PROCEEDINGS OF THE LATVIAN ACADEMY OF SCIENCES. Section B, Vol. 70 (2016), No. 3 (702), pp. 131–137.
DOI: 10.1515/prolas-2016-0021

UNDERSTORY CHANGES IN *FRAXINUS EXCELSIOR* STANDS IN RESPONSE TO DIEBACK IN LATVIA

Ilze Pušpure[1 #], Māris Laiviņš[1, 2], Roberts Matisons[1], and Tālis Gaitnieks[1]

[1] Latvian State Forest Research Institute Silava, Rīgas iela 111, Salaspils, LV-2169, LATVIA

[2] Forest Sector Competence Centre, Dzērbenes iela 23, Rīga, LV-1006, LATVIA

[#] Corresponding author; ilze.puspure@silava.lv

Communicated by Tālis Gaitnieks

Intense dieback of Fraxinus excelsior *L. has been causing rapid changes in advance growth of trees and understory shrub growth of the affected stands. In this study, changes in composition and density of understory were studied in 15 permanent plots (each 235.6 m²), repeatedly sampled in 2005, 2010, and 2015. Within each plot, the number and average height of understory individuals were determined. The successional changes in understory were assessed by Detrended Correspondence Analysis. In total, 11 advance growth and 20 undergrowth species were recorded. A significant increase in the density of understory was observed only in 2015, mainly due to understorey growth of* Corylus avellana *L.,* Padus avium *Mill., and* Lonicera xylosteum *L. Regarding advanced growth, the highest density was observed for* Ulmus glabra *Huds.,* F. excelsior *and* Acer platanoides *L.; the density of* A. platanoides *and* F. excelsior *increased particularly in the period from 2010–2015. The observed successional changes suggested individuality of development of the affected stands according to the composition of the remaining and neighbouring canopy trees.*

Key words: Fraxinus excelsior*, succession, advance growth, undergrowth,* Hymenoscyphus fraxineus*, recovery.*

INTRODUCTION

Studies of understory dynamics, i.e. advance growth of trees (AG) and understory growth of shrubs (UG), are mostly related to the changes fallowing disturbance of canopy (Klinka *et al*., 1996) caused by weather, harvesting (Mallik, 2003), pests (Ehrenfeld, 1980) or disease (Mackey and Sivec, 1973; McCormick and Platt, 1980; Lygis *et al*., 2014). Since the mid-1990s, in Europe, intense dieback caused by the pathogenic fungus *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz, Hosoya, comb. nov. has severely decreased the abundance of *Fraxinus excelsior* L. (Vasiliauskas *et al*., 2006). Studies conducted prior to the dieback showed successful self-regeneration of *F. excelsior* (Laiviņš and Mangale, 2004; Anonymous, 2005; Dobrowolska *et al*., 2011), but since the dieback, the regeneration has decreased sharply (Bakys, 2013). Simultaneously, changes in the understory species composition and density have been observed in the affected stands (Lygis *et al*., 2014). A similar succession was observed also in stands after Dutch elm disease (*Ophiostoma novo-ulmi* Brasier), as significant changes in UG were observed in stands with severe dieback, while minor changes were observed in healthy stands (Dunn, 1986). Huenneke (1983) showed that after Dutch elm disease, species composition and its change were influenced by the progression of individual tree dieback, the number of dead trees, gap size and the presence of adjacent gaps. McCormick and Platt (1980) suggested that changes in species composition after chestnut-blight mainly depended on the time since the disturbance and on local conditions. A dense UG layer is also known to strongly compete with AG regeneration (Beckage *et al*., 2000; Royo and Carson, 2006), thus altering the rate and direction of the succession (Givnish, 2002).

Considering that *F. excelsior* planting has been stopped (Kirisits *et al*., 2011, Bakys, 2013), knowledge about the natural succession of affected stands is crucial for assessment of their potential and for planning of further management. The future development of stands might be already guessed from the present composition of understory. Bakys (2013) and Lygis *et al.* (2014) showed that damaged *F. excelsior* stands tend to transform to stands dominated by early successional tree species like *Betula pendula* Roth, *Alnus incana* L. and *Populus tremula* L. The absence of predisturbance data is a major problem for many studies on forest response to sudden changes; therefore, long-term vegetation surveys are useful for understanding of successional processes (Sulser, 1971; Henry and Swan, 1974; Brewer, 1980; Sheil, 2001). The aim of the study was to evaluate changes in AG and UG species composition in affected *F. excelsior* stands during the recent decade and to assess potential transformations in the future. We hypothesised that the incidence of *F. excelsior* regeneration in previously *F. excelsior* dominated stands has decreased, and hence the species might be replaced by others (early successional tree species).

MATERIALS AND METHODS

Studied sites, sampling, and measurements. In this study, 15 permanent plots were established in 2005 in uneven-aged stands initially dominated by *F. excelsior*, but later subjected to a different degree of dieback. The age of the stands ranged from 51 to 138 years. The plots were scattered across the territory of Latvia (Fig. 1) to characterize the climatic differences and the prevailing site types of *F. excelsior* stands. Most of the plots were situated on soils with a normal moisture regime and a few plots (e.g. Ķemeri, Ainaži) were located on over-moist soils. Site types of the plots mostly were *Aegopodiosa, Dryopteriosa, Oxalidosa turf. mel,* and *Filipendulosa* (Bušs, 1976). The climate can be classified as moist continental. The mean annual temperature is +7.2 and +6.1 °C, with January being the coldest (–1.8 and –4.5 °C) and July being the warmest (+17.4 and +17.9 °C) months in the western and eastern region of Latvia, respectively. The mean annual precipitation in western Latvia is 748, and in eastern Latvia — 665 mm.

The data were collected in three observation periods during the recent decades, i.e. in 2005, 2010, and 2015. For the description of the overstorey, in each stand, one circular plot with a radius of 15 m was established, where all trees with diameter at breast height (DBH) exceeding 6 cm were measured and their health condition (living or dead) recorded. Within each plot, three smaller circular plots with the total area of 235.6 m^2 were placed in three directions (0°, 120°, 240°) at seven meter distance from the centre for the description of understory. In these plots, height of all UG and AG individuals with DBH ≤ 6 cm was measured with the precision of 0.5 m.

Data analysis. The composition of the understory and separately of AG and UG species among the sites and observation periods was compared using a chi-square test. The *t*-test was used to assess the significance of differences in mean height between the three periods for the understory as well as for individual species. ANOVA was used to assess the differences in total and individual species density between the observation periods. The relationships between understory as well as AG and UG density separately and the density of dead *F. excelsior* were determined by Pearson correlation analysis. Detrended Correspondence Analysis (DCA), based on the AG density, was used to assess the successional changes in species composition during the observation period following canopy *F. excelsior* dieback. A randomization test with 10^5 iterations was performed to determine the significance of DCA components. All analyses were calculated in the software R v. 3.1.2 (Anonymous, 2014) at the significance level $\alpha = 0.05$.

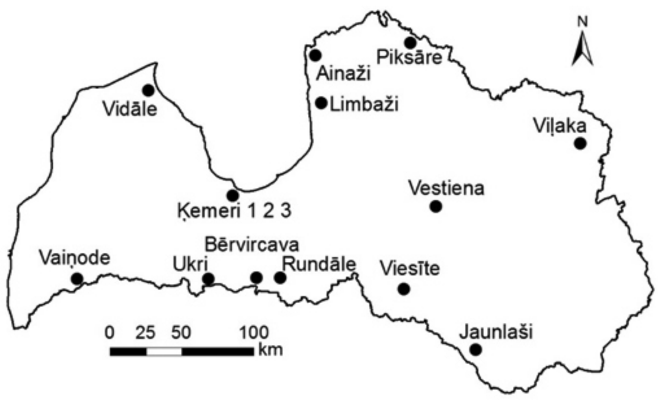

Fig. 1. The location of the studied sites (plots).

RESULTS

In total, in all observation periods, 13 canopy species were recorded (Table 1), but their distribution differed among the sites; e.g. *P. tremula* and *Tilia cordata* Mill., *Quercus robur* L., and *Alnus glutinosa* (L.) Gaertn. occurred only in three, four and five sites, respectively; *F. excelsior*, *Ulmus glabra* Huds., *Acer platanoides* L., and *Picea abies* (L.) H. Karst. occurred in more than eight sites. The highest density (> 70 trees ha^{-1}) was observed for *F. excelsior*, *P. abies*, *U. glabra,* and *A. glutinosa* (Table 1), although, after the second observation period, the density of *F. excelsior* decreased sharply (Fig. 2a). A slight decrease in the density of canopy *U. glabra* was observed after the second observation period, as in the Ainaži, Piksāre, and Viesīte sites, many *U. glabra* entered the canopy from AG to canopy, while in the third observation period, a dieback (mortality of 35%) occurred in the Ķemeri2 and Ķemeri3 sites. In the Vidāle site, a decrease (65%) of *P. abies* density occurred due to a windfall in the second period. An increase in number of *T. cordata* (from 142.86 trees ha^{-1} in 2005 to 285.71 trees ha^{-1} in 2015), *P. tremula* (from 1.00 trees ha^{-1} in 2005 to 242.68 trees ha^{-1} in 2015) and *A. platanoides* (from 28.57 trees ha^{-1} in 2005 to 471.42 trees ha^{-1} in 2015) was observed in the Viļaka, Jaunlaši, and Limbaži sites, respectively.

In total, 11 AG and 20 UG species were recoded (Table 1). Significant differences (*p*-value 0.001) in the composition of understory species were observed between all observation periods. *A. incana* was observed in AG only in 2005; *Cerasus avium* (L.) Moench and *Crataegus curvisepala* Gand. were observed in UG only in 2010. The highest number of species was in 2015, when seven species, which were absent before, were found (Table 1). Species with the highest occurrence in all three periods remained unchanged; in the AG layer — *F. excelsior*, *A. platanoides* and *U. glabra*, but in the UG — *Padus avium* Mill., *Corylus avellana* L., and *Sorbus aucuparia* L. (Table 1). The occurrence of *Q. robur*, *A. glutinosa*, *T. cordata,* and *Viburnum opulus* L. increased gradually. Nevertheless, the proportion of AG and

Table 1

UNDERSTORY AND CANOPY SPECIES DENSITY (D, INDIVIDUALS HA^{-1}) AND OCCURRENCE (O, %) CALCULATED BASED ON ALL PLOTS IN THREE OBSERVATION PERIODS

	Understory						Canopy		
	2005		2010		2015		2005	2010	2015
	D	O	D	O	D	O	D	D	D
Acer platanoides	920.03	73	696.39	73	1729.65	73	24.52	42.44	60.36
Alnus glutinosa	22.65	13	16.99	20	373.67	20	71.68	71.68	72.62
Alnus incana	14.15	13	0.00	0	0.00	0	-	-	-
Betula pendula	11.32	13	22.65	13	16.99	13	25.46	21.69	17.92
Fraxinus excelsior	645.44	73	871.90	80	1930.64	100	256.53	131.10	94.31
Picea abies	87.76	33	79.26	33	62.28	40	106.57	99.97	101.86
Populus tremula	93.42	27	56.62	27	192.50	20	8.49	18.86	21.69
Quercus robur	31.14	27	33.97	33	53.79	53	12.26	11.32	13.20
Tilia cordata	62.28	13	121.73	20	124.56	20	18.86	26.41	29.24
Ulmus glabra	1554.14	47	1406.94	60	1208.78	73	96.20	105.63	83.94
Cerasus avium	0.00	0	2.83	7	0.00	0			
Cornus sanguinea	25.48	7	0.00	0	110.40	7			
Corylus avellana	2692.14	73	2697.81	80	3204.53	73			
Crataegus curvisepala	0.00	0	2.83	7	0.00	0			
Dafne mezereum	0.00	0	0.00	0	2.83	7			
Euonymus europaeus	90.59	33	59.45	33	110.40	33			
Frangula alnus	16.99	13	8.49	20	48.12	13			
Lonicera xylosteum	266.10	33	418.97	33	854.92	33			
Malus sylvestris	8.49	13	8.49	13	59.45	27	0.94	0.94	2.83
Padus avium	2635.53	100	2525.12	100	4996.46	100	11.32	9.43	18.87
Prunus divaricata	0.00	0	0.00	0	2.83	7			
Rhamnus cathartica	5.66	7	2.83	7	5.66	13			
Ribes nigrum	90.59	27	62.28	27	342.53	40			
Ribes pubescens	0.00	0	0.00	0	2.83	7			
Ribes rubrum	0.00	0	0.00	0	11.32	7			
Salix caprea	0.00	0	0.00	0	2.83	7	1.89	1.89	1.89
Sambucus nigra	0.00	0	0.00	0	2.83	7			
Sorbaria sorbifolia	0.00	0	0.00	0	14.15	7			
Sorbus aucuparia	67.94	67	124.56	67	229.30	67	7.55	6.60	4.72
Viburnum opulus	53.79	10	50.96	33	325.55	53			

UG individuals remained relatively stable (36 and 64%, respectively), with fluctuations of only up to 2%.

In most of the sites, density of understory individuals was quite similar in 2005 (688 ± 221 and 1190 ± 178, respectively) and 2010 (660 ± 145 and 1192 ± 183, respectively), but in 2015, it was higher (p-value 0.001) and nearly doubled (1138 ± 228 and 2065 ± 312, respectively) (Fig. 3), except for the Ķemeri3 site, where a decrease was observed (Fig. 2b). During all periods, *U. glabra* (1390 trees ha^{-1}), *F. excelsior* (1149 trees ha^{-1}) and *A. platanoides* (1115 trees ha^{-1}) had the highest densities in AG (Fig. 4), but in 2015, significantly higher density was observed for *A. platanoides*, *F. excelsior,* and *A. glutinosa* (Fig. 4, Table 1). In UG, density of *P. avium* (3386 individuals ha^{-1}), *C. avellana* (2865 individuals ha^{-1}), and *Lonicera xylosteum* L. (513 individuals ha^{--1}) remained stable during all observation periods. However, their density, as for *Ribes nigrum L., V. opulus*, *Frangula alnus* Mill., and *Euonymus europaeus* L. was significantly higher in 2015 (Fig. 4). Thus, the increase of UG or AG density was caused by a particular species (Table 1). With the rapid increase in number of recruits, the average height of AG and UG decreased, particularly in the third observation period (mean height of AG decreased from 2.21 to 0.94 cm in 2005 and 2015, respectively) (Fig. 3).

The DCA ordination (Fig. 5) showed that the sites had an expressed grouping according the composition of AG species, hence three groups were arbitrarily distinguished. The first group consisted of the Ainaži (Fig. 5, site 1), Piksāre (8), Ķemeri1 (4) and Ķemeri2 (5) sites, which were dominated by *U. glabra*. The second group was characterized by the Bērvircava (2), Vidāle (13), Ukri (10), Vestiena (12), Jaunlaši (3) sites, which were distinguished by the dominance of *F. excelsior* with *Q. robur,* and *B. pendula*. The third group consisted of the Viesīte (14), Vaiņode (11), Limbaži (7), Viļaka (15) and Rundāle (9) sites, in which, however, AG was dominated by many species. The successional changes in AG were the most expressed in the

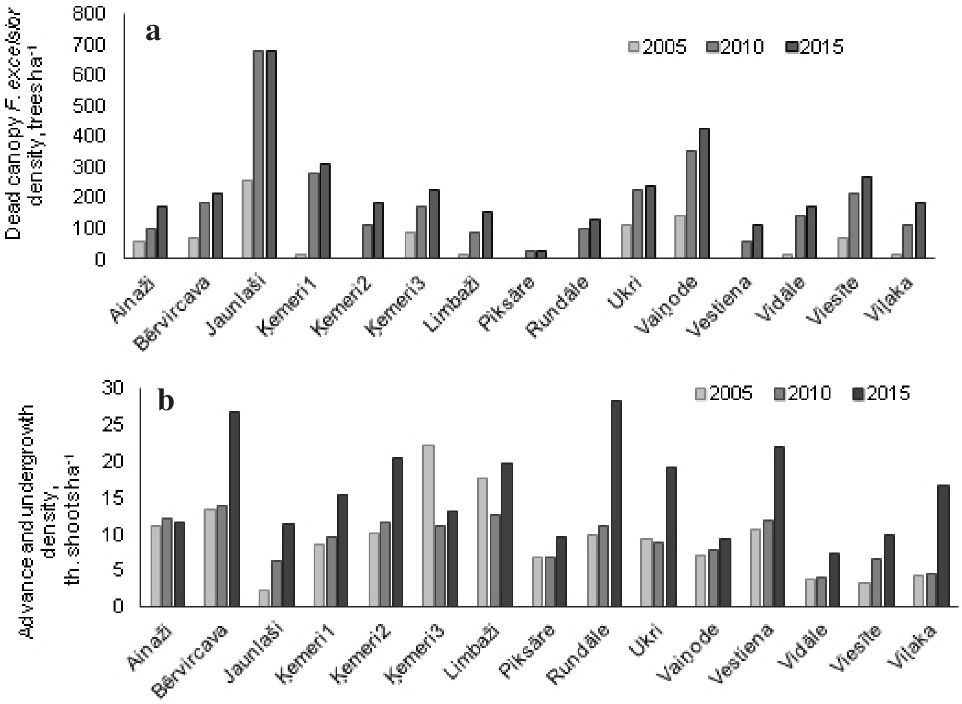

Fig. 2. Changes in the number of declining (dead) canopy *F. excelsior* trees (a) and total density of understory tree advance growth and shrubs (b) in the studied plots during the three observation periods.

first and second group, but the third group showed the weakest changes. Hence, the direction of changes were site specific. The sites from the first group showed the changes characterized by increasing abundance of *A. glutinosa* or *T. cordata*. The successional vectors of the sites from the second and third group mainly had opposite directions indicating changes among the broadleaved species, suggesting interchange of AG composition. Nevertheless, the abundance of *F. excelsior* increased in the Bērvircava (2), Ukri (10) and Jaunlaši (3) sites as shown by similarity of the vectors. Some sites (Ainaži (1), Ķemeri1 (4) and Vaiņode (11)) had only slight and reversing vectors, suggesting stability of the species composition in AG. The AG composition and its changes mainly coincided with the canopy species in the particular sites (Table 1). The correlation between understory density and the amount of dead canopy *F. excelsior* was not significant in any period (Fig. 6), although in a few sites, density of understory increased with the *F. excelsior* dieback (Jaunlaši, Ķemeri1, Ķemeri2) (Fig. 2a, b).

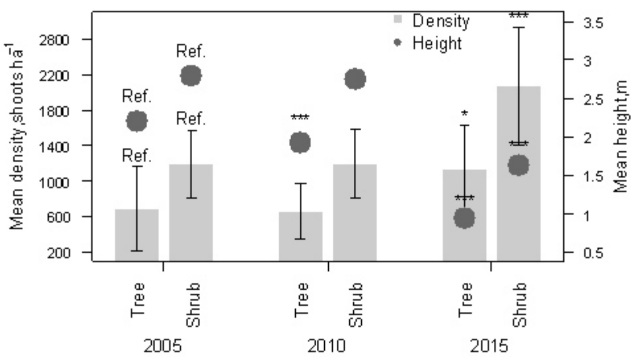

Fig. 3. Average density and height of understory tree advance growth and shrubs in the studied plots.

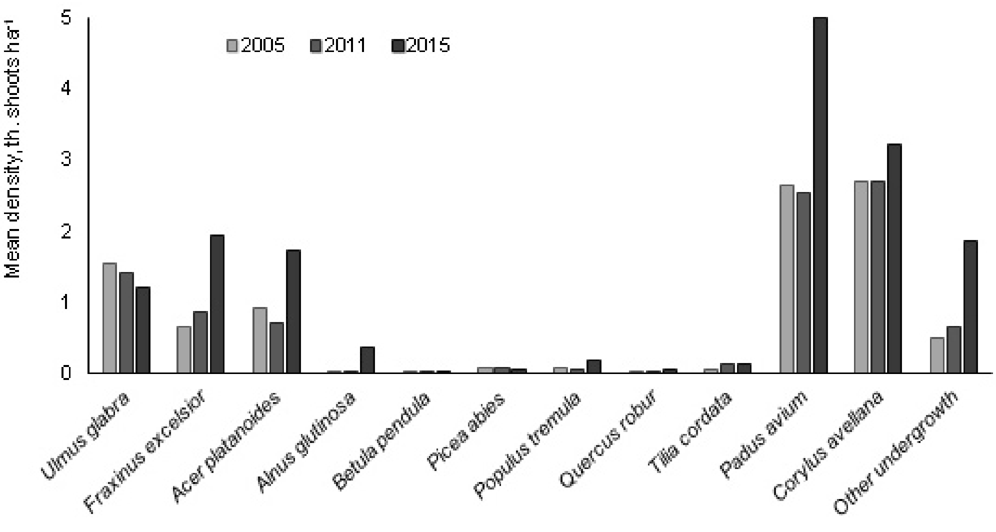

Fig. 4. Mean density of the main understory tree advance growth and shrub species.

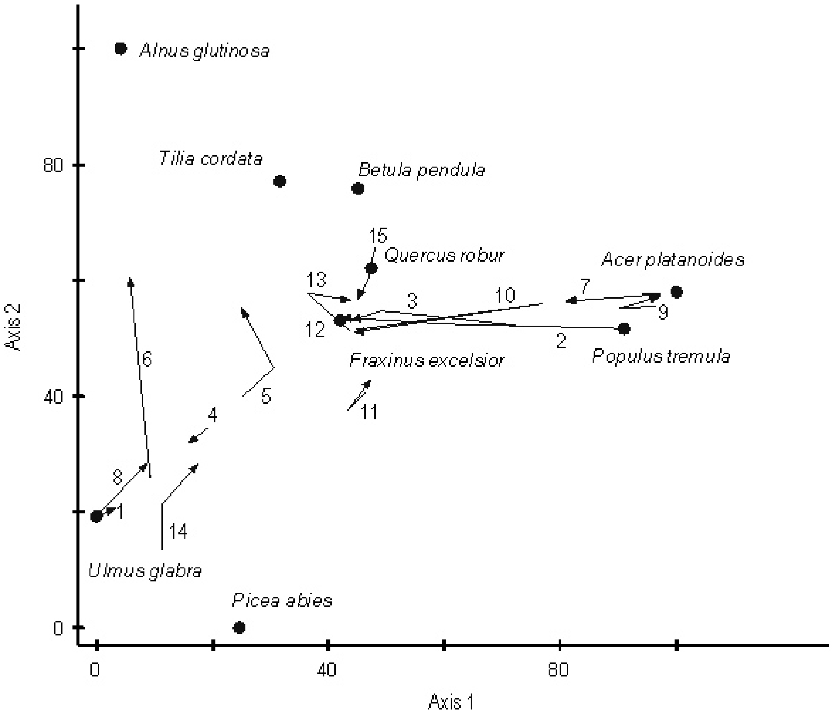

Fig. 5. DCA ordination of advance growth density in 2005, 2010, and 2015 in 15 studied plots (numbers) and species (dots). Site codes: 1 – Ainaži, 2 – Bērvircava, 3 – Jaunlaši, 4 – Ķemeri1, 5 – Ķemeri2, 6 – Ķemeri3, 7 – Limbaži, 8 – Piksāre, 9 – Rundāle, 10 – Ukri, 11 – Vaiņode, 12 – Vestiena, 13 – Vidāle, 14 – Viesīte, 15 – Viļaka. The successional changes in species composition among the observation periods are indicated by the vectors.

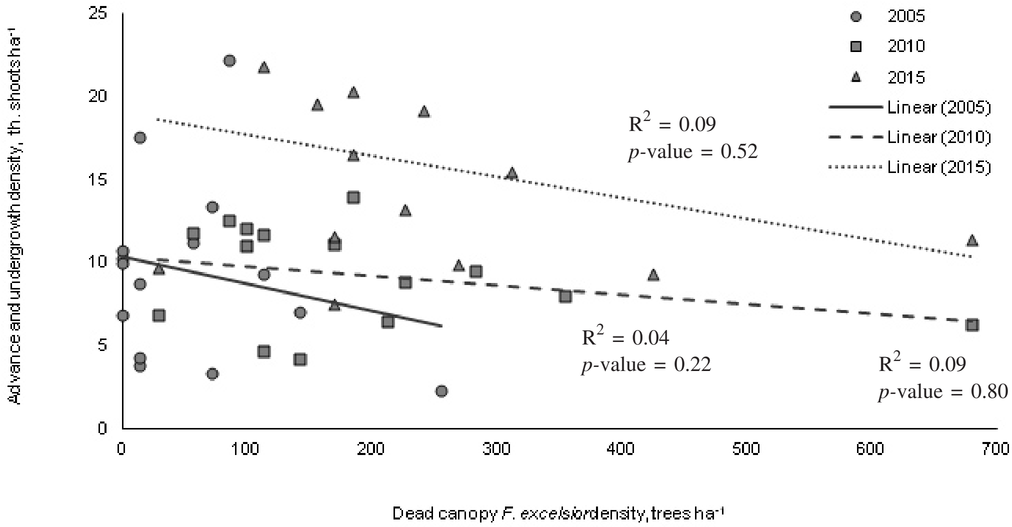

Fig. 6. Linear regression of understory tree advance growth and shrub density vs. dead canopy *F. excelsior* density in 15 studied plots in three observation periods.

DISCUSSION

Although understory is known to form a monodominant layer with abundant ground cover vegetation after the dieback of canopy trees (Royo and Carson, 2006), our results indicated the opposite, as an increase in number of UG species followed the dieback of canopy *F. excelsior*, while the number of AG species remained the same (Table 1). This could be explained by the fact that UG species, which are adventitious and/or temporary (e.g. *Prunus divaricate* Ehrh., *Sorbaria sorbifolia* (L.) A. Braun and *Ribes sp*.), can adapt to altered environmental conditions more quickly than AG (Gonzales *et al*., 2002). Changes in species composition were minimal in the sites where the mortality of canopy *F. excelsior* was low, e.g., Piksāre and Viļaka (Fig. 2a), as observed after Dutch elm disease, when abundance of UG increased only in larger gaps (after death of two or more canopy trees) (Huenneke, 1983). Hence, changes in understory after disturbance can alter the course of succession, and diversification of stand composition might be expected in future (de la Cretaz and Kelty, 2002; Mallik, 2003).

The DCA, and particularly directions of the successional vectors, showed that the course of succession in the affected *F. excelsior* stands was diverse (Fig. 5), likely due to the differences in growing conditions and seed sources. The DCA also showed that in the first observation period *U. glabra* was a major species in AG in several sites (e.g. Ainaži, Piksāre, and Ķemeri3), but afterwards its abundance decreased due to poor health condition and dieback of the canopy trees, reducing the seed source (Fig. 5), probably due to *Ophiostoma novo-ulmi* (Huenneke, 1983). At present, *U. glabra* is being rapidly replaced by *A. glutinosa* (Fig. 5), likely due to moist conditions, for which alder is better adapted. In the third period, in sites where *A. platanoides* co-occurred in canopy, i.e. Limbaži and Rundāle, the growth of AG *A. platanoides* was released by the *F. excelsior* dieback (Figs. 4, 5), suggesting that it could become the dominant species there.

In Lithuania a rapid increase in the number of primary species (*P. tremula*, *B. pendula*) has been observed after canopy *F. excelsior* dieback, (Bakys, 2013; Lygis *et al*., 2014), but this was observed only in the Rundāle site (Figs. 4, 5), probably due to lack of these species in the canopy of the surrounding stands of other sites. Nevertheless, the increase in the number of AG *F. excelsior*, especially in the third observation period (Fig. 4), suggested recovery of *F. excelsior*, which might be explained by the natural selection of the most resistant genotypes (Pliura *et al*., 2015).

Many studies indicate that the increase of understory density has been caused by canopy thinning, hence reduction of competition and the improvement of light conditions (de la Cretaz and Kelty, 2002; Coomes *et al*., 2003; Royo and Carson, 2006). In contrast, in this study, the increase of understory density was not associated with the dieback of canopy *F. excelsior* (Fig. 6), suggesting that *F. excelsior* has had minimal effect on the UG species, except in the Jaunlaši, Ķemeri1 and Ķemeri2 sites, where such tendencies persisted. Alternatively, this could be related to delayed response of UG to such changes, as the strongest dieback was observed between first two observations (132.98 shoots ha^{-1}), hence the increase in understory density might still be expected. Some UG species are also known to persist within a territory for a long time after the disturbance, competing with AG in longer term (Latham, 2003; Mallik, 2003; Royo and Carson, 2006), hence making AG more susceptible to other disturbances (Pallardy, 2008).

Increase of UG due to canopy disturbance can suppress AG regeneration directly through competition, allelopathy, limited seedling germination and growth (Runkle, 1990; Gillman *et al*., 2003; Royo and Carson, 2006), thus stalling succession for decades (Schnitzer *et al*., 2000). However, the proportion of AG and UG varied little (Fig. 3), suggesting similar competitiveness of the species under altered conditions following the disturbance. This might be also explained by a quite rapid growth of AG that reached the canopy, hence shaded the understory, as observed for *A. platanoides* and *T. cordata* and *U. glabra* in the Limbaži, Viļaka and Ķemeri3 sites, respectively.

Our results showed that the changes of species composition and density after the *F. excelsior* dieback have been occurring with different rates in relation to the local conditions. Therefore it is difficult to generalize further transformation of *F. excelsior* stands. The temporal stability of AG and UG composition and density suggested similar competitiveness of the species, contraindicating the formation of shrub land. Although the dieback of canopy trees has been progressing, increase of *F. excelsior* AG in the later observation period suggested improvement of regeneration, and hence there is a chance that *F. excelsior* could remain as an admixture species in these stands in the future. Still, monitoring of the stands is necessary to assess further recovery.

ACKNOWLEDGEMENTS

This study was carried out within the scope of Latvian State Forest project "Ash forest destruction and regeneration in Latvia" (No 5.5.-5.1_0017_101_14_28) and by the Forest Sector Competence Centre project "Methods and technologies for increasing forest capital value" (No L-KC-11-0004)".

REFERENCES

Anonymous (2005). *Ash Species in Europe: Biological Characteristics and Practical Guidelines for Sustainable Use*. FRAXIGEN project. UK: Oxford Forestry Institute, University of Oxford. 128 pp.

Anonymous (2014). R: A language and environment for statistical computing. R Core Team. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/ (accessed 11.02.2016).

Bakys, R. (2013). *Dieback of Fraxinus excelsior in the Baltic Sea Region, Associated Fungi, Their Pathogenicity and Implications for Silviculture*. Doctoral Thesis No. 10. Swedish University of Agricultural Sciences, Uppsala. 48 pp.

Beckage, B., Clark, J. S., Clinton, B. D., Haines, B. L. (2000). A long-term study of tree seedling recruitment in southern Appalachian forests: The effects of canopy gaps and shrub understories. *Can. J. For. Res.*, **30**, 1617–1631.

Brewer, R. (1980). A half-century of changes in the herb layer of a climax deciduous forest in Michigan. *J. Ecol.*, **68**, 823–832.

Bušs, K. (1976). *Latvijas PSR mežu klasifikācijas pamati* [Basis of Forest Classification in the Latvian SSR]. Latvijas zinātniski pētnieciskais mežsaimniecības problēmu institūts, Rīga. 34 pp. (in Latvian).

Coomes, D. A., Allen, R. B., Forsyth, D. M., Lee, W. G. (2003). Factors preventing the recovery of New Zealand forests following control of invasive deer. *Conserv. Biol.*, **17**, 450–459.

de la Cretaz, A. L., Kelty, M. J. (2002). Development of tree regeneration in fern-dominated forest understories after reduction of deer browsing. *Restor. Ecol.*, **10**, 416–426.

Dobrowolska, D., Hein, S., Oosterbaan, A., Wagner, S., Skovsgaard, J. P. (2011). A review of European ash (*Fraxinus excelsior* L.): Implications for silviculture. *Forestry*, **84** (2), 133–148.

Dunn, C. P. (1986). Shrub layer response to death of *Ulmusa americana* in southeastern Wisconsin lowland forests. *Bull. Torrey Bot. Club*, **113** (2), 142–148.

Ehrenfeld, J. G. (1980). Understory response to canopy gaps of varying size in a mature oak forest. *Bull. Torrey Bot. Club*, **107** (1), 29–41.

Gillman, L. N., Wright, S. D., Ogden, J. (2003). Response of forest tree seedlings to simulated litterfall damage. *Plant Ecol.,* **169**, 53–60.

Givnish, T. J. (2002). On the adaptive significance of evergreen vs. deciduous leaves: Solving the triple paradox. *Silva Fennica*, **36**, 703–743.

Gonzalez, M. E., Veblen, T. T., Donoso, C., Valeria, L. (2002). Tree regeneration responses in a lowland *Nothofagus*-dominated forest after bamboo dieback in south-central Chile. *Plant Ecol.*, **161**, 59–73.

Henry, J. D., Swan, J. M. A. (1974). Reconstructing forest history from live and dead plant material — an approach to the study of forest succession in southwest New Hampshire. *Ecology*, **55**, 772–778.

Huenneke, L.F. (1983). Understory response to gaps caused by the death of *Ulmus americana* in central New York. *Bull. Torrey Bot. Club*, **110** (2), 170–175.

Kirisits, T., Freinschlag, C. (2011). Ash dieback caused by *Hymenoscyphus pseudoalbidus* in a seed plantation of *Fraxinus excelsior* in Austria. *J. Agr. Extension Rural Devel.*, **4** (9), 184–191.

Klinka, K., Chen H. Y. H., Wang, Q., de Montigny, L. (1996). Forestc and their influence on understory vegetation in early-serial stands on West Vancouver Island. *Northwest Sci.*, **70** (3), 193–199.

Laiviņš, M., Mangale, D. (2004). The distribution of young growth of the common ash (*Fraxinus. excelsior*) in Latvia [Parastā oša (*Fraxinus excelsior*) paaugas izplatība Latvijā]. *Mežzinātne,* **13** (46), 61–69 (in Latvian).

Latham, R. E. (2003). Shrubland longevity and rare plant species in the northeastern United States. *Forest Ecol. Man.*, **185**, 21–39.

Lygis, V., Bakys, R., Gustiene, A., Burokiene, D., Matelis, A., Vasaitis, R. (2014). Forest self-regeneration fallowing clear-felling of dieback-affected *Fraxinus excelsior*: Focus on ash. *Eur. J. For. Res.*, **133**, 501–510.

Mackey, H. E., Sivec, N. (1973). The present composition of a formwork-chestnut forest in the Allegheny Mountains of western Pennsylvania. *Ecology*, **54**, 915–919.

Mallik, A. U. (2003). Conifer regeneration problems in boreal and temperate forests with ericaceous understory: Role of disturbance, seedbed limitation, and keystone species change. *Crit. Rev. Plant Sci.*, **22** (3&4), 341–366.

McCormick, J. F., Platt, R. B. (1980). Recovery of an Appalachian forest following the chestnut blight, or, Catherine Keever-You were right! *Amer. Midland Natur. J.*, **104**, 264–273.

Pallardy, S. G. (2008). *Physiology of Woody Plants*. Elsevier, London. 464 pp.

Pliura, A., Lygis, V., Suchockas, V., Marčiulyniene, D., Suchockas, V., Bakys, R. (2015). Genetic variation of Fraxinus excelsior half-sib families in response to ash dieback disease following simulated spring frost and summer drought treatments. *iForest*, **9**, 12–22.

Royo, A. A., Carson, W. P. (2006). On the formation of dense understory layers in forests worldwide: Consequences and implications for forest dynamics, biodiversity, and succession. *Can. J. For. Res.*, **36**, 1345–1362.

Runkle, J. R. (1990). Gap dynamics in an Ohio *Acer-Fagus* forest and speculations on the geography of disturbance. *Can. J. For. Res.*, **20**, 632–641.

Schnitzer, S. A., Dalling, J. W., Carson, W. P. (2000). The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. *J. Ecol.*, **88**, 655–666.

Sheil, D. (2001). Long-term observations of rain forest succession, tree diversity and responses to disturbance. *Plant Ecol.*, **155** (2), 183–199.

Sulser, J. A. S. (1971). The vegetation of the William L. Hutcheson Memorial Forest: A quantitative comparison of twenty years. *William L. Hutcheson Memor. For. Bull.*, **2**, 15–24.

Vasiliauskas, R., Bakys, R., Lygis, V., Barklund, P., Ihrmark, K., Stenlid, J. (2006). Fungi associated with the decline of *Fraxinus excelsior* in the Baltic States and Sweden. In: Oszako, T., Woodward, S. (eds.). *Possible Limitation of Dieback Phenomena in Broadleaved Stands*. Forest Research Institute, Warsaw, pp. 45–53.

Received 24 February 2016

KRŪMU STĀVA IZMAIŅAS PARASTĀ OŠA AUDŽU DESTRUKCIJAS REZULTĀTĀ LATVIJĀ

Pēc *Fraxinus excelsior* L. audžu destrukcijas, šajās audzēs novērotas straujas pameža un paaugas (krūmu stāva) sugu sastāva un biezuma izmaiņas. Šajā pētījumā sugu sastāva un biezuma izmaiņas krūmu stāvā pētītas 15 ilglaicīgajos parauglaukumos (katrs 235,6 m^2) 2005., 2010. un 2015. gadā. Katrā parauglaukumā uzskaitītas visas krūmu stāva sugas un nomērīts to augstums. Sukcesionālās izmaiņas krūmu stāvā novērtētas, izmantojot detrendēto korespondentanalīzi. Kopā uzskaitītas 11 pameža un 20 paaugas sugas. Būtiska krūmu stāva biezuma palielināšanās novērota tikai 2015. g., galvenokārt pieaugot pamežam — *Corylus avellana* L.*,* *Padus avium* Mill. un *Lonicera xylosteum* L. Paaugā lielākais biezums konstatēts *Ulmus glabra* Huds.*,* *F. excelsior* un *Acer platanoides* L.; turklāt *A. platanoides* un *F. excelsior* biezums 2015. gadā palielinājās. Novērotā sukcesija norāda, ka katrai slimības skartajai audzei raksturīga individuāla attīstība atkarībā no palikušās un blakus esošās audzes sastāva.