NEMORALISATION OF *PINUS SYLVESTRIS* AND *PICEA ABIES* FOREST STANDS IN THE HEMI-BOREAL ZONE: A CASE STUDY FROM LATVIA

Māris Laiviņš^{1,#}, Gunta Čekstere², and Dārta Kaupe¹

¹ Latvian State Forest Research Institute “Silava”, 111 Rīgas Str., Salaspils, LV-2169, LATVIA

² Institute of Biology, University of Latvia, 4 O. Vācieša Str., Rīga, LV-1004, LATVIA

Corresponding author, maris.laivins@silava.lv

Communicated by Viesturs Melecijs

*At the beginning of the 21st century, in extensively managed mature and over-mature conifer stands (*Pinus sylvestris* and *Picea abies*) in Latvia, establishment of native deciduous broad-leaved (*Acer platanoides*, *Tilia cordata*, *Quercus robur* and *Ulmus laevis*), as well as alien broad-leaved species (*Acer pseudoplatanus* and *Tilia platyphyllos*) has been observed. The establishment of deciduous broad-leaved species in coniferous stands is a process known as nemoralisation of coniferous stands, which is characterised by a large number of seedlings of broad-leaved species, young trees and the formation of a subcanopy layer in stands. Based on the age measurements of individuals of broad-leaved species trees, the establishment of some individuals into the studied coniferous stands occurred 40–50 years ago — in the 1970s–1980s. However, the predominant age of alien broad-leaved tree species in the study plots was 15–25 years, i.e. the introduction of large numbers of seedlings of these species in the coniferous stands occurred at the end of the 20th century. In this manner, in the final phase of the conifer replacement process, stable, mostly shade tolerant, mixed stands consisting of 3–4 species have formed, in which spruce is often found together with broad-leaved species.*

Keywords: coniferous species, deciduous species, forest stand dynamic, *Acer* sp., *Tilia* sp.

INTRODUCTION

In recent decades, many countries in Europe and North America have amassed extensive evidence of the invasion of alien and native deciduous broad-leaved tree species (*Acer*, *Tilia*, *Quercus*, *Robinia*, *Sambucus*, *Corylus* and other genera) into extensively managed forest and non-forest lands in urban, suburban and protected (reserve) forests, in ruderal habitats, wastelands and elsewhere (Wyckoff and Webb, 1996; Pyšek, 1998; Hunter and Mattice, 2002; Alberti, 2005; Lapointe and Brisson, 2012; Sjöman *et al.*, 2012; Kowarik *et al.*, 2013; Kokareviča *et al.*, 2016; Palo and Gimbutas, 2017). The investigations show that, e.g., invasion of *Acer platanoides* trees has a detrimental impact on species richness and tree regeneration in the understory (Fang, 2005; Galbraith-Kent and Handel, 2008). In addition to *A. platanoides*, other deciduous broad-leaved species, like *Ulmus glabra*, *U. laevis*, *Tilia cordata*, *Quercus robur*, *Fraxinus excelsior*, are often found in admixture in the

shrub layer, as well as alien species such as *Tilia platyphyllos* and *Acer pseudoplatanus*, which sometimes form even the subcanopy layer of stands. These broadleaf species successfully compete with the species growing in the forest stand, limiting their vitality and distribution, thus gradually forming a new species composition in the forest stand. Extremely intensive introduction of broad-leaved tree species into coniferous stands has occurred in the nemoral and boreal forest contact zone (Götmark *et al.*, 2005; Liira *et al.*, 2011; Hamberg *et al.*, 2015).

Currently, almost a half (45.1%, calculated based on the State Forest Service data from 2018) of the total Latvian forest area in oligo-, meso- and eutrophic soils is occupied by coniferous forest stands, where the edificator (environment forming plants) species are Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). In Latvia, due to intensive forest management, as well as changing environmental conditions, coniferous forest stands are dynamic.

At the end of the 20th century, the main species composition transformation processes in coniferous stands in Latvia were identified based on studies of meso- and meso-eutrophic *P. sylvestris* and *P. abies* forest plant communities, determining the diversity of their species composition, as well as analysing species and species groups as indicators of environmental status. These transformation processes are related to natural, as well as to anthropogenic forest stand development processes. It was found that eutrophication and synanthropisation of the soil, as well as changes in the composition of forest stand species, reflected the following leading, interrelated transformation processes: ruderalisation, graminification and fruticification of forest stands (Laiviņš, 1998). Forest ruderalisation is the expansion of aggressive ruderal and weed plant communities in semi-natural and natural forest stands. Graminification of forest stands is intensive spread of grasses and is mainly related to the increase of total nitrogen content in the environment, which is caused by atmospheric deposition, as well as by more intensive decomposition and mineralisation of litter. Fruticification (encroachment) is the formation of a thick shrub layer (understorey and young growth) in forest stands when trees reach their natural age-span and leave gaps in the tree stand, or intensive development of shrubs in the stand after extensive forest disturbance, such as due to wind, forest fires, and clear cuts. Of native shrub species, *Corylus avellana*, *Padus avium* and *Sorbus aucuparia* have the largest edificator role in deforested stands, and the most common alien species are *Amelanchier spicata*, *Sambucus racemosa*, *S. nigra*, and *Cotoneaster lucidus* (Lange, 1949; Laiviņš and Laiviņa, 1991; Laiviņš, 2002a, 2002b; Rūrāne, 2004). Shrub development in unmanaged grassland sites, fallows and abandoned ruderal areas is also a process of vegetation fruticification and initial stages of forest communities, such as the shrub formation by *Acer negundo*, *Robinia pseudoacacia*, *R. luxurians*, *Sambucus nigra*, *Aronia x prunifolia* and other species on extensively managed lands (Laiviņš, 2002a; Priede, 2008; Laiviņš and Čekstere 2014; Rutkovska, 2014; Jankovska *et al.*, 2015; Laiviņš and Čekstere, 2015; Marozas *et al.*, 2015; Straygite *et al.*, 2015).

Thus, currently, mainly in mature and overmature coniferous stands in Latvia, there is an intensive invasion of native and alien broad-leaved tree species. This process in our study is called “the process of forest stand nemoralisation”.

The research aim was to identify the initial stages of deciduous broad-leaved forest stands, which are formed by the transformation of coniferous stands in the hemi-boreal climate zone, based on investigation of the composition of the shrub and tree layer of pine and spruce stands, the age of individuals and the features of stand structure.

MATERIALS AND METHODS

Study plots. Intensive invasion of deciduous broad-leaved tree species is currently observed in urban and suburban extensively managed coniferous (mainly pine) forest stands.

Fig. 1. Location of study plots in Latvia.

Therefore, eight forest stands were selected as examples to characterise the transformation process of coniferous forest stands by invasion of broad-leaved species. In these forest stands, permanent study plots for long-term research of forest stand dynamics were established (Fig. 1).

The invasion of *A. platanoides* in *P. sylvestris* forest stands was studied in study plot 5 (Speļģi) in the Gauja National Park and in *P. abies* forest stands in natural forest habitats in plots 3 (Saldus) and 7 (Augštaurene). Replacement of *P. sylvestris* with *T. cordata* was studied in plot 6 (Leukādijas) in Gauja National Park, with *Q. robur* in plot 2 (Dzirkalags — peninsula of Lake Usma), and with European white elm *U. laevis* in plot 8 (Kalnasmidži) in the natural forest habitat of riparian forests of the Gauja River valley (riparian forests). In addition, urban forest stands in plots 1 (Ventspils) and 4 (Ogre) were selected to characterise the invasion of alien broad-leaved species *T. platyphyllos* and *A. pseudoplatanus*, respectively, in *P. sylvestris* forest stands.

The studied forest stands are located in various ecological regions of Latvia, and therefore the climatic conditions in the study plots are different (Table 1). The Baltic coastal *P. sylvestris* forests in plot 1 with *A. platanoides* and *A. pseudoplatanus* in the understory have a milder climate with higher monthly and annual temperatures. With increasing distance from the sea, the monthly and annual temperature amplitudes increase, and a more continental climate background characterises the mixed stand of *P. sylvestris* and *U. laevis* in plot 8 located in the Gauja River valley in north-east Latvia.

Stand plots. To characterise forest stand structure, a circular permanent plot (radius 15 m, area 706.5 m²) was established in each forest stand. A 1.7-m long and 15–20 cm thick pole was positioned in the centre of the sample plot. The geographical coordinates of the centre of the plot were recorded in the LKS-92 coordinate system with a GPS/eXplorist 500 Magellan device (Table 1, Fig. 2).

Canopy trees. All live and dead trees higher than 5 m, as well as broken standing stems longer than 0.5 m, were num-

Table 1. Coordinates of the study plots and climatic data of the nearest meteorological station

Plot No.	Study plot	Location in Latvia	Geographical coordinates, LKS-92		Meteorological station	Mean air temperature (1981–2010), °C					Annual precipitation (mm)
			X	Y		Annual	July	February	Min	Max	
1	Ventspils	Western	6365126	354224	Ventspils	7.3	17.2	-1.6	4.9	10.1	709
2	Dzirkaļrags	Western	6341563	387319	Stende	6.3	16.9	-3.3	2.5	10.6	724
3	Saldus	Western	6278488	410530	Saldus	6.4	17.1	-3.3	2.4	10.4	682
4	Ogre	Central	6296698	537584	Skriveri	6.3	17.6	-4.2	2.5	10.4	739
5	Speļģi	North-eastern	6358420	583140	Priekuļi	6.1	17.5	-4.5	2.6	9.8	705
6	Leukādijas	North-eastern	6358768	583227							
7	Augštaurene	North-eastern	6337181	602408							
8	Kalnasmidži	North-eastern	6373065	641645	Alūksne	5.2	17.1	-5.8	1.8	9.0	758

Fig. 2. Design of the forest stand plots. (1 – center of permanent plots (R – 15 m), 2 – trees, 3 – center of shrub inventory plots (R – 5 m), 4 – seedling inventory plots (1 × 1 m).)

bered in each study plot. The numbers were painted on the trunk with white colour on the side facing the centre of the plot 1.5–1.6 m above the ground. The location of live trees, dead trees, stems and stumps in the plot was obtained by measuring the distance from the centre of the plot with a Vertex IV and determining the azimuth (compass SUONTO). Processing of measurement data and calculation of coordinates were performed in MS Excel.

The following parameters were determined for live trees, deadwood, and broken standing stems in each plot:

- trunk diameter at 1.3 m height (Hultafors Talmeter 3 M);
- tree height measured in leafless condition in autumn or spring (Vertex IV, Haglöf, Sweden);
- the longest (L_1) axis of the tree crown projection and perpendicular (L_2) axis (Vertex IV); based on these mea-

surements the average crown radius $(L_1 + L_2) / 2$ as well as crown asymmetry (L_2 / L_1) were calculated for each tree;

- tree-ring width samples (wood cores) were collected with a Presler increment drill at a height of 1.3 m to determine the number and width of annual increment. Radial growth was measured using the equipment LNTAB IV, at the Latvian State Forest Research Institute “Silava”. Computer software TSAP WIN Scientific 0.55 was used for data pre-processing.

Shrub layer. Trees up to 5 m high and all shrubs were recorded in three smaller circular sub-plots (radius 5 m) located within the plot. The distance of the centre of the sub-plot from the centre of the plot was 7 m, and the azimuth was 0, 120 and 240 degrees from the centre of the plot, respectively. In each sub-plot, all young trees (< 5 m) and shrubs (shoots) and their height were classified in the following height classes: 0.6–1.0 m, 1.1–1.5 m, 1.6–2.0 m, 2.1–3.0 m, 3.1–4.0 m, and 4.1–5.0 m.

In order to describe the distribution of young trees of *T. platyphyllos* on the slope of the esker, a transect was established and a 50 m long measuring tape was stretched from the mother tree in eight directions every 45 degrees, divided by stakes in 5 m long sections. In each section, in a 0.5 m wide band on both sides of the measuring tape, young trees of *T. platyphyllos* (< 5 m) were counted in the same height intervals as in the sub-plots of young trees of the permanent plot.

Seedlings. Counting of seedlings of *A. platanooides*, *A. pseudoplatanus*, *Q. robur*, *P. sylvestris* and other tree species with height less than 0.5 m was done in 16 systematically arranged 1 × 1 m sub-plots. The sub-plots were selected at distances of 4 and 8 m from the centre of the study plot in directions of 0, 90, 180, and 270 degrees, as well as 5 and 10 m from the centre of the study plot in directions of 45, 135, 225, and 315 degrees. Seedlings with height up to 10 cm (less than 1-year-old seedlings), 11–30 cm (1-year- and 2-year-old seedlings) and 30–50 cm (2-year-old and three-year-old seedlings) were counted in each 1 m² plot.

Crown volume and stand layers. Trees were divided into 5-m height classes: 5.1–10.0, 10.1–15.0, and 15.1–20.0 m,

etc. The relative volume of each species in each layer and of each layer in the total volume was calculated using the following formula:

$$V_{crown} = 0.614 \cdot \pi \cdot \left(\frac{L_1 + L_2}{2} \right) \cdot L_{crown}, \text{ where}$$

V_{crown} – crown volume (m^3), L_1, L_2 – axis of the tree crown projection, L_{crown} – crown length, 0.614 – crown shape coefficient (Frank, 2010; Mikšis, 1988).

Statistical analysis. Data were stored in a structured database in EXCEL format. Data Analysis — Descriptive Statistics in MS EXCEL 2019 version was used to calculate statistical parameters for the study stands (mean values, standard error, standard deviation, etc.). A map of plot locations was created using ArcView 6.1 software.

Calculation of stock volume. Wood volume was calculated as follows (Liepa, 1996):

$$= 2.3106 \cdot 10^{-4} \cdot H_g^{0.78193} \cdot D_g^{0.34175 \cdot \lg(H_g) + 1.18811} \cdot N, \text{ where}$$

M, stand stock volume, $\text{m}^3 \cdot \text{ha}^{-1}$;

Hg, average height of forest stand, m;

Dg, average diameter of the forest stand at 1.3 m high, cm;
N, number of trees in a stand, ha^{-1} .

RESULTS

Replacement of coniferous stands with *A. platanoides* and *A. pseudoplatanus*.

Of the broad-leaved species, the most common colonising species was *A. platanoides*. To characterise the expansion process of *A. platanoides* and *A. pseudoplatanus* in *P. sylvestris* forests, an overmature *P. sylvestris* stand in Ventspils city (plot 1) and a mature stand in Gauja National Park (plot 5) were chosen. The establishment of *A. platanoides* in *P. abies* stands of different ages also occurred in plot 7 and in a middle-aged natural habitat with mixed broad-leaved species (*A. platanoides*, *Q. robur*) and *P. abies* stand in plot 3 (Table 2).

Invasion of *A. platanoides* occurs in coniferous forest stands of different ages. Formation of a dense *A. platanoides* seedling cover, young understory, as well as the subcanopy occurs in both middle-aged, pre-mature and mature stands.

Table 2. Parameters of coniferous forest stands with invasion of *Acer* species

Permanent plots	Species	Number of trees		Mean trees parameters		Age, years			Volume	
		N, ha^{-1}	%	D, cm	H, m	Mean	Minimal	Maximal	$\text{m}^3 \text{ha}^{-1}$	%
Spelgi	<i>Pinus sylvestris</i>	438	26.7	36.7 ± 1.5	30.5 ± 0.9	77	65	94	684.5	74.9
	<i>Picea abies</i>	42	2.6	8.1 ± 1.6	7.4 ± 1.6	45	41	49	1.1	0.1
	<i>Acer platanoides</i>	806	49.2	10.3 ± 0.7	15.1 ± 0.6	36	24	57	81.2	8.9
	<i>Quercus robur</i>	57	3.5	14.6 ± 2.4	16.1 ± 0.9	52	48	55	8.5	0.9
	<i>Tilia cordata</i>	28	1.7	20.7 ± 10.3	22.5 ± 0.3	45	33	56	12.3	1.3
	<i>Betula pendula</i>	212	12.9	22.5 ± 3.2	22.6 ± 1.4	57	39	70	124.3	13.6
	<i>Padus avium</i>	42	2.6	8.8 ± 1.7	8.5 ± 1.5	*			1.4	0.2
	<i>Sorbus aucuparia</i>	14	0.9	8.2	11.8	*			0.5	0.1
	Total	1639	100.0						913.8	100.0
Ventspils	<i>Pinus sylvestris</i>	297	72.4	38.7 ± 1.3	18.9 ± 0.3	138	124	150	302.6	98.6
	<i>Acer platanoides</i>	71	17.3	10.5 ± 1.1	5.9 ± 0.3	25	16	33	2.3	0.7
	<i>Acer pseudoplatanus</i>	42	10.2	12.3 ± 0.2	6.7 ± 0.1	22	16	28	2	0.7
	Total	410	100.0						306.9	100.0
Augštaurene	<i>Pinus sylvestris</i>	57	7.4	41.5 ± 1.6	31.3 ± 2.6	153	147	164	105.1	12.6
	<i>Picea abies</i> I layer	127	16.5	52.1 ± 3.6	34.3 ± 1.1	129	102	159	666.5	80.1
	<i>Picea abies</i> II layer	226	29.4	10.8 ± 1.5	10.7 ± 1.3	42	34	49	21.9	2.6
	<i>Acer platanoides</i>	156	20.3	10.2 ± 2.8	13.4 ± 1.9	41	30	62	26	3.1
	<i>Ulmus glabra</i>	42	5.5	12.0 ± 4.0	14.3 ± 3.7	27	23	31	5.3	0.6
	<i>Padus avium</i>	14	1.8	6.7	8.2	*			0.2	0.1
	<i>Sorbus aucuparia</i>	147	19.1	8.6 ± 1.1	10.8 ± 0.9	55	66		6.6	0.8
	Total	769	100.0						831.6	100.0
Saldus	<i>Picea abies</i>	71	14.4	20.3 ± 4.1	16.3 ± 3.0	49	41	59	80.4	16.2
	<i>Acer platanoides</i>	311	63.0	24.0 ± 2.7	22.0 ± 1.6	58	43	65	226.8	45.7
	<i>Quercus robur</i>	28	5.7	50.4 ± 6.2	32.9 ± 1.6	65	64	65	84.7	17.1
	<i>Malus sylvestris</i>	14	2.8	32.7	21.3	*			12.2	2.5
	<i>Betula pendula</i>	42	8.5	39.3 ± 3.8	35.8 ± 2.1	64	60	68	84.1	16.9
	<i>Alnus incana</i>	14	2.8	12.2	20.6	43			1.6	0.3
	<i>Populus tremula</i>	14	2.8	22.6	24.4	*			6.7	1.3
	Total	494	100.0						496.5	100.0

*no measurements

Fig. 3. Distribution of different age and stem diameter of maple individuals in the studied pine (Spelģi, plot 5) and spruce (Augštaurene, plot 7) stands (possible mother tree marked in red).

The main prerequisite for the rapid invasion of *A. platanoides* is *A. platanoides* individuals growing in or near conifer stands and producing seeds. For example, in study plots 5 and 7 there are at least one or a few 50–60-year-old *A. platanoides*, which produce sufficiently abundant seeds and ensure the growth of *A. platanoides* seedlings and young trees (Fig. 3).

The number of *A. platanoides* seedlings can be very variable. The largest amount of seedlings was recorded in the middle-aged mixed *A. platanoides* and *P. abies* stand in plot 4 in central Latvia (Table 3). The most typical number of

seedlings in *P. sylvestris* stands was several tens of thousands of seedlings per ha. In the young understory (height 0.5–5.0 m), the number of young *A. platanoides* trees (as well as the number of seedlings) varied from a few hundred in plot 7 to several thousand individuals in plot 4 (Table 4).

In the *P. sylvestris* stand in the Ventspils urban forest (plot 1), invasion of *A. platanoides* and *A. pseudoplatanus* occurred simultaneously. It was observed that mother-trees for seed production of *A. platanoides* and *A. pseudoplatanus* at approximately 50 m distance in the nearby cemetery. The number of *A. platanoides* individuals in the seedling and shrub layers was slightly higher than for the *A. pseudoplatanus*.

Replacement of *P. sylvestris* stands with *T. cordata*. Replacement of different age *P. sylvestris* stands with deciduous broad-leaved tree species, especially *T. cordata*, was observed in plot 6 in the Gauja National Park (Table 5). In this forest stand, 12 species were recorded. The edificator species was *P. sylvestris*, having the largest volume (91.7% of total stand volume), while deciduous broad-leaved species comprised only 7.5%. According to the number of individuals in the stand, the proportion of *P. sylvestris* was

Table 3. Number of seedlings in the permanent plots (individuals per ha)

Species	Permanent plots							
	Urban forests		Suburban forests					
	Ventspils	Ogre	Spelģi	Saldus	Augštaurene	Leukādijas	Kalnasidži	Dzirkaļrags
<i>Acer platanoides</i>	51666	171250	66875	260625	1250	5000	1875	625
<i>Acer pseudoplatanus</i>	18125							
<i>Tilia cordata</i>		625	4375			2500		
<i>Tilia platyphyllos</i>		22500						
<i>Quercus robur</i>		625	625	5000		1250		1875
<i>Fraxinus excelsior</i>		1875	5000			625		
<i>Ulmus glabra</i>		1875	625					
<i>Ulmus laevis</i>							1875	
<i>Picea abies</i>				625	11875			

Table 4. Number of young trees in the shrub layer (height: 0.3–5.0 m) in the permanent plots (individuals per ha)

Species	Permanent plots							
	Urban forests		Suburban forests					
	Ventspils	Ogre	Spelģi	Saldus	Augštaurene	Leukādijas	Kalnasidži	Dzirkaļrags
<i>Acer platanoides</i>	339	3524	1698	4373	572	550	253	42
<i>Acer pseudoplatanus</i>	212							
<i>Tilia cordata</i>		166	467			2292		
<i>Tilia platyphyllos</i>		3534						
<i>Quercus robur</i>		42			42	679		1402
<i>Fraxinus excelsior</i>		42	85	212				
<i>Ulmus glabra</i>		84			212	42		
<i>Ulmus laevis</i>							297	
<i>Picea abies</i>			42	764	679	42		
<i>Betula pendula</i>						170		212
<i>Populus tremula</i>			127	3737				
<i>Alnus incana</i>							679	
<i>Salix caprea</i>				85				

Table 5. Parameters of pine stands with lime, elm and oak

Permanent plots	Species	Number of trees		Mean tree parameters		Age, years			Volume	
		N·ha ⁻¹	%	D, cm	H, m	Mean	Minimal	Maximal	m ³ ·ha ⁻¹	%
Leukādijas	<i>Pinus sylvestris</i> Canopy layer	113	7.7	38.9 ± 4.1	31.0 ± 2.1	86	80	90	217.9	32.5
	<i>Pinus sylvestris</i> Subcanopy layer	495	33.7	26.8 ± 0.9	28.9 ± 0.8	64	50	65	397.1	59.2
	<i>Picea abies</i>	42	2.9	8.4 ± 1.8	8.0 ± 2.3	20	17	23	1.3	0.2
	<i>Tilia cordata</i>	198	13.5	10.8 ± 1.5	12.7 ± 1.1	23	16	38	20.5	3.1
	<i>Acer platanoides</i>	156	10.6	12.0 ± 1.8	13.9 ± 1.2	34	26	61	17.3	2.6
	<i>Fraxinus excelsior</i>	71	4.8	11.7 ± 2.0	14.9 ± 1.6	34	26	40	7.1	1.1
	<i>Quercus robur</i>	14	1.0	5.9	7.9	33			0.2	0.1
	<i>Ulmus glabra</i>	71	4.8	9.8 ± 0.9	12.9 ± 0.9	24	21	27	3.9	0.6
	<i>Betula pendula</i>	28	1.9	8.3 ± 0.2	11.5 ± 1.7	49	44	63	0.9	0.1
	<i>Salix caprea</i>	28	1.9	11.1 ± 0.1	14.5 ± 0.3	26	25	26	2.0	0.3
	<i>Padus avium</i>	142	9.7	6.2 ± 0.4	7.9 ± 0.6	29	13	25	1.9	0.3
	<i>Sorbus aucuparia</i>	99	6.7	5.3 ± 0.4	6.8 ± 0.3	26	23	30	0.9	0.1
	<i>Rhamnus cathartica</i>	14	1.0	5.7	7.0	*			0.1	0.0
	Total	1471	100.0						671.1	100.0
Ogre	<i>Pinus sylvestris</i>	85	9.4	49.7 ± 2.2	24.8 ± 1.2	119	102	132	187.2	54.8
	<i>Picea abies</i>	14	1.5	57.2	28.6	*			49.4	14.5
	<i>Tilia platyphyllos</i> Canopy layer	14	1.5	51.3	24.3	82			31.8	9.3
	<i>Tilia platyphyllos</i> Sapling layer	467	51.6	8.0 ± 0.8	7.9 ± 0.4	14	10	45	15.9	4.7
	<i>Acer platanoides</i> Subcanopy layer	297	32.8	16.2 ± 1.4	14.6 ± 0.7	43	17	51	57.3	16.8
	<i>Ulmus glabra</i>	28	3.1	4.5 ± 0.7	6.7 ± 0.2	12			0.2	0.1
	Total	905	100.0						341.8	100.0
Kalnasmidži	<i>Pinus sylvestris</i>	226	18.8	38.9 ± 3.2	28.7 ± 1.0	64	62	66	379.2	63.7
	<i>Ulmus laevis</i>	934	77.7	13.8 ± 0.9	13.9 ± 0.7	49	33	63	179.4	30.1
	<i>Betula pendula</i>	14	1.2	40.4	29.5	*			23.9	4.0
	<i>Alnus incana</i>	28	2.3	22.8 ± 0.7	25.2 ± 0.7	50	45	55	12.9	2.2
	Total	1202	100.0						595.4	100.0
Dzirkaļrags	<i>Pinus sylvestris</i>	127	20.9	44.5 ± 3.3	28.7 ± 1.2	119	98	119	271.6	83.1
	<i>Quercus robur</i>	481	79.1	13.7 ± 0.7	12.3 ± 0.5	41	34	57	55.2	16.9
	Total	608	100.0						326.8	100.0

*no measurements

41.4%, and of deciduous broad-leaved species — 34.7%. Currently the stand is very dynamic and intensive decay of *P. sylvestris* is occurring (volume of dead *P. sylvestris* was 119.4 m³·ha⁻¹ or 19.4% of volume of living *P. sylvestris*), as well as expansion of deciduous broad-leaved species, especially, *T. cordata*, *A. platanoides*, and *Q. robur*. The number of *T. cordata* seedlings and young growth trees was about 2500 individuals·ha⁻¹, the density of *A. platanoides* seedlings and shrub layer trees differed by ten times, *Q. robur* by two times. Individuals of *F. excelsior* and *U. glabra* were also found in the seedling, shrub and tree layers (Tables 3, 4).

Replacement of *P. sylvestris* stands with *T. platyphyllos*.

Plot 4 was located in a stand containing *P. sylvestris* trees and *T. platyphyllos* in a small area (approximately 1000 m²), in the upper part of the southern slope of the Zilie kalni esker in Ogre (slope 12°, exposition 180°). This is a unique

Fig. 4. Distribution of individuals in forest stand layers in the Ogre study plot (33 *Pinus sylvestris*, 33 *Acer platanoides*, 33 *Tilia platyphyllos*).

and currently rare case in Latvia. The canopy layer of the stand (24–25 m) consists of mature and over-mature *P. sylvestris* trees and one 82-year-old *T. platyphyllos* (Table 5, Fig. 4). The subcanopy layer consists of 15–20 m high *A.*

Fig. 5. Distribution of young large-leaved limes in the vicinity of the mother tree (number of individuals and distance from the mother tree).

platanoides, and the sapling layer of 5–10 m high *T. platyphyllos*.

The tallest *A. platanoides* in the subcanopy layer had age of 40–50 years. The average defoliation of tree crowns was 30%, but several individuals had severely thinned crown (defoliation > 60%). The sapling layer consisted of a large number of young vigorous *T. platyphyllos* with height 5–10 m (average crown defoliation — 12%) with a mixture of some *A. platanoides* and *U. glabra*. The largest number of seedlings was for *A. platanoides* and for *T. platyphyllos*, and in the shrub layer the number of individuals for *A. platanoides* and *T. platyphyllos* was similar (Tables 3, 4). *T. cordata* individuals were also found in the seedling and shrub layers.

The counting of *T. platyphyllos* in the seedling and shrub layers, carried out by the transect method on the esker, indicated the rapid spread of individuals of this species in the vicinity of the 82-year-old mother tree (Fig. 5). Young *T. platyphyllos* were found in larger numbers (up to 50 m from the mother tree) in the eastern and south-eastern direction (down the slope).

Replacement of *P. sylvestris* trees with *U. laevis*. The establishment of *U. laevis* in *P. sylvestris* stands was observed on the southern slope of the Gauja River terrace on dolomite bedrock (study plot 8). In the mixed *P. sylvestris* and *U. laevis* forest stand, *P. sylvestris* individuals had approximately the same age (average age 64 years, and the age difference of individuals did not exceed five years) (Table 5). The height and diameter of *P. sylvestris* did not differ significantly. Some of the largest *U. laevis* had age similar to that of *P. sylvestris* trees, but most *U. laevis* had different age, diameter, and height. Currently, *P. sylvestris* dominates the stock volume, but according to the number of individuals, *U. laevis* is dominant. The stand is dense with poor light conditions under the canopy layer (closure of 90–95%), and therefore the ground cover is poor and the number of seedlings and young trees in the shrub layer is small. Three species with a small number of individuals had

Fig. 6. Distribution of the proportion of crown volume in the layers of Leukādija study plot.

established — *Alnus incana*, *U. laevis* and *A. platanoides* (Table 4). *P. sylvestris* does not regenerate in such shaded conditions. Numerous and vigorous *U. laevis* individuals of different ages in the stand indicated the increase in the edifier role of this species in the stand and formation of an *U. laevis* stand in the future.

Replacement of a *P. sylvestris* stand with *Q. robur*. Transformation of *P. sylvestris* stands into *Q. robur* stands is currently less common in Latvia, as *P. sylvestris* forests are intensively managed. *P. sylvestris* forest stands with a *Q. robur* shrub and sapling layers are found in mesotrophic growing conditions, as in plot 2 in the Dzirkalags stand. The number of stand forming species is small and consisted of two species — in the canopy layer the edifier species was *P. sylvestris*, and *Q. robur* occurred in the subcanopy (Table 5). The number of *Q. robur* individuals in the seedling and shrub layers is small, and a few *A. platanoides* occur (Tables 3, 4). *P. sylvestris* does not regenerate in the stand due to shading.

Layering of mixed coniferous-broad-leaved stands. In the process of transformation of coniferous stands, the formation of composite stands is characteristic, in which the tallest dominant layer is formed by conifers — *P. sylvestris* or *P. abies*, and the subcanopy layer by one of the broad-leaved tree species (Fig. 6). In better growing conditions (study plots: 5–8) the dominant height of *P. sylvestris* and *P. abies* in the first layer is 25–35 m, and in lower quality conditions (plots 4 and 1) — 20–30 m. The subcanopy layer trees (broad-leaved tree species with a small admixture of other deciduous tree species) are usually 20–25 m high.

Below the conifer canopy layer, broad-leaved species have wide, thick crowns that ensure intensive physiological processes. Currently, in most of the surveyed forest stands, the crown volume of the subcanopy layer of broad-leaved and other deciduous tree species exceeded the volume of *P. sylvestris* or *P. abies* crowns of the dominant canopy layer. For example, in plot 6 the total crown volume of *T. cordata*, *A. platanoides*, *F. excelsior*, *U. laevis*, *Q. robur*, other deciduous tree species up to height of 25 m was 54.7%, and

the crown volume of *P. sylvestris* was 45.3% of the total crown volume (Fig. 6).

DISCUSSION

A. platanoides is particularly prevalent in urban and suburban forests, successfully competing with the dominant species, limiting their vitality and distribution, and thus gradually forming a new species composition in the stand (Kowarik *et al.*, 2013; Rogers, 2013; Fang and Wang, 2020). Our results showed that intensive invasion of *A. platanoides* in intensively managed forest stands, forests of protected nature territories, and specially protected forest districts, urban and suburban forests is also occurring in Latvia. *A. platanoides* seedlings form a large proportion of the seedling cover, young *A. platanoides* dominate in the shrub layer, but in the subcanopy below the *P. sylvestris* and *P. abies* upper layer. The subcanopy layer is formed by vigorous *A. platanoides* individuals, often mixed with other deciduous broad-leaved species (*T. cordata*, *Q. robur*, *U. glabra*).

Generally, *A. platanoides* is suitable for growing in dry and sandy soils, and it is also tolerant of long drought periods, which are typical in urban environments (Roloff *et al.*, 2009; Sjöman *et al.*, 2015). In the 21st century, not only in cities, but also in many regions in Latvia, long periods of drought and heat lasting up to 2–3 weeks have been observed (Avotniece *et al.*, 2010; Kļaviņš *et al.*, 2012). Such conditions are favourable for the spread of *A. platanoides* and *A. negundo*, especially in the more continental regions in the south-east part of the country. Moreover, according to climatic forecasts for native forest tree species in Lithuania, the climate will be suited for development of *A. platanoides* and other deciduous tree species, and will be less suited for growth of *P. sylvestris* (Ozolinčius *et al.*, 2014).

In Latvia, *A. platanoides* colonises *P. sylvestris* and *P. abies* stands of various age, from middle-aged stands with age 40–80 years to overmature stands with age 140 years and older (Table 2). In coniferous stands, individuals of *A. platanoides* have different age; the older individuals reach 60–70 years (Fig. 3; Table 2). These were the first to be established in the stand and have been donors to future generations of *A. platanoides*. Coniferous stands with a subcanopy of *A. platanoides* have a very large number of seedlings (max. > 260 000 ind.·ha⁻¹, average 95 104 ind.·ha⁻¹). Comparing the number of *A. platanoides* individuals in the seedling layer and shrub layer, it is clear that in coniferous forest stands the majority of seedlings decay before reaching a height of 0.5 m.

Some cases of naturalisation of *A. pseudoplatanus* in pine forests were already observed in southern Latvia in the 1990s (unpublished data, M. Laiviņš geobotanical descriptions in 1997). This tree species was probably spontaneously introduced in Latvia from Lithuania. *A. pseudoplatanus* plantations in forests in Lithuania were established since the 19th century (Straigyte and Baliuckas, 2015), but

the first case of its naturalisation was noted in 1950 in south-western Lithuania (Gudžinskas, 1998). In Lithuania, the species grows in fertile moist sites and in secondary forests, it is frost and shade tolerant (Navasaitis, 2004). The largest density of *A. pseudoplatanus* was observed in plots dominated by pine with birch, maple, and lime (Straigyte and Baliuckas, 2015). In *P. sylvestris* stands with either beech (*P. sylvestris* – *F. sylvatica*) or spruce (*P. sylvestris* – *P. abies*) in the subcanopy layer, frequency of *A. platanoides* frequency in the subcanopy layer was 71% and 0%, and for *A. pseudoplatanus* – 28% and 0%, respectively, while in other layers, no *Acer* was found (Marozas *et al.*, 2014). Currently, *A. pseudoplatanus* is an alien tree species with intensive naturalisation potential in Latvia.

Higher air temperature (on average above +15 °C) promotes better germination of *T. cordata* and *T. platyphyllos* seeds and faster seedling growth. Good soil drainage/aeration and nutrient content, especially nitrogen and potassium, contribute to vitality and faster dispersal of *Tilia* sp. (Pigott, 2012; Jaegre *et al.*, 2016). Falinski (1986) attributes the fast dispersal of *T. cordata* in the Puszcza Białowiesza and throughout Europe to environmental eutrophication and global warming. Indeed, the formation of *T. platyphyllos* plant communities in Latvia occurs on well-drained eutrophic and warmer southern exposure slopes, such as on the esker slope in Ogre (in this publication) and the Bārta River terrace slope (Laiviņš 2017). Increased expansion of *T. platyphyllos* in southern Baltic forest stands is forecast for the middle of the 21st century (Ozolinčius *et al.*, 2014). In the coming years, a significant increase in the influence of *Tilia* species in forest stands is expected, which confirms the hypothesis of the edificator (environment forming plants) role of shade tolerant species in the development of forest plant communities, in relation with the environment, that are close to the climax stage (Smirnova, 1998; 2004a; 2004b).

The determined ages of broad-leaved species in the mixed *P. sylvestris* and *T. cordata* stand in plot 6 located in north-east Latvia showed that *A. platanoides* was the first species to establish in the stand. The oldest *A. platanoides* was 61 years old, and after a period of 20 years, other *A. platanoides* individuals established. In plot 6, as well as in plots 5 and 7 (Fig. 3), one vigorous individual was initially established, which was the basis for the development of future generations of *A. platanoides*. The oldest *T. cordata* and *F. excelsior* trees were at least 20 years younger than the oldest *A. platanoides* (Table 5). Currently, the number of young trees in the seedling and shrub layers indicate that *T. cordata* trees had the greatest vitality among deciduous broad-leaved tree species. In the future, it is likely to become the dominant species in the forest stand.

Similar trends in broad-leaved species change are seen in the stand of *P. sylvestris* and *T. platyphyllos* (plot 4). The dominant species in different layers differ in light requirements. The species of the canopy layers, i.e. *P. sylvestris* and also *A. platanoides*, are more light demanding, while *T. platyphyllos* in the sapling layer is a shade tolerant species.

In the following years, a significant increase in the role of *T. platyphyllos* in the stand is expected. The prevailing west winds and the slope facilitate the dispersal of *T. platyphyllos* seeds.

Replacement of *P. sylvestris* with *U. laevis* is also predicted on the slopes of river terraces, where vital *U. laevis* stands can be found next to the high floodplain. The mixed stand of *P. sylvestris* and *U. laevis* apparently formed from a *P. sylvestris* stand that had developed on xerophytic grassland (dominant species *Helictotrichon pratense*). Presumably, some individuals of forest and shrub species like *U. laevis* and *A. incana*, which are characteristic of river valleys, have also become established in the young *P. sylvestris* stand, and later when the stand was formed, began to compete with *P. sylvestris* of the dominant stand. Fragments of xerophytic grasslands at a few hundred meters distance from the plot contain a few vigorous young *P. sylvestris* (the early stage of the *P. sylvestris* stand) and *Juniperus communis*, as well some young *U. laevis*, indicating the developmental course for such stands.

The study showed a decline in the role of pioneer species (*Betula pendula*, *Populus tremula*, *Alnus incana*) in dynamic forest stabilisation processes and an increasing role of broad-leaved species (more so for *A. platanooides* and *U. glabra*, less for *T. cordata*, *F. excelsior*, *U. laevis* and *Q. robur*) in the replacement processes of tree species. Such an increase in the role of broad-leaved species in the development of coniferous stands can be seen in all the described examples of replacement of *P. sylvestris* and *P. abies* in our study plots.

Study of tree regeneration in mature and old forests in boreo-nemoral forests in Estonia have also revealed that seedlings of temperate broad-leaved trees prevailed in productive boreonemoral forests. Sapling abundance was determined by forest site-type, and facilitated by forest stand diversity, variability in stand closure, abundant moss, lying dead wood, as well as a thick organic layer (Liira *et al.*, 2011).

Our study showed that the replacement of *P. sylvestris* and *P. abies* stands with broad-leaved species begins with the stable establishment of broad-leaved species into the stand. When trees reach their reproductive age, self-sowing occurs and usually a large number of seedlings occur and develop into the shrub layer. With further growth the young trees reach the tree layer in the stand relatively quickly. Based on the age measurements of individuals of broad-leaved species trees, the establishment of some individuals into the studied coniferous stands took place 40–50 years ago, in the 1970s–1980s. In the beginning, this process is slower and less noticeable, but with the seed propagation of broad-leaved species, it intensifies. The predominant age of alien broad-leaved tree species in the study plots was 15–25 years, indicating that the mass introduction of seedlings of these species in coniferous stands occurred at the end of the 20th century. In this manner, in the final phase of the conifer replacement process, stable, mostly shade tolerant, mixed

stands consisting of 3–4 species are formed, in which *P. abies* is often found together with broad-leaved species.

30–40 years ago, the nemoralisation process in extensively managed coniferous forests involved changes in the composition of ground cover species (ruderalisation and graminification) and often also the formation of a thick layer of native and alien species. However, at present, the species composition and stand structure of the understory is uncharacteristic of coniferous forests. Complex multi-storey stands are formed, in which the seedling layer is formed by broad-leaved species.

In the first half of the 20th century, K. Melderis (1939), and later K. Bush (Bush and Ievinsh, 1984; Bush, 1989), wrote about the natural change of species in Latvia, mainly replacement of conifers (especially *P. sylvestris*) with pioneer species species. The replacement of *P. sylvestris* stands with *Q. robur*, *T. cordata*, *A. platanooides* and *A. campestre* and *Carpinus betulus* in the ecotone of forest and steppe biomes was also analysed in 20th century Russian and Ukrainian forestry textbooks (Nesterov, 1954; Morozov, 1949; Pogrebnak, 1963). It is important to emphasise that environmental factors and forest stand syngenetic processes influenced species change in forest stands in Eastern Europe, Russia, and Ukraine several hundred kilometres southeast of the territory of Latvia 60–100 years ago, and these changes have now become prevalent in Latvia. This indicates not only the migration of species and plant communities, but also the migration of spontaneous forest stand development processes from south to north.

ACKNOWLEDGMENTS

This study was financially supported by the Latvian State Forests Stock Company Research Project (2016–2020) “Role of Broad-leaved Forest Stands in Sustainable Forestry in Latvia”. The authors are grateful to Dr. Dainis Edgars Ruņģis for English corrections of the manuscript.

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Received 10 February 2021

Accepted in the final form 22 July 2021

PINUS SYLVESTRIS UN *PICEA ABIES* MEŽAUDŽU NEMORALIZĀCIJA HEMI-BOREĀLĀ ZONĀ: LATVIJAS PIEMĒRS

Latvijā 21. gs. sākumā ekstensīvi apsaimniekotās pieaugušās un pāraugušās skujkoku (*Pinus sylvestris* un *Picea abies*) audzēs ieviešas vietējās platlapju — *Acer platanoides*, *Tilia cordata*, *Quercus robur* un *Ulmus laevis*, kā arī svešzemju platlapju — *Acer pseudoplatanus* un *Tilia platyphyllos* sugas. Platlapju sugu ieviešanās skujkoku audzēs nosaukta par skujkoku audžu nemoralizācijas procesu, kam raksturīga lielu platlapju sugu sējeņu, jauno kociņu skaitu un otrā stāva veidošanās kokaudzē. Pamatojoties uz platlapju sugu indivīdu vecuma mērījumiem, atsevišķu indivīdu ieviešanās pētītajās skujkoku audzēs notikusi pirms 40–50 gadiem — 20. gs. 70.–80. gados. Savukārt svešzemju platlapju koku sugām valdošais vecums ir 15–25 gadi, šo sugu masveida sējeņu ieviešanās skujkoku audzēs varētu būt saistīta ar 20. un 21. gs. miju. Noslēdzošajā skujkoku nomaiņas procesa fāzē veidojas stabila 3–4 galvenokārt ēncietīgu, sugu mistrotas audzes, kurās kopā ar platlapju sugām nereti ir sastopama arī egle.