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Characteristics of *Pinus sylvestris* stands infected by *Viscum album* subsp. *austriacum*

Merkmale von *Pinus-sylvestris*-Beständen infiziert durch *Viscum album* subsp. *austriacum*

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Keywords: drought, European mistletoe, forest phytopathology, plant parasites, Scots pine, Czech Republic

Schlüsselbegriffe: Dürre, weißbeerige Mistel, Waldphytopathologie, Pflanzenparasiten, Waldkiefer, Tschechische Republik

Abstract

The infection rate (assigned in classes 0–6) of European mistletoe (*Viscum album* subsp. *austriacum* [Wiesb.] Vollm.) on Scots pine (*Pinus sylvestris* L.) in the Czech Republic was analysed from May 2019 to June 2020 in relation to Forest Infrared Index (FII: low, high), stand age (21–50, 51–70 and 71–90 years), tree position (at stand edge, within stand), stem diameter at breast height (DBH) and defoliation (0–10%, > 10–25%, > 25–60% and > 60–99%) in five natural forest areas (NFA). In each NFA, the analysis were done at two locations, one with a low FII and one with a high FII. At each locality and in each of the three stand age categories, the DBH, defoliation and mistletoe infection rate were assessed for 25 trees in the stand edge and 25 trees within the stand. Statistically significant higher mistletoe infection rate was recorded in stands with high FII (higher drought stress), in older stands (highest for 71–90 years followed by 51–70 years) and on trees at the stand edge, that have higher DBH and higher defoliation (highest for > 60–99% followed by > 25–60% and lowest for > 10–25%). The differences between NFAs were also significant. Our results suggest, that (1) selecting drought- and heat-resistant *P. sylvestris* varieties, (2) focussing plan-

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tation efforts to areas with lower temperatures and higher precipitation and (3) the reduction of the rotation period are recommended for *Pinus sylvestris* forest management in Central Europe.

Zusammenfassung

Der Befall (eingeteilt in Klassen 0–6) der Kiefern-Mistel (*Viscum album* subsp. *austriacum* [Wiesb.] Vollm.) auf der Waldkiefer (Pinus sylvestris L.) wurde im Zeitraum Mai 2019–Juni 2020 analysiert für 5 natürliche Waldbestände (NFAs) hinsichtlich des Infrarotindex des Waldes (FII: niedrig, hoch), der Altersklasse (21–50, 51–70, 71–90 Jahre), der Position im Bestand (am Bestandesrand, innerhalb des Bestandes), dem Stammdurchmesser in Brusthöhe (DBH) und der Kronenverlichtung (Defoliation, 0–10%, > 10–25%, > 25–60% und > 60–99%). In jedem NFA wurde die Auswertung in einem Gebiet mit niedrigem FII sowie einem mit hohem FII durchgeführt. An jeder Lokalität wurden innerhalb jeder der drei Altersklassen an 25 Bäumen am Rand und an 25 Bäumen in Bestandesinneren der DBH, Kronenverlichtung und Mistelbefall gemessen. Ein statistisch signifikant höherer Mistelbefall wurde in Beständen mit hohem FII (höherer Stress durch Trockenheit), in älteren Beständen (am stärksten in Beständen mit 71–90 Jahre, gefolgt von Kategorie 51–70 Jahre), an Bäumen am Rand des Bestandes, mit einem höheren DBH und einer höheren Kronenverlichtung festgestellt. Der Einfluss der NFAs war ebenfalls statistisch signifikant. Die Ergebnisse dieser Studie legen folgende Maßnahmen zur Bewirtschaftung von Waldkiefernbeständen in Mitteleuropa nahe: (1) Einsatz von trockenheitsresistenten Waldkiefer Sorten, (2) Fokussierung des Anbaus in kühleren und niederschlagsreicheren Gebieten und (3) Verkürzung der Umtriebszeit.

1 Introduction

European mistletoe (*Viscum album* L.) is a dioecious, evergreen, hemi-parasitic plant from the family Santalaceae. *Viscum album* is insect pollinated. The white fleshy berries are eaten and dispersed by birds, the most important are the mistle thrush (*Turdus viscivorus* L.), fieldfare (*Turdus pilaris* L.), Bohemian waxwing (*Bombycilla garrulous* L.) and Eurasian blackcap (*Sylvia atricapilla* L.) (Zuber 2004). *Viscum album* grows on stems and branches of woody plants, from which it drains water and inorganic compounds. Mistletoe haustorial system cause tubular corridors in the host's wood, leading to the technical degradation of the wood (Příhoda 1959). Woody plants heavily infested with mistletoe show reduced radial growth (Noetzli *et al.* 2003; Barbu 2009; Rigling *et al.* 2010; Sangüeesa-Barreda *et al.* 2013; Pilichowski *et al.* 2018; Bilgili *et al.* 2018). On Scots pine (*Pinus sylvestris* L.), *Viscum album* infection can lead to crown degradation in its host, reduction in primary production, decrease in carbohydrate availability (Rigling *et al.* 2010), reduction in needle length, weight (Mutlu *et al.* 2016b; Bilgili *et al.* 2020a), area and width (Bilgili *et al.* 2020a), reduction of nitrogen content in needles (Galiano *et al.* 2011), reduction of size and mass of the cones, the number and weight of seeds, and the height and weight of the seedlings (Jasiczek *et al.* 2017).

The degrading crown have reduced the length, the radial increment, the ramification, and the number of needle years of the infested branches (Rigling *et al.* 2010). *Viscum album* infection on *P. sylvestris* affects both the host's anti-oxidative defense system and the phytohormone profile after establishment of the xylem tapping haustorium (Hu *et al.* 2017) and causes inhibition of chlorophyll (Mutlu *et al.* 2016b). Hosts heavily infested with mistletoe may die (Noetzli *et al.* 2003; Mutlu *et al.* 2016a). Mistletoe is a serious threat for host trees, especially during drought periods, because it increases their hydric stress by draining water (Dobbertin and Rigling 2006; Rigling *et al.* 2010; Mutlu *et al.* 2016b), decreaces the availabitity of nutrients (Mutlu *et al.* 2016b) and increases their risk of bark beetle infestation (Tsopelas *et al.* 2004). Mistletoe-induced stomatal closure is a successful mechanism of the hosts against dying from hydraulic failure in the short term but increases the risk of carbon starvation in the long term (Zweifel *et al.* 2011). *Viscum album* produces viscotoxins, small proteins with three reducible disulfide bonds. The most abundant *Viscum album* subsp. *austriacum* viscotoxin (1-PS) is positively correlated with summer precipitation and autumn irradiance ratios, and negatively correlated with the host´s leaf nitrogen and sulfur status (Seegmueller 2012).

Hosts of *Viscum album* include over 150 genera, and the genus *Pinus* is a common host (Barney *et al.* 1998). *Viscum album* includes several subspecies, differing in habitat and the hosts. Three of the subspecies occur in the Czech Republic. *Viscum album* L. subsp. *album* attacks deciduous trees, especially *Malus* spp., *Populus* spp., *Tilia* spp., *Acer* spp., and *Pyrus* spp., *Sorbus* spp., *Jungans* spp., *Quercus* spp. and *Robinia* spp. (Zuber 2004; Box 2019; EPPO 2021). *Viscum album* subsp. *abietis* (Wiesb.) Abrom. with broad green leaves occurs only on firs (*Abies* spp.) (Zuber 2004; EPPO 2021). *Viscum album* subsp. *austriacum* (Wiesb.) Vollm. with narrow yellow-green leaves parasitizes conifers, especially on *Pinus* spp., including *P. sylvestris* and Austrian pine (*P. nigra* J.F. Arnold) (Zuber 2004; Box 2019; EPPO 2021), but it may also occurs on *Larix* spp. and *Picea* spp. (Zuber 2004; Schrack and Döring 2004; EPPO 2021).

Viscum album naturally occurs in Europe, mostly in the lowlands and hilly areas, but it is absent in many areas (especially those with high altitudes). In recent decades, there has been a marked increase in the occurrence of all *Viscum album* subspecies on both forest and non-forest trees (Dobbertin *et al.* 2005). In Poland, the occurrence of *Viscum album* increased continuously throughout the period of 2008–2018, the most on *P. sylvestris*, silver fir (*Abies alba* Mill.) and white birch (*Betula pendula* Roth) (Lech *et al.* 2020). In *P. sylvestris* forest in southeast Berlin (Germany), approximately 25% reduction in basal area increment of trees during the last 9 years of heavy infection of *Viscum album* (Kollas *et al.* 2017). In many dry inner-Alpine valleys, the increasing mistletoe abundance was reported to accelerate the ongoing pine decline (Zweifel *et al.* 2011). In the Klagenfurt (Austria), *Viscum album* subsp. *album* has been recorded on various deciduous trees for the first time (Leute and Perko 1999). In Hungary, the area infested by *Viscum album* has almost tripled since the beginning of the 20th century (Varga *et al.* 2014). The increase in the occurrence of *Viscum album* is probably due to long-term high temperatures. If these weather conditions persist, *Viscum* *album* can be expected to continue to spread to higher altitudes and to be an increasingly important factor involved in the decline and mortality of individual trees and entire stands, including pine stands (Dobbertin *et al.* 2005).

Pruning and tree removal are the primary control measurements for *Viscum album* (Butin 1995). However, thinning favors the growth of *Viscum album* by increasing light levels in thinned stands (Noetzli *et al*. 2003). Mistletoe shoots can be broken off or cut off, but due to new sprout growth from the cortical haustoria it must be done repeatedly. Effective chemical preparations against *Viscum album* are growth regulators, which can be used while the host is dormant (Sinclair and Lyon 2005). The hosts most susceptible to Viscum album infection can be replaced by more resistant species, *e. g.* Norway spruce (*Picea abies* [L.] H. Karst.) or European beech (*Fagus sylvatica* L.), or by more resistant cultivars (Noetzli *et al.* 2003; Zuber 2004). The aims of this study were: 1) to evaluate the occurrence of *Viscum album* subsp. *austriacum* on *P. sylvestris* stands in the areas of highest occurrence of *Viscum album* subsp. *austriacum* in the Czech Republic based on the Forest Infrared Index (FII), stand age, tree position in the stand, defoliation and stem diameter at breast height (DBH) in five natural forest areas, 2) to assess which factors are related to *Viscum album* infection and 3) to formulate management recommendation for the protection and management of *P. sylvestris* stands against *Viscum album* infection in the climatic conditions of the Central Europe.

2 Materials and methods

From May 2019 to June 2020, one-time evaluations of *Viscum album* infection rates on *P. sylvestris* trees in forest stands in the Czech Republic were conducted. Natural forest areas (NFAs) in the Czech Republic have been established based on geological, climatic, orographic and phytogeographical conditions (ÚHÚL 2021). We selected five NFAs with an abundance of *P. sylvestris* (Figure 1). These were Západočeská pahorkatina, Středočeská pahorkatina, Jihočeské pánve–část Třeboňská pánev, Polabí, Jihomoravské úvaly (Figure 2). Predisposition to *Viscum album* infection rate due to drought stress was evaluated using the forest infrared index (FII), which has been established as a basic indicator of forest health. FII is defined as the normalized ratio of water content to the state of the cellular structure of the assimilation apparatus in the stand. A higher FII means a worse state of cell structure and lower water content in the assimilation apparatus (ÚHÚL 2021). The FII values were obtained from the Map Information Catalog. The FII values from the catalog for year 2017 were used (ÚHÚL 2021), as maps with FII for years 2019–2020 were not available. At each NFA, one locality with a low FII and one locality with a high FII were studied (Table 1). At each locality, three stands were evaluated according to their ages: 20–50 years, 51–70 years and 71–90 years. Stands less than 20 years (due to minimal or no infection by mistletoe) and trees with ages, that did not correspond with the stand age, were excluded from the analysis. In each stand, 25 trees along the stand edge were measured. Theses trees were adjacent to each other, hence no tree along the stand edge was left out until 25 trees were measure. Likewise, we measured 25 trees within the stand, along a line dividing the stand into two approximately equal parts, using a compass. The stem diameter of each tree was measured at a height of 1.3 m above ground (DBH) using a forest calliper with an accuracy of 0.5 cm. Percentage defoliation of each tree was estimated in 5% steps and then assigned to one of four categories: 0–10%, > 10–25%, > 25–60% or > 60–99% (CEC-UN/ECE 1993). Dead trees (100% defoliation) were excluded from the analysis. For this reason, the number of sampled trees was lower than 25 in some stands (especially at locality Čelina; Table 1). The *Viscum album* infection rate of each tree was evaluated using the internationally recognized six-class dwarf mistletoe rating system (Hawksworth 1977). This rating system was developed for lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.), but it has already been successfully used to evaluate infection rates of *Viscum album* on Greek fir (*Abies cephalonica* Loudon) (Tsopelas *et al.* 2004), and on *P. sylvestris* (Bilgili *et al.* 2018; Bilgili *et al.* 2020b). The tree crown was visually divided into three equal parts. Each third was rated 0 for no mistletoe infection, 1 for light mistletoe infection (less than 50% of the branches infected) or 2 for heavy mistletoe infection (50% or more of the branches or stem infected). The ratings of the three parts were summed to obtain a total value for the whole tree (ranging from 0–6) (Hawksworth 1977; Figure 3).

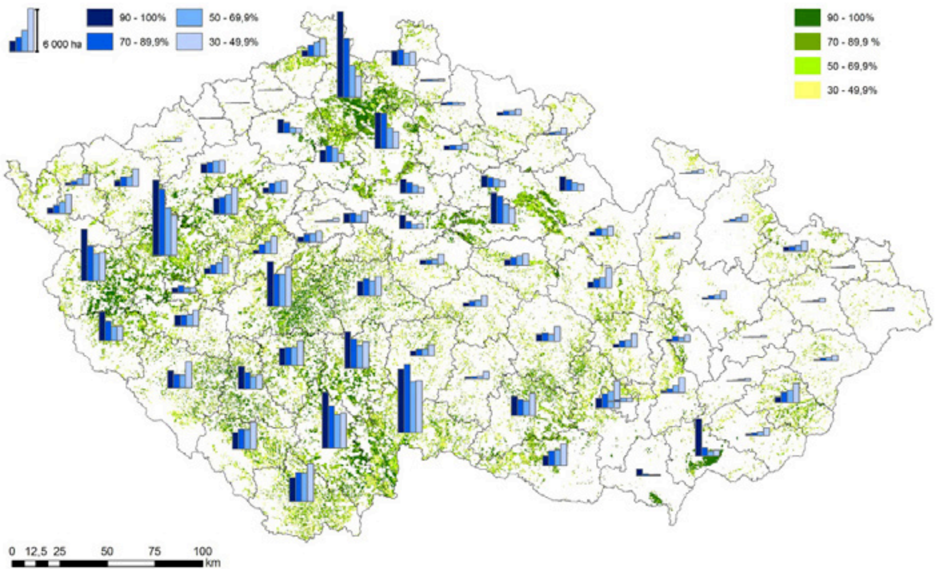

Figure 1: Share of Pinus sylvestris at forest area in districts of the Czech Republic according to the pine percentage (blue columns, length of columns show covered area), and percentage of the pine in the stand (yellow – green points) (Neudertová Hellebrandová et al. 2020).

Abbildung 1: Anteil von Pinus sylvestris an Waldfläche in den Bezirken der Tschechischen Republik nach dem Kiefernanteil (blaue Säulen, Länge der Säulen symbolisiert bedeckte Fläche), und der Kiefernanteil in dem Bestand (gelb – grüne Flächen) (Neudertová Hellebrandová et al. 2020).

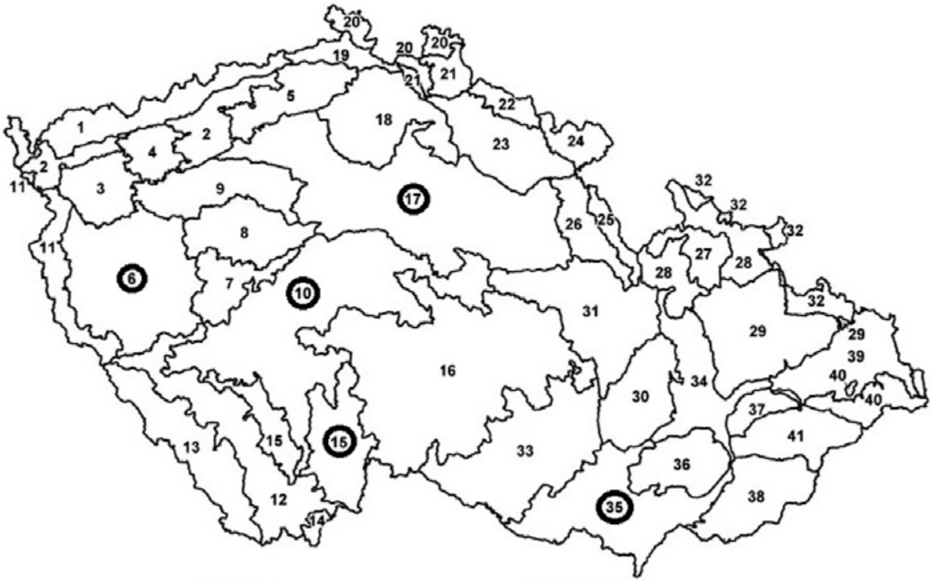

Figure 2: Natural forest areas (NFA) in the Czech Republic (ÚHÚL 2021). The numbers of the NFAs analysed in this study are circled: 6—Západočeská pahorkatina, 10—Středočeská pahorkatina, 15b—Jihočeské pánve—část Třeboňská pánev, 17—Polabí, 35—Jihomoravské úvaly.

Abbildung 2: Natürliche Waldbestände (NFAs) in Tschechien (ÚHÚL 2021). Die Nummern der NFA, die in dieser Studie analysiert wurden, sind eingekreist: 6—Západočeská pahorkatina, 10—Středočeská pahorkatina, 15b—Jihočeské pánve—část Třeboňská pánev, 17—Polabí, 35—Jihomoravské úvaly.

Table 1: Summary information for all research plots. NFA – natural forest area; FII – Forest Infrared Index; Age – stand age (years); Position – tree position in the stand; DBH (cm) – diameter at breast height (cm); Viscum album – Viscum album subsp. austriacum infection rate (values 0-6); N – number of sampled trees. We show arithmetic mean plus-minus Standard Deviation (SD).

Tabelle 1: Zusammenfassung für alle Untersuchungsflächen. NFA – natürliches Waldgebiet; FII – Infrarotindex des Waldes; Age – Alter des Bestands; Position – Position des Baumes im Bestand; DBH – Brusthöhendurchmesser; Viscum-Album-Infektionsrate (Werte 0–6); N – Anzahl der beprobten Bäume. Wir zeigen arithmetische Mittelwert plus-minus Standardabweichung.

NFA	Locality GPS	FII	Age	Position	Defoliation (%)		DBH (cm)		*V. album*	
					N	mean ± SD	N	mean ± SD	N	mean ± SD
6	Semošice 49.5446786N, 12.9864403E	low	21-50	edge	25	52.23 ± 23.27	25	30.60 ± 6.87	25	0.84 ± 1.11
				within	25	61.00 ± 18.37	24	22.96 ± 6.74	24	0.72 ± 1.24
			51-70	edge	25	49.60 ± 23.05	25	35.72 ± 6.81	25	1.08 ± 1.26
				within	25	64.80 ± 19.23	25	28.52 ± 5.62	25	0.44 ± 0.82
			71-90	edge	25	52.40 ± 23.85	25	32.04 ± 20.37	25	1.64 ± 1.68
				within	25	60.60 ± 20.33	25	27.28 ± 4.22	25	1.84 ± 2.01
	Čečovice 49.5964183N, 13.0137133E	high	21-50	edge	25	30.00 ± 17.68	25	21.06 ± 6.82	25	0.24 ± 0.88
				within	25	45.60 ± 17.16	25	17.48 ± 4.34	25	0.28 ± 0.84
			51-70	edge	25	43.80 ± 15.29	25	33.76 ± 6.04	25	0.96 ± 1.24
				within	25	49.40 ± 20.63	25	33.16 ± 5.21	25	0.92 ± 1.38
			71-90	edge	25	44.20 ± 18.41	25	33.02 ± 4.64	25	1.20 ± 1.47
				within	25	63.40 ± 18.12	25	34.10 ± 7.07	25	0.24 ± 0.73
10	Drásov 49.7005250N, 14.1066297E	low	21-50	edge	25	51.80 ± 19.52	25	11.56 ± 5.43	24	0.60 ± 1.26
				within	25	45.40 ± 15.06	25	11.92 ± 3.56	25	0.16 ± 0.80
			51-70	edge	25	44.40 ± 21.33	25	24.33 ± 5.11	24	0.20 ± 0.50
				within	25	53.00 ± 15.81	25	19.76 ± 3.65	25	0.28 ± 0.84
			71-90	edge	25	46.40 ± 18.90	25	29.48 ± 6.01	25	0.20 ± 0.50
				within	25	53.40 ± 17.95	25	25.36 ± 3.32	25	0.00 ± 0.00
	Čelina 49.7356172N, 14.3289978E	high	21-50	edge	24	48.13 ± 21.51	24	14.15 ± 2.41	24	0.42 ± 0.78
				within	24	57.08 ± 21.96	24	13.58 ± 3.22	24	0.63 ± 1.24
			51-70	edge	23	68.26 ± 16.41	23	26.46 ± 4.91	23	2.43 ± 1.50
				within	7	85.71 ± 10.18	7	28.00 ± 5.24	7	1.14 ± 1.07
			71-90	edge	25	56.60 ± 19.43	25	33.84 ± 10.17	25	1.60 ± 1.38
				within	19	80.26 ± 15.68	19	28.55 ± 4.70	19	1.47 ± 1.50

NFA	Locality GPS	FII	Age	Position	Defoliation (%)		DBH (cm)		*V. album*	
					N	mean ± SD	N	mean ± SD	N	mean ± SD
15	Drahov 49.1787631N, 14.7733806E	low	21-50	edge	25	34.00 ± 8.54	25	13.92 ± 2.91	25	0.00 ± 0.00
				within	25	40.40 ± 9.89	25	14.12 ± 3.46	25	0.28 ± 0.89
			51-70	edge	25	43.80 ± 18.67	25	23.70 ± 4.37	25	0.16 ± 0.80
				within	25	39.60 ± 8.41	25	23.40 ± 4.39	25	0.00 ± 0.00
			71-90	edge	25	43.60 ± 13.96	25	37.02 ± 6.27	25	1.96 ± 1.65
				within	25	50.20 ± 14.47	25	36.37 ± 8.93	25	2.2 ± 1.87
	Stráž nad Nežárkou 49.0719200N, 14.8677075E	high	21-50	edge	25	25.40 ± 5.19	25	16.34 ± 4.51	25	0.00 ± 0.00
				within	25	45.20 ± 20.67	25	12.06 ± 3.03	25	0.16 ± 0.80
			51-70	edge	25	36.80 ± 7.62	25	20.58 ± 3.34	25	0.68 ± 1.89
				within	25	47.60 ± 14.30	25	16.40 ± 3.34	25	0.32 ± 0.95
			71-90	edge	25	36.60 ± 14.41	25	32.84 ± 6.81	25	1.44 ± 1.53
				within	25	40.20 ± 10.46	25	31.02 ± 5.40	25	1.56 ± 1.98
17	Sruby 50.0078394N, 16.1794006E	low	21-50	edge	25	45.20 ± 17.59	25	19.18 ± 4.37	25	0.00 ± 0.00
				within	25	39.80 ± 13.65	25	18.14 ± 5.17	25	0.08 ± 0.40
			51-70	edge	25	32.80 ± 5.02	25	21.48 ± 4.82	25	0.00 ± 0.00
				within	25	42.80 ± 14.15	25	21.28 ± 4.04	25	0.00 ± 0.00
			71-90	edge	25	42.20 ± 16.59	25	31.98 ± 7.13	25	1.12 ± 2.01
				within	25	52.20 ± 16.21	25	24.98 ± 5.28	25	0.24 ± 0.66
	Sokoleč 50.0973531N, 15.0952514E	high	21-50	edge	25	31.60 ± 7.60	25	16.70 ± 6.62	25	1.24 ± 1.88
				within	25	56.20 ± 18.44	25	11.86 ± 3.12	25	0.48 ± 1.19
			51-70	edge	25	53.20 ± 21.40	25	27.92 ± 5.78	25	2.60 ± 2.02
				within	25	72.80 ± 19.58	25	31.34 ± 4.97	25	3.08 ± 1.88
			71-90	edge	25	67.20 ± 20.52	25	30.08 ± 6.69	25	2.52 ± 2.06
				within	25	74.60 ± 13.14	25	26.56 ± 5.00	25	2.80 ± 2.25
35	Ratíškovice 48.9224258N, 17.1773706E	low	21-50	edge	25	29.40 ± 6.18	25	25.54 ± 8.02	25	0.00 ± 0.00
				within	25	41.80 ± 15.54	25	19.14 ± 3.62	25	0.00 ± 0.00
			51-70	edge	25	32.40 ± 10.81	25	35.98 ± 7.30	25	0.16 ± 0.55
				within	25	60.60 ± 17.22	25	33.46 ± 5.49	25	1.28 ± 1.84
			71-90	edge	25	39.60 ± 13.69	25	40.28 ± 9.47	25	0.00 ± 0.00
				within	25	55.80 ± 23.70	25	34.26 ± 4.87	25	0.84 ± 1.57
	Valtice 48.7599211N, 16.8139458E	high	21-50	edge	25	29.80 ± 9.84	25	24.86 ± 6.20	25	2.04 ± 2.21
				within	25	44 ± 14.36	25	18.54 ± 4.06	25	0.56 ± 1.61
			51-70	edge	22	56.40 ± 18.68	25	31.52 ± 7.82	25	4.56 ± 1.58
				within	25	58.20 ± 21.55	25	24.66 ± 4.24	25	3.24 ± 2.22
			71-90	edge	25	49.20 ± 19.72	25	30.20 ± 8.08	25	4.60 ± 1.94
				within	25	52.40 ± 22.09	25	22.80 ± 4.67	25	3.20 ± 2.31

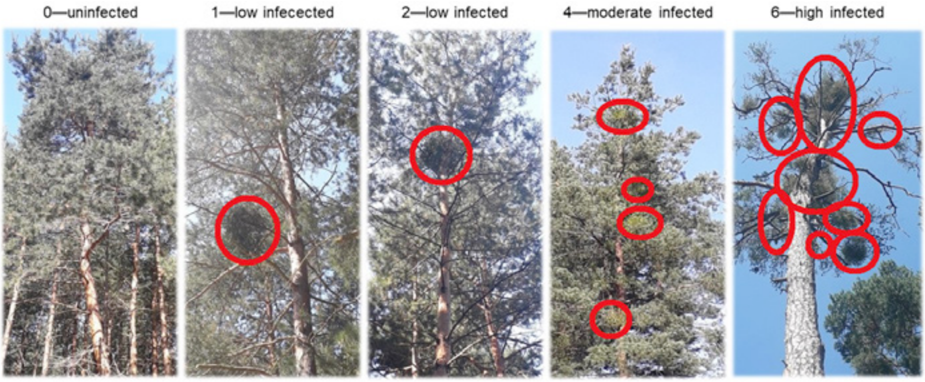

Figure 3: The examples of trees according to six-class dwarf mistletoe rating system classes according to Hawksworth (1977): 0 – uninfected, 1,2 – low, 4 – moderate 6 – high infected.

Abbildung 3: Die Beispiele für Bäume nach sechs Klassen der Zwergmistel-Bewertungssystem-Klassen nach Hawksworth (1977): 0 – nicht infiziert, 1,2 – gering (1-2), 4 – mäßig 6 – hoch infiziert.

A statistical evaluation for the whole trees was performed using SPSS Statistics Version 27 software from the IBM company. A generalized linear model (GLM) was used to test the significance of the predictors (NFA, FII, stand age, tree position in the stand, defoliation and DBH) to *Viscum album* infection rate (Denis 2019) (Table 2). Differences between the *Viscum album* occurrence (0–2) in crown thirds (upper, middle, lower was analysed with Kruskal-Wallis and subsequent pairwise Dunn's tests was performed using Statistica 10 from StatSoft company.

Table 2: Generalized linear model (GLM) of Viscum album subsp. austriacum infection rate.Total number of observations were 1470. Effect – tested variables, df – degrees of freedom, Wald – value of the Wald Chi-square test, p – significance level (P < 0.05 *** P < 0.001), NFA – natural forest area, FII – Forest Infrared Index, Age – stand age, Position – tree position in the stand, Defoliation – percentage tree defoliation, DBH – diameter at breast height.*

Tabelle 2: Verallgemeinertes lineares Modell (GLM) des Mistelbefalls. Anzahl der Beobachtungen ist 1470. Effect – getestete Variable, df – Freiheitsgrade, Wald – Wert des Wald-Chi-Quadrat-Tests; P – Signifikanzniveau (* p < 0.05 *** p < 0.001); NFA – natürliches Waldgebiet; FII – Infrarotindex des Waldes; Age – Alter des Bestands; Position – Position des Baumes im Bestand; Defoliation – prozentuelle Kronenverlichtung der Bäume; DBH – Brusthöhendurchmesser.

Effect	df	Wald	P	Significantly different groups
NFA	4	21.36	***	
FII	1	102.64	***	high > low
Age	2	9.09	*	71–90 > 51–70 > 20–50
Position	1	5.40	*	edge > within
Defoliation	3	43.13	***	60–99 % > 25–60 % > 10–25 %
DBH	1	64.93	***	positive correlation

3 Results

The *Viscum album* subsp. *austriacum* infection rate differed statistically significantly between NFA (Table 1). We observed the highest infection rate in NFA Jihomoravské úvaly and the lowest in NFA 10 Středočeská pahorkatina, but the differences between individual NFAs were not significant (Table 2; Figure 2; Figure 4a). Infection rates were significantly higher in localities with high FII (Table 1; Table 2; Figure 4b). We further observed significant differences between all age categories and the highest infection rate was for 71–90 years, followed by 51–70 years and lowest in the 21–50 years (Table 1; Table 2; Figure 4c). The infection rate was higher at the stand edge than within the stand (Table 1; Table 2; Figure 4d). For higher defoliation there were higher infection rates. Only the 0–10% category did not differ significantly from the other defoliation categories, all other categories differed significantly from each other with the highest infection rate observed in the > 60–99% category, followed by the > 25–60% category and lowest in the > 10–25% category (Table 1; Table 2; Figure 4e). DBH was positively correlated with mistletoe infection (Table 1; Table 2; Figure 4f – shown as classes). Kruskal-Wallis test confirms differences between *Viscum album* subsp. *austriacum* infection rate in relation to crown part ($H = 17.28$, $p < 0.001$) with significantly higher infection rates in the upper and middle part compared to lower part (Dunn's test: middle > low, $z = 2.78$, $p < 0.05$; high > low, $z = 2.41$, $p < 0.05$) (Figure 5).

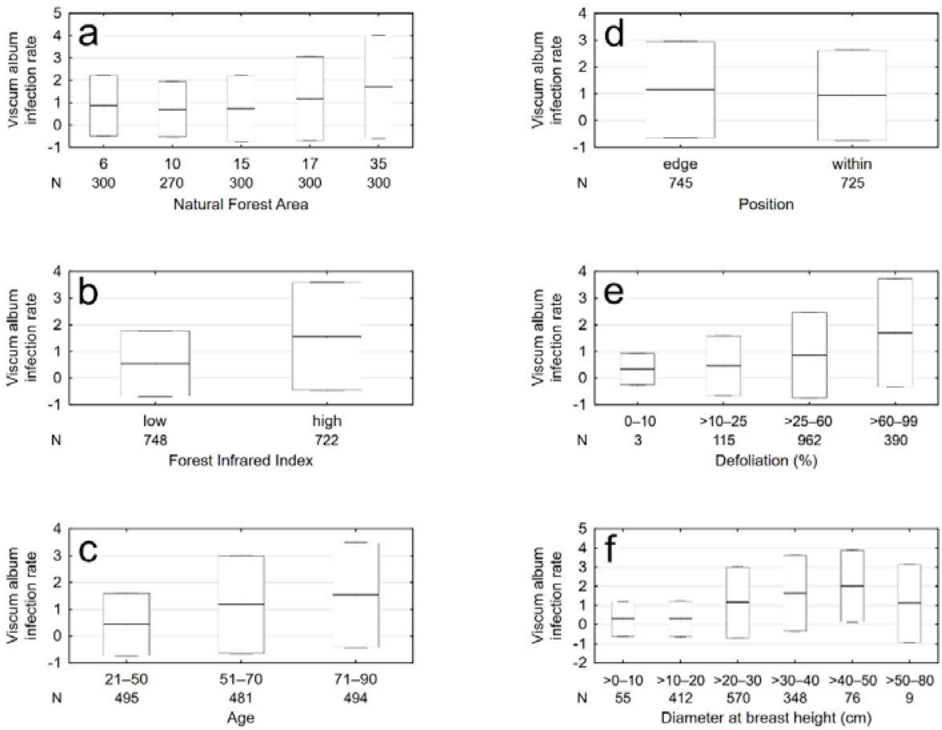

Figure 4: Box plots of Viscum album infection rate (range of values 0–6) for natural forest areas (NFA), the Forest Infrared Index (FII), stand age, tree position in the stand, defoliation and diameter at breast height (DBH). Center line – arithmetic mean, box – standard deviation. NFAs: 6 – Západočeská pahorkatina, 10 – Středočeská pahorkatina, 15b – Jihočeské pánve – část Třeboňská pánev, 17 – Polabí, 35 – Jihomoravské úvaly. N – number of observations.

Abbildung 4: Boxplot des Viscum-album-Befalls (Wertebereich 0–6) für natürliche Waldbestände (NFA), zum Infrarotindex des Waldes (FII), zum Alter des Bestandes, zur Position des Baumes im Bestand, zur Defoliation und zum Brusthöhendurchmesser (DBH). Mittelstrich – arithmetisches Mittel, Kasten – Standardabweichung, NFAs: 6 – Západočeská pahorkatina, 10 – Středočeská pahorkatina, 15b – Jihočeské pánve – část Třeboňská pánev, 17 – Polabí, 35 – Jihomoravské úvaly. N – Anzahl der Beobachtungen.

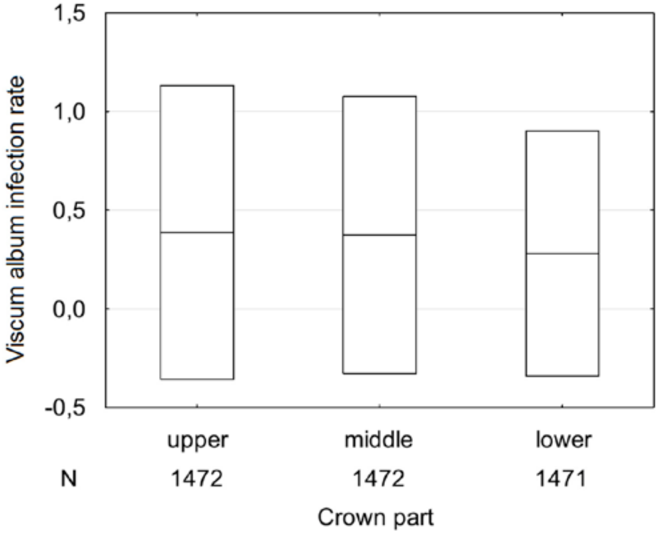

Figure 5: Box plots of Viscum album infection rate (range of values 0–2) in relation to crown part (thirds). For details of display see Fig. 4.

Abbildung 5: Boxplots zum Viscum album Befall (Wertebereich 0–2) bezogen auf Kronendrittel. Für Details zur Darstellung siehe Fig. 4.

4 Discussion

The highest *Viscum album* subsp. *austriacum* infection rate in our study was recorded in NFA Jihomoravské úvaly (South Moravia) due to high values at locality Valtice (with high FII – more drought stress). NFA 35 is located in the climatic region T4, which is the warmest in the Czech Republic. Only the edges of this NFA with higher altitude are located in the warm T2 region (Quitt 1971; ÚHÚL 1999). The average annual temperature in NFA 35 is within the range of 8.4–9.5 °C, and the average annual precipitation varies between 495 mm and 625 mm (ÚHÚL 1999). The high mistletoe infection rate in NFA 35 at locality Valtice may be attributed to its very warm and dry climate. Altitude and stand volume were the most significant predictor of the distribution of *Viscum album* subsp. *austriacum* at stand level on *P. sylvestris* in the Eastern Black Sea Region of Turkey (Bilgili *et al.* 2020b). It is commonly known that temperature decreases with higher altitude, which also applies to NFA 35 (Quitt 1971; ÚHÚL 1999). Several outbreaks of *Viscum album* subsp. *album* in NFA 35 regions have been previously reported, especially in the Lednice castle park on deciduous trees (Procházka 2004; Bulíř 2017), which is located ca 3 km from the research locality Valtice included to our study. These data indicate long-term favourable conditions for the growth of *Viscum album sensu lato* in NFA 35 in the warm and drought stressed areas of South Moravia.

Viscum album subsp. *austriacum* infection was significantly higher in trees in localities with high FII (more stressed by drought) in our study. Stands generally kept relative low or relative high FII for a long time (in comparison with other stands in the same year) (see ÚHÚL 2021). Moreover, research localities with high FII were obviously more drought stressed than the localities with low FII during our study. So, although the FII values were obtained from the Map Information Catalog for year 2017 (ÚHÚL 2021), it should not affect our study. No previous studies focused on relationship between FII and *Viscum album* infection are available. However, *Viscum album* subsp. *austriacum* infection lead to massive loss in photosynthetic tissue (Rigling *et al.* 2010) and FII depends on water content in assimilation apparatus of the stand (ÚHÚL 2021). So, massive mistletoe infection can contribute to higher FII values. On the other hand, drought is an important factor which conducive to weakening trees and making them more susceptible to the spread of biotic pests (Oliva *et al.*, 2014), including *Viscum album* (Szmidla *et al.* 2019). Lech *et al.* (2020) reported a statistically significant higher *Viscum album* subsp. *austriacum* infection rate in *P. sylvestris* in dry sites compared to fresh, moist and very moist sites in Poland. Szmidla *et al.* (2019) recorded a higher occurrence of *Viscum album* subsp. *austriacum* in *P. sylvestris* in sites with lower precipitation in Poland. Therefore, the infection of *P. sylvestris* by *Viscum album* subsp. *austriacum* is higher in drier or more drought-stressed sites.

Viscum album subsp. *austriacum* infection was significantly higher in older trees in our study, which have larger DBH and tree height. Birds, which are the main vectors of mistletoe species, prefer taller trees for nesting and resting (Aukema and del Rio 2002). This could be one reason for more frequent infections for older and larger trees (Kołodziejek and Kołodziejek 2013; Lech *et al.* 2020). Our study confirms evidence in the lierature, as higher *Viscum album* infection rates for older *P. sylvestris*, *Abies alba* and *Betula pendula* trees were found in Poland (Lech *et al.* 2020). On *Abies cephalonica*, *Viscum album* infection was highest in trees over 100 years old in Greece (Tsopelas *et al.* 2004). On field maple (*Acer campestre* L.) and small-leaved linden (*Tilia cordata* Mill.) in Lednice Castle Park (South Moravia, Czech Republic), the number of *Viscum album* shrubs increased with tree age and lower tree vitality, with large differences between the two species (Baltazár *et al.* 2013). On broadleaved trees, *Viscum album* infection possitively correlated with tree age in the Kalingrad City (Russia) (Skrypnik *et al.* 2020). Thus, higher infection rate with *Viscum album* for older trees appears to be a general feature in Eurasian forests.

Viscum album subsp. *austriacum* infection was significantly higher on the trees in the stand edge than on those within the stand in our study. Kołodziejek and Kołodziejek (2013) recorded a higher *Viscum album* infection in stands with lower density and on the outer branches of the tree crown in *P. sylvestris* in Poland. Kartoolinejad *et al.* (2007) recorded significantly higher *Viscum album* infection rate in the stand edge on *Parrotia persica* (DC) C.A. Mey in Caspian Forests (Iran). Zuber (2004) reported that *Viscum album* prefers to grow in sunlit parts of the crown. Mellado and Zamora (2014) noted that excess radiation and high temperatures have a negative effect on *Viscum* *album* seeds and thus prevent its spread in warm areas on *P. nigra*, maritime pine (*P. pinaster*) and *P. sylvestris* in the Sierra de Baza (Spain). However, our study was performed in Central Europe, where the low temperature is a limiting factor for *Viscum album* (Zuber 2004). *Viscum album* is also a light-demanding species, especially for germination (Zuber 2004). Thus, in the climatic conditions of Central Europe, the higher occurrence of *Viscum album* on *P. sylvestris* in the stand edge can be explained by the positive effect of sunlight.

Heavily defoliated trees were the most infected by *Viscum album* subsp. *austriacum* in our study. The only exception was defoliation in the 0–10% category, due to the very low number of trees (only three). For the other defoliation categories, the numbers of trees were sufficient (115, 962, 390). Significantly higher defoliation in *P. sylvestris* trees infected by *Viscum album* was recorded also in urban area in Viernheim (Germany) (Hülsmann *et al.* 2013) and in forests in Teruel (Spain) (Sangüeesa-Barreda *et al.* 2013). Lech *et al.* (2020) recorded significantly higher defoliation in *P. sylvestris* and *B. pendula* trees infected by *Viscum album* compared with uninfected trees; in *A. alba*, this difference was on the border of statistical significance. The positive correlation between mistletoe infection and defoliation can be interpreted in two ways: 1) mistletoe causes higher defoliation of trees (Sangüeesa-Barreda *et al.* 2013); 2) heavily defoliated trees are more often infected by mistletoe, either due to the greater lightening of crowns (*i.e.*, to favourable conditions for mistletoe growth) (Zuber 2004), or due to deteriorating health and, consequently, higher susceptibility to mistletoe attack (Dobbertin and Rigling 2006; Rigling *et al.* 2010). These interpretations are not mutually exclusive. Thus, the relationship between the rate of *Viscum album* infection and defoliation may not be unequivocally causal and consequential and is therefore a feedback relationship.

Viscum album subsp. *austriacum* infection increased with increasing DBH in our study, which is in line with previous studies. Sangüeesa-Barreda *et al*. (2013) recorded higher stem and crown diameters in *P. sylvestris* trees infected with *Viscum album* compared with uninfected ones, but trees with long-term infections of *Viscum album* showed reduced radial growth. Lech *et al.* (2020) recorded statistically significant higher DBH on trees infected with *Viscum album* compared with uninfected ones in *P. sylvestris* and *A. alba*; in *B. pendula*, the difference was on the border of statistical significance. According to the Kraft classification, predominant trees and dying or dead trees were the most infected in all three tree species (Lech *et al.* 2020). Significant positive correlation between *Viscum album* infection rate and DBH was recorded also on genera *Acer*, *Crataegus*, *Junglans*, *Robinia* and *Tilia* in the Lednice Castle Park (Czech Rebublic) (Baltazár *et al.* 2019) and on *Parrotia persica* in Caspian Forests (Iran) (Kartoolinejad *et al.* 2007). Trees with higher DBH could be more infected due to preference of bigger trees for perching it (Aukema and del Rio 2002; Kołodziejek and Kołodziejek 2013; Lech *et al.* 2020). Therefore, dominant trees with a higher stem diameter are more susceptible to *Viscum album* infection.

Viscum album subsp. *austriacum* infection rate in relation to crown part was lower in lower part compared to both middle and upper part in our study. This could have been caused by preference of birds for higher trees and crown sections for nesting and resting (Aukema and del Rio 2002), Moreover, *Viscum album* is a light-demanding species (Zuber 2004) and more light is available in upper parts of the crown compared to lower parts. Bilgili *et al.* (2020b) recorded gradually increasing distribution of *Viscum album* subsp. *austriacum* from lower to upper part of the crowns on *P. sylvestris* in Eastern Black Sea Region of Turkey, which was evaluated by the same method like in our study. Sangüeesa-Barreda *et al.* (2012) recorded that age and basal diameter of *Viscum album* subsp. *austriacum* increased towards the crown apex on P. sylvestris in Eastern Spain. Vallauri (1998) recorded the highest infection by *Viscum album* subsp. *austriacum* in upper third of the crown on *Pinus nigra* in the Saignon watershed (southwestern Alps). So, upper parts of tree crown are more susceptible to to *Viscum album* subsp. *austriacum* infection than the lower parts.

5 Conclusion

Results in our study showed that significantly higher *Viscum album* subsp. *austriacum* infection was recorded in stands with high FII (higher drought stress), in older stands (highest: 71–90 years followed by 51–70 years), on trees in the stand edge, on trees with higher DBH and higher defoliation (highest: > 60–99% then > 25–60 %, lowest: > 10–25 %), and in the upper and middle part of tree crown. These results can be explained mainly due to 1) preference of dominant trees by birds which are vectors of the mistletoe seeds, 2) lightness of the *Viscum album* subsp. *austriacum*, 3) higher susceptibity of drought stressed trees to the mistletoe infection.

In cases of continuing trends of rising temperature, more frequent drought periods and overgrowth of biotic pests, an even higher infection rate of *P. sylvestris* trees by *Viscum album* subsp. *austriacum* can be expected (Dobbertin *et al.* 2005). Therefore, planting woody varieties more resistant to drought and to high temperatures and planting in sites with lower temperatures and higher precipitations is recommended for *P. sylvestris* forest protection in Central Europe. The felling of infected trees leads to the lightening of stands, which may result in the further development of mistletoe on existing trees in the stand (Noetzli *et al.* 2003). Thus, the reduction of the rotation period can be an effective measure for *P. sylvestris* stand protection against *Viscum album* subsp. *austriacum*.

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