PROCEEDINGS OF THE LATVIAN ACADEMY OF SCIENCES. Section B, Vol. 70 (2016), No. 3 (702), pp. 124–130.
DOI: 10.1515/prolas-2016-0020

SPREAD OF *HYMENOSCYPHUS FRAXINEUS* IN LATVIA: ANALYSIS BASED ON DYNAMICS OF YOUNG ASH STANDS

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Communicated by Pēteris Zālītis

In Latvia, during the last 15 years (2000–2015), the area of common ash Fraxinus excelsior *forest stands has decreased by 40.6%. The dieback was predominantly caused by the fungal pathogen* Hymenoscyphus fraxineus*. Mostly young stands (up to 40 years old) were affected, accounting for 77.3% of the area of dieback. In this paper, we analysed the dynamics of young ash stand area within nature regions in Latvia to attempt to determine patterns of spread and the major migration routes of* H. fraxineus*. As suggested by the available data, the invasion of the fungal pathogen began in the southern part of Latvia, and then gradually dispersed across the country. The largest decline of young ash stands, during the period 2000–2010, occurred in lowlands. According to our estimate, the average rate of dispersal in Latvia was 40 km per year. At the scale of Latvia, the dispersal routes of fungal pathogen* H. fraxineus *largely coincide with the major migration corridors of biota and are related to macro-relief forms and their configuration.*

Key words: *dieback,* Fraxinus excelsior*, young stands, migration routes.*

INTRODUCTION

Common ash *Fraxinus excelsior* is the most widespread deciduous broadleaved woody species in Latvia. According to the data of the State Forest Service (Anonymous, 2015), in 2015 the total cover of ash stands was 13 011.1 ha (0.4% of the total forest cover or 53.1% of the broadleaved deciduous forest area in Latvia).

During the last century, the absolute and relative area of ash stands in forests of Latvia varied considerably. In the first half of the 20th century, the cover of ash stands did not exceed 1000 ha (Anonymous, 1926; 1937; Kundziņš, 1937; Eihe, 1940; Kronītis, 1966) or 0.1% of the total forest area. However, in the 1960s to 1970s, targeted silvicultural measures resulted in a rapid increase of the total ash stand area (Saks, 1957; Sakss, 1958; Grauziņš, 1969, 1971; Grauzinsh, 1971) with a peak at the end of the 20th century (in 1998, the total area was 21 905.3 ha or 0.8% of the total forest area). On the basis of the literature sources mentioned above and forest statistics, the dynamics (change in area) of ash stands was estimated (Fig. 1).

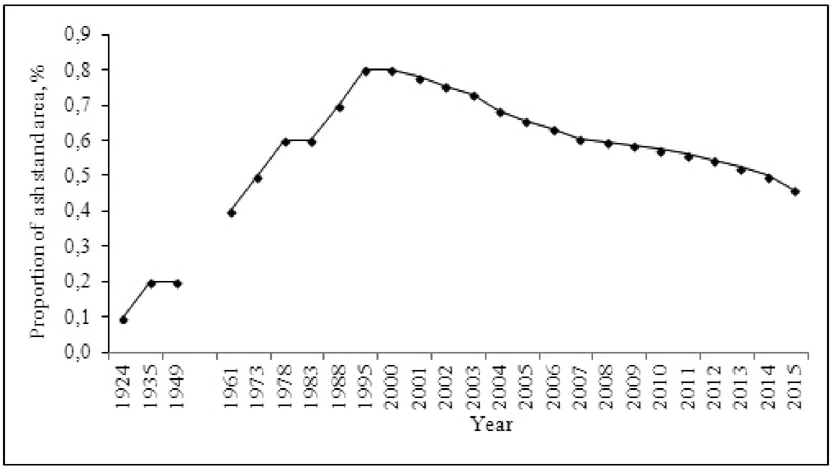

Fig. 1. Dynamics of common ash stands in the forests of Latvia within the last 90 years. Data summarized from the following sources: Anonymous, 1926; 1937; Kundziņš, 1937; Eihe, 1940; Saks, 1957; Kronītis, 1966; Sakss, 1958; Grauziņš, 1969; 1971; Grauzinsh, 1971; Anonymous, 2015.

Regeneration of ash and increase of the ash stand area were perhaps promoted also by environmental changes, particularly eutrophication of soil and synanthropization of vegetation, as suggested also by numerous studies in Europe (e. g. Kuhn *et al*., 1983; Fangmeier *et al*., 1994; Diekmann *et al*., 1999) including Latvia (Laiviņš, 1997, 1998).

The first cases of common ash dieback in Poland were recorded in the beginning of the 1990s (Przybyl, 2002). In Lithuania, the first cases of ash dieback were noted at the end of the 1990s (Juodvalkis and Vasilauskas, 2002; Kowalski and Lukomska, 2005). Soon the fungal pathogen *Hymenoscyphus fraxineus* was discovered to be the cause of the extensive ash dieback (Bakys *et al*., 2013; Pautasso *et al*., 2013; Gross *et al*., 2014). In the first decade of the new millenia, the fungi species was present in ash stands most of the European countries (Pautasso *et al*., 2013).

In Latvia, numerous cases of ash dieback were recorded in the end of the 20^{th} century and in the beginning of the 21^{st} century. However, the actual cause of dieback, *H. fraxineus*, was first proven in the western part of the country near Liepāja in 2006 and in the central part near Tukums in 2007 (Kēnigsvalde *et al*., 2010), several years after the massive dieback throughout the country. Thus, no precise data on the first establishment and dispersal rate of this fungi species in Latvia are available.

During the last 15 years (2000–2015), ash stands in Latvia are being damaged and die mostly due to infection caused by *H. fraxineus*. As a result, the total cover of ash stands has decreased by 8878.0 ha (40.6% of the area in 2000). The pathogen has affected mostly young ash stands (younger than 40 years) causing a loss of area of this age class by 77.3%, and of middle-aged stands by 51.1%, compared to the area in 2000. Similar patterns were observed also in Lithuania, where young and middle-aged stands were the most affected by pathogen infection (Juodvalkis and Vasilauskas, 2002). In mature and old-growth stands, the destruction and dieback is considerably slower.

In literature, the scientific name of the fungal pathogen species has changed several times. Currently, *Hymenoscyphus fraxineus* has been adopted as the taxonomically correct name (previously, *Chalara fraxinea* and *Hymenoscyphus pseudoalbidus*, currently used as synonyms) (Baral *et al*., 2014). In this paper, we used the latest accepted scientific name, *Hymenoscyphus fraxineus*.

In our study, we focused on the dynamics of young ash stands, which are known as the most susceptible against pathogen infections (Kowalski, 2006) and consequently the most dynamic age group among ash stands. Thus far, the cause of massive ash dieback in Europe has not cast doubt since the main reason was discovered. Therefore, in this paper we assume that this was the cause of young ash dieback also in Latvia, though the cause in each stand was not determined. The aim of this study was to describe regional differences of ash dieback caused by *H. fraxineus* and to determine the migration routes and the dispersal rate. We hypothesized that its dispersal routes in Latvia coincided with the major migration routes of biota largely defined by the pattern and configuration of macro-relief forms.

MATERIAL AND METHODS

Forest inventories and age groups of ash stands. In order to determine the dynamics of young ash stand area in different regions of Latvia within the time period from 2000 to 2015, data from the State Forest Service (Anonymous, 2015) were used. For each of the smallest administrative units (counties), data on the area and volume of ash stands (within time intervals 1–10, 11–20, ... > 201 years) were available. The ash stands are classified into five age groups: young stands (< 41 years), middle-aged stands (41–60 years), pre-mature stands (61–80 years), mature stands (81–120 years), and overmature stands (>121 years). Only data on the area per county of young stands (< 41) years) were selected and used in the analysis.

Nature regions and groups of regions. The selected data on young ash stands in 506 counties were used in a spatial analysis at the regional level. Using ArcView 9.1 software the counties were grouped within the borders of physiogeographical districts, or nature regions (Fig. 2) as defined by K. Ramans (Ramans, 1994), others (Sleinis, 1937; Zelčs and Šteins, 1989). If a county was crossed by the border of nature region, the county was joined to the region with the largest proportional area of the county.

The nature regions (Fig. 2) were merged into larger units: Southern, Central, and Northern Latvia. The Eastern Zemgale Plain (VII) and Augšzeme Upland (VIII) as well as Western Zemgale Plain (VI), Eastern Kursa Upland (IV), and Western Kursa Upland II were grouped into a unit

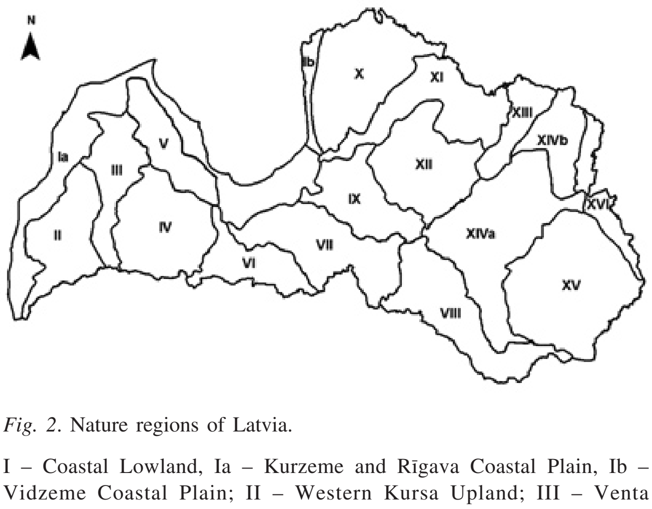

Fig. 2. Nature regions of Latvia.

I – Coastal Lowland, Ia – Kurzeme and Rīgava Coastal Plain, Ib – Vidzeme Coastal Plain; II – Western Kursa Upland; III – Venta River-land; IV – Eastern Kursa Upland; V – Northern Kursa Upland; VI – Western Zemgale Plain; VII – Eastern Zemgale Plain; VIII – Augšzeme Upland; IX – Southern Vidzeme Tilted Plain; X – Northern Vidzeme Plain; XI – Gauja River-land; XII – Vidzeme Upland; XIII – Eastern Vidzeme Upland; XIV – Aiviekste River-land, XIVa – Lubāna and Jersika Plain, XIVb – Adzele Rise; XV – Latgale Upland; XVI – Eastern Latgale (Mudava) Lowland. In the text the region numbers are given in parentheses.

called Southern Latvia, south of the Daugava River. The Southern Vidzeme Tilted Plain (IX), Lubāna and Jersika Plain (XIVa), and Vidzeme Upland (XII) were merged into a group called Central Latvia. The Northern Kursa Upland (V), Vidzeme Coastal Plain (Ib), Northern Vidzeme Plain (X), and Adzele Rise (XIVb) were combine in a Northern Latvia group of regions. The Northern Latvia and Southern Latvia groups were analysed in detail.

Data from nature regions in which the area of young ash stands in 2000 was smaller than 200 ha (Kurzeme and Rigava Coastal Plain (Ia, Ib), Venta River-land (III), Gauja River-land (XI), Latgale Upland (XV), Eastern Vidzeme Upland (XIII), and Eastern Latgale Lowland (XVI)) were excluded from the analysis. In these regions, the distribution of ash is limited by climatic or edaphic factors (von Sievers 1903; Sakss 1958; Laiviņš and Mangale 2004).

Data analysis. For each region, the annual increase (+) or decrease (-) of young ash stand area was calculated in hectares (transformed into percent) as compared to the previous year. This analysis was performed for each region over the time period from 2000 to 2010. The distribution maps were prepared using Arc View 9.1 software.

RESULTS

Dynamics of young ash stand areas in Latvia. In comparison to 2000, in 2015 the total area of young ash stands in Latvia had decreased by 4.4 times (Fig. 3). The rate of decline during the last 15 years was uneven: in 2000–2006, the decline was rapid (average 805 ha/year), while in 2007–2015 the rate had declined (average 279 ha/year).

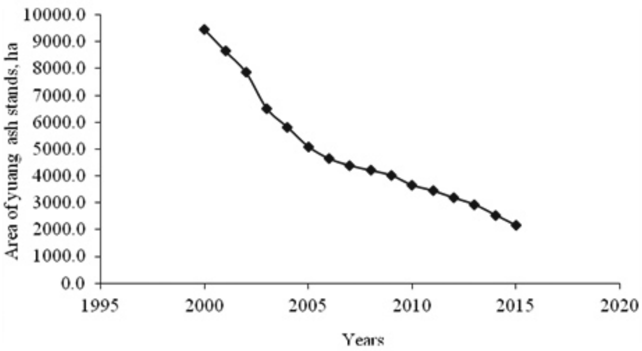

Fig. 3. Total area of young ash stands in Latvia (2000–2015).

During the last 16 years, the damage caused by *Hymenoscyphus fraxineus* has dramatically changed the age structure of ash stands at the national scale. In 2000, young ash stands comprised nearly one half (43%) of all ash stands in Latvia. In 2015, the area of young ash stands was only 17% of the total ash stand area in the country.

Regional differences in young ash stand dynamics. Intensive dieback of young ash stands began in Southern Latvia. In 2000, the highest rate of dieback was observed in the Eastern Zemgale Plain (VI) where a loss of 2333 ha had occurred (decrease of the total young ash stand area by 4.3 times), and in the Eastern Zemgale Plain (loss of 1083 ha; decrease by 3.1 times) (Fig. 4).

A year later, in 2001, the total area of young ash stands had decreased by one half (373 ha or 34.4% of the area in 2000). In Augšzeme (VIII), during the period from 2000 to 2002, the total area of young ash stands decreased almost

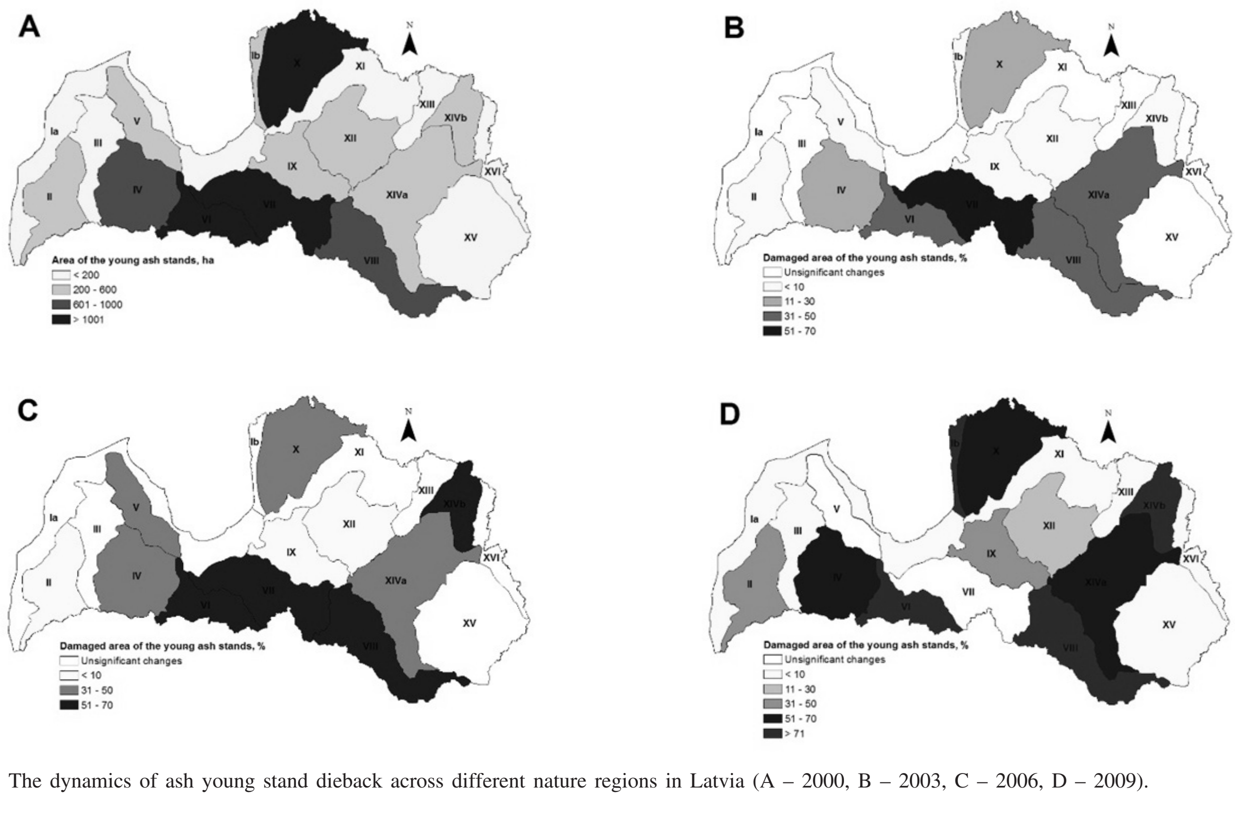

Fig. 4. The dynamics of ash young stand dieback across different nature regions in Latvia (A – 2000, B – 2003, C – 2006, D – 2009).

Table 1

THE DYNAMICS OF THE YOUNG ASH STAND AREAS IN NATURE REGIONS OF LATVIA*

Year	Nature regions in Southern Latvia					Nature regions in Central Latvia			Nature regions in Northern Latvia			
	II**	IV	VI	VII	VIII	IX	XIVa	XII	Ib	V	X	XIVb
2001	+5.8	+2.7	–17.4	–34.4	–1.6	+5.6	–21.7	–0.1	+2.3	+2.7	+11.2	+0.2
2002	+0.6	+0.7	–1.2	–7.1	–47.3	–0.6	–15.7	+1.7	–6.6	–3.0	–12.2	–8.1
2003	–5.5	–25.0	–31.8	–32.2	–0.2	–17.4	–2.7	–4.1	–2.1	–2.2	–13.6	–1.1
2004	–4.7	–9.5	–7.0	0.0	–1.8	–0.6	–2.8	+3.2	–66.2	–1.7	–28.7	–1.3
2005	–1.1	–3.0	–17.1	–1.7	–12.3	–2.9	–4.6	+1.5	–1.1	–36.1	–3.7	–65.2
2006	–0.4	–4.7	–29.3	–3.3	–3.1	–3.9	–10.0	0.0	–1.5	–5.2	–4.6	–1.6
2007	–8.1	–0.2	–8.7	–9.8	–2.0	–7.0	–0.1	–4.5	–5.1	–9.3	–4.5	–3.3
2008	–5.7	–2.7	–4.6	+0.4	–3.6	–9.4	–9.8	+0.8	–6.5	+0.2	–5.0	–0.9
2009	–1.9	–7.6	–3.2	–1.5	–7.4	–0.3	12.4	–0.3	+3.4	–19.3	+3.6	–3.1
2010	–2.6	5.0	–9.4	–7.4	–15.5	–9.6	–7.8	–6.4	–15.1	+3.7	–17.5	–9.2

* ±, % as compared to the previous year; ** The number code of regions are presented in Fig. 2. Annual decreases exceeding –10% are underlined.

twice — loss of 354 ha (48.8% of the area in 2000). In the Western Kursa (II) Upland and Eastern Kursa (IV) Upland, where the total area in 2001 was 236 ha and 967 ha, respectively, the total area slightly increased (Table 1).

In the nature regions of Central Latvia, the total area of young ash stands in 2001 decreased only in the Lubāna and Jersika Plain (XIVa) — by 106 ha (21.6% of the area in 2000). In the Vidzeme Upland (XII), the area of young ash stands did not change, while in the Southern Vidzeme Tilted Plain (IX) it slightly increased.

In all nature regions of Northern Vidzeme, the total area of young ash stands in 2001 increased in the next year, but only a year later, in 2002, in all these regions a slight decrease of the area was observed, with the largest decline in the Northern Vidzeme Plain (X) — loss of 160 ha (12.2%) from the area in 2000 (Table 1).

Spread of *H. fraxineus* can be modelled by the dynamics of young ash stand area across the nature regions of Latvia (Fig. 4). In 2003, in the Eastern Zemgale Plain more than 50% of the young ash stands recorded in statistics of 2000 were dead (Fig. 4A). In Western Zemgale, where the largest area of young ash stands was recorded in 2000 (2333 ha) as well as in Augšzeme Upland and Lubāna and Jersika Plain (total 1083 ha), two regions bordering with Eastern Zemgale, the total area of young ash stands decreased by more than 30%. Similarly, in the Northern Vidzeme Plain with relatively large areas of young ash stands in 2000 (totally 1177 ha), about 10% of them died in the period up to 2003 (Fig. 4B). This means that within three years after the outbreak in Southern Latvia, the disease had reached also the northern part of the country.

In the period up to 2006, the decline of young ash stands reached nearly 70% in the Western Zemgale Plain, Augšzeme Upland, Adzele Rise, and Vidzeme Coastal Plain, which means that massive dieback had occurred throughout the country. Loss of about one-third of young ash stands had occurred also in the Eastern Kursa Upland, Northern Kursa Upland, and Northern Vidzeme Plain (Fig. 4C). In the period from 2007 to 2010, in most of regions the dieback of young ash stands had slowed (Fig. 4D, Table 1).

DISCUSSION

In Latvia, ash dieback caused by *Hymenoscyphus fraxineus* began in the first years of the 21st century along with dispersal of spores of the fungi northward from Lithuania. In Lithuania, the first signs of dieback caused by *H. fraxineus* were recorded in 1996–1997, and massive dieback was recorded a few years later in 2001 (Juodvalkis and Vasilauskas, 2002; Vasaitis, 2012). According to Lithuanian forest monitoring data, moderately poor (crown defoliation > 25 %) condition of common ash was first recorded in 1994 and 1998 (crown defoliation 26.9 and 27.9%, respectively), and in all years since 2000 (Ozolinčius *et al.*, 2005; Stakenas *et al.*, 2013). In Poland, spreading dieback of common ash was first recorded in the second half of the 1990s, although the first signs were observed earlier with recording of the fungal pathogen *H. fraxineus* (Kowalski, 2001; Kowalski and Lukomska, 2005). Also in countries north of Latvia (Estonia and South Finland including the Åland Islands), invasion of the fungal pathogen was recorded during the first decade of the 21st century (Rytkönen *et al.*, 2011).

According to data of the State Forest Service, increased dieback of common ash began in Southern Latvia in two nature regions located south of the Daugava River. In 2001, a dramatic decline of young ash stands was recorded in Western Zemgale Plain (VI), where the young ash stand area had decreased by 405 ha (17.4% of the area in 2000), and Eastern Zemgale (VII), by 373 ha (34.4% of the area in 2000).

Both regions are located on the border of districts in Lithuania (Biržai, Panevežys, and Rokiškis forest massifs), where the majority of the damaged ash stands occurred at that time (Juodvalkis and Jankauskas, 2002). In 2001, the area of young ash stands had decreased by 106 ha (21.7% of the area in 2000) also in the Lubāna and Jersika Plain (XIVa). Thus we can assume that the diaspores of the fungal pathogen had spread northward across Daugava River and reached the Eastern Latvia Lowland. Between 2000 and 2001, the area of young ash stands did not decrease in other nature regions in Latvia, and in some cases had even slightly increased. A few years after invasion of *H. fraxineus* in Southern Latvia, dieback of common ash was recorded also in Northern Vidzeme (Fig. 5), reaching a peak in 2004 (Table 2).

The intensity of young ash stand decline in 2000–2015 was uneven: in 2000–2006, the decline was rapid (average 805 ha/year), and relatively slower in 2007–2015 (average 279 ha/year). One of the reasons for the observed young ash stand decline (loss of area) might be that the young stands had survived and were included in the category of pre-mature stands, but this would include only a small proportion of stands. The forest statistics data did not allow to estimating the area of young ash stands that transform into pre-mature stands annually. However, according to the forest statistics, the proportion of total ash stand area that transformed into the next age category did not exceed 14% during the period 2000–2015. The forest statistics do not show a notable increase of pre-mature stand area, and thus it is very probable that the area of young stands has declined, and not transformed into pre-mature stands. Although we did not analyse this in more detail, also the area of pre-mature ash stands continuously declined over the study period, allowing us to assume that the major cause of the decline of area was dieback.

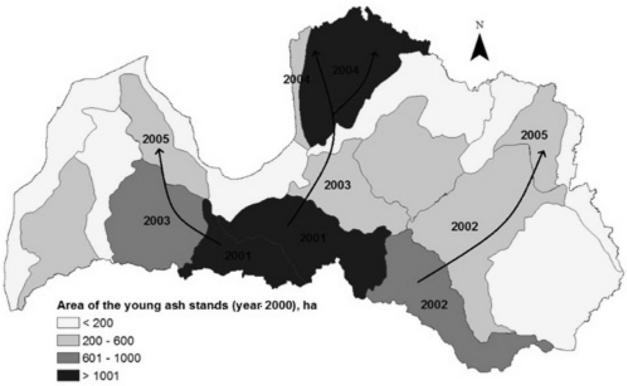

Fig. 5. Hypothesized migration routes of *Hymenoscyphus fraxinea* in Latvia.

Table 2

ANNUAL CHANGES OF THE YOUNG ASH STAND AREA IN THE SOUTHERN AND NORTHERN NATURE REGIONS OF LATVIA*

Year	Southern regions of Latvia	Northern regions of Latvia
2001	–15.0	+6.5
2002	–10.8	–9.4
2003	–24.8	–7.9
2004	–5.5	–26.9
2005	–10.2	–24.8
2006	–13.9	–4.1
2007	–6.1	–5.2
2008	–3.2	–3.9
2009	–2.0	+4.6
2010	–6.4	–13.5

* ±, % as compared to the previous year. Annual decreases exceeding –10 % are underlined.

Perhaps the high rate of decline can be explained by the large proportion of young ash stand areas in the beginning of the studied period. Being more widespread, the ash stands became easily invaded by the fungal pathogen, consequently serving as stepping stones and promoting further spread into other stands.

On the basis of map analysis, we can assume that the diaspores of the fungal pathogen spread from the south to the north, at least during the first years (2001–2003) after invading the territory of Latvia. The dispersal occurred in the south-north oriented lowlands using the landforms as migration corridors (Fig. 5). The Eastern Latvia migration corridor coincides with the Eastern Latvia Lowland. It is likely that the diaspores spread from the southern slope of Aknīste Rise (bordering with Biržai and Rokiškis forest massifs in Lithuania) toward the Jersika and Lubāna Lowland reaching and massively invading young ash stands in the Adzele Rise in 2005.

The Central Latvian migration corridor, connects Western Zemgale Lowland with Northern Vidzeme and the Coastal Lowland in Vidzeme along the coast of the Gulf of Riga and the Southern Vidzeme Tilted Plain. In 2003, the fungal pathogen caused significant damage to ash stands in Southern Vidzeme and Northern Vidzeme. Most probably, *H. fraxineus* spread into Northern Kurzeme from the Western Zemgale region (Fig. 5).

The dispersal of diaspores was less intensive and less damaging to young ash stands on uplands. In Vidzeme Upland and Western Kursa Upland, dieback of young ash stands in the period up to 2010 was recorded only in small areas. This is perhaps due to the low cover of young ash stands in the particular regions (in 2000, there were 366 ha in Vidzeme Upland, and 236 ha in Western Kursa Upland). Additionally, due to terrain conditions in uplands, the distribution pattern of ash stands has a mosaic character and they are naturally more isolated from each other. Augšzeme Upland is an exception, where intensive dieback was observed already in 2002, most probably because the region is adjacent to the most invaded districts in Lithuania at the time. Augšzeme Upland has also a relatively warm climate in comparison to many other nature regions in Latvia and early spring (Zirnītis 1956), which could be beneficial for the spread of *H. fraxineus*.

The dispersal and direction of *H. fraxineus* migration in Latvia could be well portrayed by the dynamics of young ash stands, particularly when comparing the southern and northern regions of the country (Table 2). In the northern regions (150_180 km to the north from the southern regions), the most intensive dieback started four years later than in the southern regions. Thus, we can assume that the dispersal rate was about 40 km per year. Dispersal rate estimations in other European countries differ, e. g. 50–60 km per year in North East Italy (Luchi *et al*., 2012) and 30 km in Norway (Solheim *et al*., 2012) suggesting that at the European scale the rates may increase southward.

The dispersal corridors of *H. fraxineus* in Latvia coincide with the most important migration corridors of biota. For example the migration routes of birds (e. g. northern lapwing *Vanellus vanellus*, Eurasian skylark *Alauda arvensis*, common cuckoo *Cuculus canorus*, and many other) are across northward oriented lowlands (Strautzels, 1939; Kalniņš, 1943). Also numerous non-native plant species spread along the lowland rivers, as suggested by several studies, e. g. Laiviņš and Gavrilova (2003); Laiviņš *et al*. (2006); Laiviņš and Čekstere (2014).

At the scale of Latvia, the dispersal routes of the fungal pathogen *H. fraxineus* largely coincide with the major migration corridors of biota and are associated with macro-relief forms and their configuration.

ACKNOWLEDGMENTS

This study was carried out within the scope of the project implemented by JSC Latvian State Forests „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).

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Received 8 March 2016

PATOGĒNAS SĒNES *HYMENOSCYPHUS FRAXINEUS* IZPLATĪŠANĀS LATVIJĀ: PARASTĀ OŠA JAUNAUDŽU DINAMIKAS ANALĪZE

Latvijā pēdējos 15 gados (2000–2015) oša audžu platība ir samazinājusies par 40,6%, galvenokārt patogēnās sēnes *Hymenoscyphus fraxineus* izraisīto slimību dēļ. Šajā periodā visstiprāk (par 77,3%) ir samazinājusies līdz 40 gadiem vecu oša audžu jeb jaunaudžu platība. Šajā rakstā, pamatojoties uz jaunaudžu platību izmaiņām dabas reģionos, analizēta sēnes izplatīšanās dinamika un galvenie izplatīšanās ceļi. Noskaidrots, ka oša jaunaudžu atmiršana vispirms sākās valsts dienvidu reģionos, bet pēc tam pakāpeniski aptvēra visu valsti; intensīvāk oša jaunaudžu platība 2000.–2010. gadā samazinājusies zemienēs. Parastā oša infekcijas masveida izplatīšanās Latvijā ir notikusi aptuveni ar ātrumu 40 km gadā. Kopumā slimības izplatīšanās ceļi sakrīt ar galvenajiem biotas migrācijas koridoriem Latvijā — reljefa lielformām un to konfigurāciju.