set of habitats with different irradiance levels in terms of the survival and development of different tree species.

Based on our analysis, to maintain all species and the ontogenetic diversity of trees, treefall gaps of different sizes are necessary in the forest community – from small gaps in the forest canopy to large openings that are formed after the fall of several trees.

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