The crown condition of Norway spruce and occurrence of symptoms caused by *Armillaria* spp. in mixed stands

PETR ČERMÁK*, TOMÁŠ ŽID

Department of Forest Protection and Wildlife Management, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic

*Corresponding author: cermacek@mendelu.cz

Abstract: Mixed stands are currently supported as effective management options to reduce forest vulnerability to climate change. However, our issues about benefits of mixtures, mechanisms of their incidence and conditions for their effectiveness have yet been only partly clarified. We assessed the crown condition of Norway spruce (*Picea abies* /L./ Karst) and occurrence of symptoms caused by *Armillaria* spp. on spruce in a small area in the Drahanská vrchovina Highlands (Czech Republic) in differently mixed stands in 2002 and 2019. We found that although the broadleaf abundance affected the total defoliation of Norway spruce, the effect was unstable in time. The observed effect of altitudinal zones and Norway spruce abundance on the occurrence of symptoms of *Armillaria* root rot in spruce was also unstable. The drought during recent four years and the implemented forestry measures (salvage and intermediate felling) can be reasons for the relationship instability. We did not identify any statistically significant relationship between tree species diversity (Simpson's Index) and defoliation.

Keywords: total defoliation; broadleaf abundance; tree species diversity

Recent studies have underlined the influence of species composition on forest productivity, health condition or some ecosystem services (Schuler et al. 2017). Mixed stands are often much more productive than monocultures (Zhang et al. 2012; Bielak et al. 2014). These stands can also be more resistant to insect herbivores. The effect is probably higher when mixed forests comprise taxonomically more distant tree species, and when the proportion of non-host trees is higher than that of host trees (Jactel, Brockerhoff 2007). The effect of tree diversity on pest occurrence and damage caused by them can follow a biogeographic pattern, because forest resistance to herbivory may depend on the mean annual temperature which is a key driver of plant and insect phenology (Kambach et al. 2016).

In the case of Norway spruce (*Picea abies* /L./ Karst.) as a climate-sensitive species the difference between growth and stress responses of both monocultures and mixtures is very important for sustainable timber production, disturbance risk management and also for adaptive forest management implementation. Numerous studies have indicated higher timber production of Norway spruce in mixed stands (Pretzsch et al. 2010; Bielak et al. 2014). Fewer studies have pointed to the effect of tree species diversity on health status or crown condition of Norway spruce. Iacopetti et al. (2019) observed that the tree diversity had an effect on Norway spruce defoliation in Alpine areas. The effect was not the same in different years; therefore, Iacopetti et al. (2019) presumed that particular

climate-related events and biotic attacks had different impacts on trees growing in monocultures and mixed stands. The mixtures may be able to reduce damage caused by the root decay such as *Heterobasidium annosum* (Thor et al. 2005; Žemiatis, Stakenas 2016) or *Armillaria* spp. (Morrison et al. 2014). However, other studies found no significant effect of tree species composition on the presence of *Heterobasidium annosum* and *Armillaria* spp. (Dálya et al. 2019).

Felton et al. (2010, 2016) underlined that mixed-species stands (*Picea abies*, *Pinus sylvestris*, *Betula pubescens* or *B. pendula*) can provide different benefits such as increased biodiversity, water quality, aesthetic and recreational values and reduced stand vulnerability to pest and pathogen damage. Similar benefits were also described by Pretzsch et al. (2017).

Climate change increases the vulnerability of forest stands to strong stress or disturbances evoked by extreme events like windstorm or drought. Mixed forests can be more resilient thanks to complementarities in species sensitivity (Lafond et al. 2014). The silviculture of mixed stands can be among the strategies to increase forest adaptability, but forest managers need information about the complex benefits of mixtures, conditions for their effectiveness. Research outputs about these issues can be important for forest management optimization.

The Proklest forest district (north of Brno, Moravia, Czech Republic) is characterized by stands with prevailing Norway spruce in different mixtures – the differences lie in Norway spruce proportion as well as in tree species composition. We assessed the crown condition and health of Norway spruce in the district in 2002 and in 2019 after repeated droughts. Our aims were to i) to compare the condition of Norway spruce in 2002 and 2019; and ii) to identify possible effects of tree species composition and other selected site and stand parameters on the crown condition of Norway spruce and occurrence of symptoms caused by *Armillaria* spp.

MATERIAL AND METHODS

Study plots and research design. The study area is a part of the Drahanská vrchovina Highlands – the Proklest forest district, Training Forest Enterprise called Masaryk Forest at Křtiny (TFE). Norway spruce (*Picea abies* /L./ Karst) covers about 60% of the total stand area.
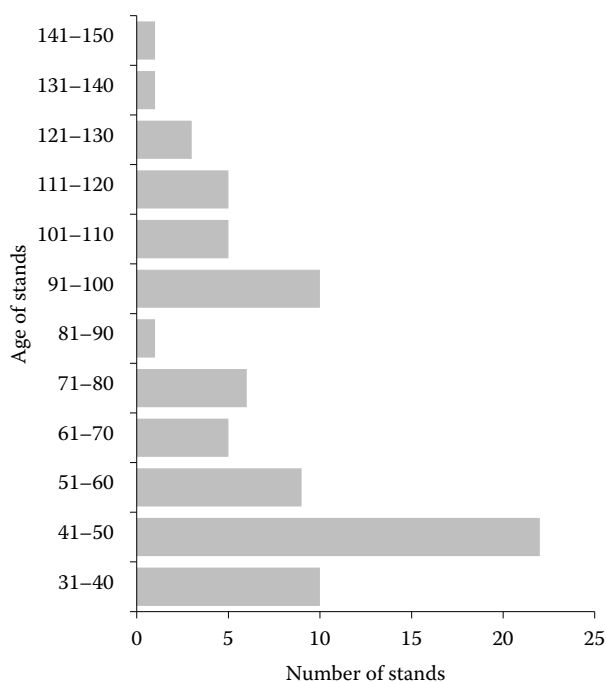

Figure 1. Age distribution of forest stands in 10-year age classes in 2019

In both years 78 stands were evaluated. The plots are in the beech altitudinal zone (62) and in the oak-beech forest altitudinal zone (16). The age of stands ranged from 36 years to 146 years in 2019 (Figure 1).

Norway spruce was the prevailing tree species (> 50% in species composition) in all the stands in the first assessed year 2002. Most of the stands were mixed. The mixed stands were composed of *Picea abies* (50% and more in 2002) and 1–6 other species: *Larix decidua*, *Pinus sylvestris*, *Abies alba*, *Pseudotsuga menziesii*, *Fagus sylvatica*, *Quercus petraea*, *Carpinus betulus*, *Fraxinus excelsior*, *Acer pseudoplatanus*, *Betula pendula* and *Alnus glutinosa*.

Our research plot was based on a simplified ICP Forest network – Level I design (Eichhorn et al. 2010). The plots were situated inside the assessed stands to minimize the edge effect. We selected twenty trees and used a simplified visual assessment – modified methods of Cudlín et al. (2001) and Eichhorn et al. (2010), see Table 1. The widely defined assessment categories shortened the time spent in the field so as to evaluate all stands in the same conditions. The same trees were not assessed in the two investigated years because many trees had disappeared from the stands due to mortality, salvage and intermediate felling (elimination of

Table 1. The evaluated parameters

Defoliation of primary structure		Total defoliation	
Degree	Value area	Degree	Value area
1	< 20%	1	< 10%
2	21–40%	2	11–20%
3	41–60%	3	21–30%
4	61–80%	4	31–40%
5	81–100%	5	41–50%
		6	51–60%

Occurrence of symptoms attributable to infection by *Armillaria* spp.	
Degree	Description
1	symptoms attributable to infection by *Armillaria* spp. are not evident
2	0–25% trees show symptoms attributable to infection by *Armillaria* spp.
3	26–50% trees show symptoms attributable to infection by *Armillaria* spp.
4	51–75% trees show symptoms attributable to infection by *Armillaria* spp.
5	> 75% trees show symptoms attributable to infection by *Armillaria* spp.

trees damaged by drought and accompanying factors like bark beetles or root rots). The same forestry measures were implemented also in the period before the study period. The present attack of stands by *Armillaria* sp. was assessed in the same plots. A tree displaying visual symptoms attributable to infection by *Armillaria* spp. such as butt swelling, fruit bodies, syrrotium or rhizomorphs was evaluated as symptomatic. All other trees were classified as non-symptomatic.

The site and stand parameters were compared with the defoliation of primary structure –defoliation of primary shoots produced by regular growth (Kozlowski 1971; Cudlín et al. 1999, 2000), the total defoliation and occurrence of symptoms caused by *Armillaria* spp. in both assessed years using one-way analysis of variance (ANOVA). Stand parameter values (age, Norway spruce abundance, broadleaf abundance) were taken over from forest management plans and forest records. Tree diversity was quantified using Simpson's index (Simpson 1949).

Climate conditions. We used climate data from gridded (0.5° × 0.5°) meteorological measurements calculated by the Climate Research Unit (CRU TS4.03; via http://climexp.knmi.nl) covering the study area (Harris et al. 2014). The climate conditions changed during the period (Figure 2). The annual temperature was above-average in all the years since 2011 (compared with 1981–2010 climate normal period). Severe drought periods were detected in the growing seasons (March–September) in 2003, 2015 and 2018. Notably below-average seasonal precipitation totals were recorded also in 2004, 2012 and 2017.

RESULTS

Species composition

The portion of the tree species changed in time because of forestry measures (salvage and usual intermediate felling), interspecific competition and dying caused by occurring chronic stress. The abundance of Norway spruce increased in 32 stands between 2002 and 2019, decreased in 36 stands, and 10 stands showed no change between 2002 and 2019. The broadleaf abundance increased in 31 stands between 2002 and 2019, decreased in 24 stands, and 23 stands were without change between 2002 and 2019. The more detailed data about species composition are in Figure 3. The average abundance of Norway spruce decreased from78.2% to 75.8% between 2002 and 2019. The average broadleaf abundance increased from12.6% to 15.7%.

Crown condition

The total defoliation of Norway spruce increased in 57 stands between 2002 and 2019, decreased in 1 stand only, and 20 stands were without change (Figure 4). The defoliation of primary structure increased in 43 stands between 2002 and 2019, decreased in 4 stands only, and 31 stands were without change (Figure 4).

Effect of site and stand parameters on the Norway spruce condition

The total defoliation, the defoliation of primary structure and the occurrence of symptoms attributable to infection by *Armillaria* spp. increased with the age of stand in both assessed years. The stands with higher broadleaf abundance had significantly lower total defoliation in 2002. In the same year, the more intensive presence of *Armillaria* spp. symptoms was found in stands in the oak-beech forest altitudinal zone (compared to the beech zone) and in stands with higher Norway spruce abundance (Table 2). In 2019, the three relationships were not
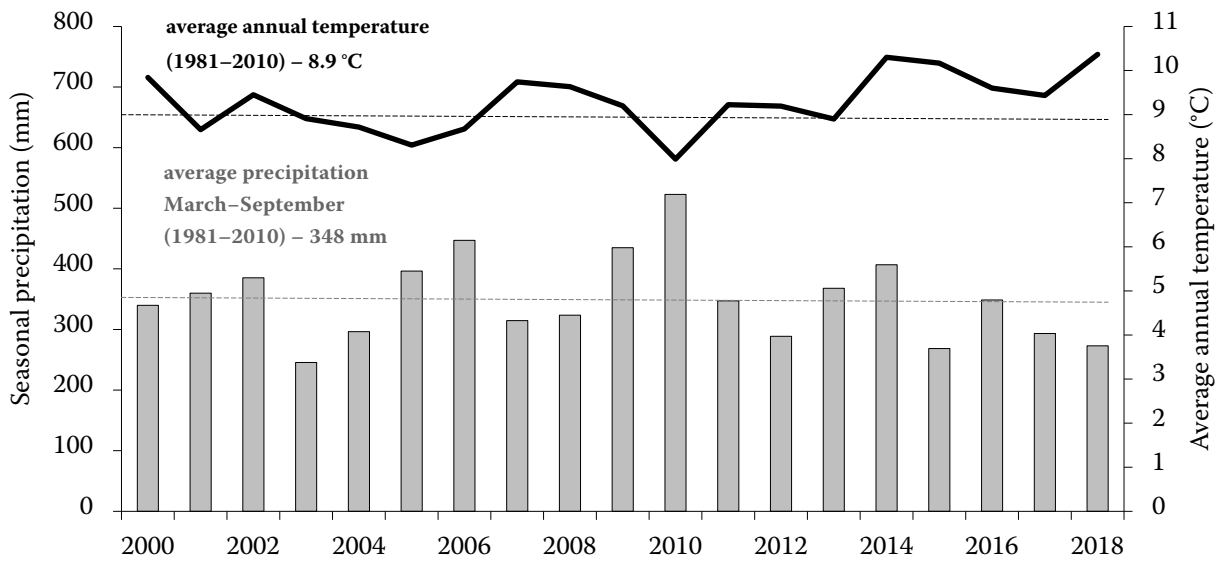
Figure 2. Annual average temperatures and seasonal (March–September) precipitation in 2000–2018 compared with 1981–2010 climate normals

found. However, we identified a significant relationship between the broadleaf abundance in 2019 and the change in the total defoliation of Norway spruce between 2002 and 2019 (Table 3). Fifteen out of twenty stands which showed the same defoliation degree between 2002 and 2019 had a 15% share of broadleaved trees and more in 2019. One stand which was classified in a lower defoliation degree in 2019 than in 2002 had a 61% share of broadleaves in 2019.

DISCUSSION

The total defoliation and the defoliation of primary structure increased with age in both assessed years (Table 2). These relationships are common for Norway spruce, as has been identified in many European areas (Vitale et al. 2014; Čermák et al. 2019; Eickenscheidt et al. 2019). Natural senescence plays a role in the age effect on defoliation with respect to the fact that the social status and the occurring
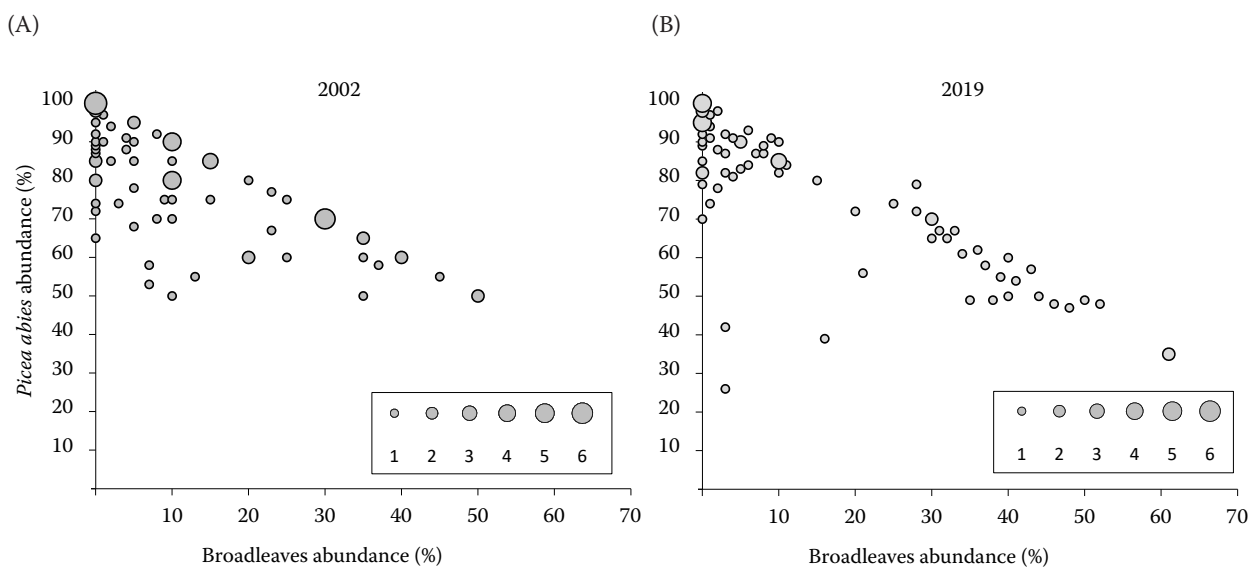
(A)

(B)

Figure 3. The abundance of Norway spruce and broadleaf species in 2002 and 2019. The bubble size represents the number of stands – a continuum from the smallest bubble representing one stand to the largest bubble representing six stands
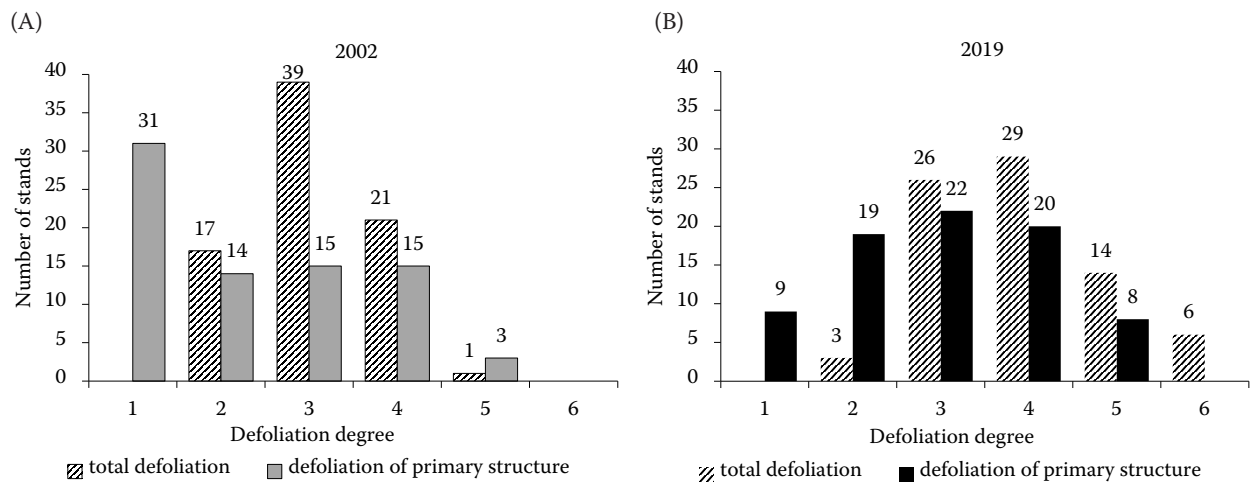
Figure 4. Total defoliation and defoliation of primary structure (the defoliation degrees are defined in Table 1)

Table 2. Effect of site and stand parameters on the health condition of *Picea abies* in 2002 and 2019 using one-way ANOVA

Source	2002		2019	
	F	*P*	*F*	*P*
Effect on the defoliation of primary structure				
Age	10.3080	**0.0000**	32.2654	**0.0000**
Altitudinal zone	3.8712	0.0524	0.9257	0.4539
P. abies abundance	1.4687	0.1096	0.9648	0.5478
Change of *P. abies* abundance	–	–	1.0971	0.3850
Broadleaf abundance	1.5142	0.1123	1.3518	0.1748
Change of broadleaf abundance	–	–	1.9619	0.0813
Simpson's Diversity Index	1.4220	0.2373	1.0971	0.3845
Effect on total defoliation				
Age	4.2851	**0.0000**	2.4863	**0.0042**
Altitudinal zone	0.0842	0.7725	0.0531	0.8184
P. abies abundance	1.5128	0.4035	0.7210	0.8454
Change of *P. abies* abundance	–	–	0.7966	0.7541
Broadleaf abundance	1.9966	**0.0218**	1.1307	0.3501
Change of broadleaf abundance	–	–	0.9162	0.5990
Simpson's Diversity Index	1.9531	0.6598	0.7701	0.7661
Occurrence of symptoms attributable to infection by *Armillaria* spp.				
Age	8.8554	**0.0000**	3.9321	**0.0001**
Altitudinal zone	5.0483	**0.0265**	0.9528	0.3321
P. abies abundance	1.7757	**0.0200**	0.6595	0.9000
Change of *P. abies* abundance	–	–	0.7248	0.8348
Broadleaf abundance	1.5844	0.0894	1.2399	0.2516
Change of broadleaf abundance	–	–	0.8856	0.6383
Simpson's Diversity Index	0.8014	0.7563	0.4554	0.9824

Statistically significant values ($P < 0.05$) are in bold

Table 3. Effect of site and stand parameters on the change of the health condition of *Picea abies* between 2002 and 2019 analysed using one-way ANOVA

Source	F	P
Effect on the change of the defoliation of primary structure		
Age	1.1055	0.3895
Altitudinal zone	0.3877	0.5354
Change of *P. abies* abundance	1.5775	0.0793
Broadleaf abundance 2019	1.3445	0.1791
Change of broadleaf abundance	1.0800	0.4010
Effect on the change of total defoliation		
Age	1.0255	0.4769
Altitudinal zone	0.1953	0.6598
Change of *P. abies* abundance	1.1542	0.3269
Broadleaf abundance 2019	1.8799	**0.0258**
Change of broadleaf abundance	1.6873	0.0524

Statistically significant values ($P < 0.05$) are in bold

stress determine the tree senescence (de Vries et al. 2014). The age did not have any effect on the change of total defoliation and the defoliation of primary structure between 2002 and 2019 (Table 3). The finding is in accordance with Eickenscheidt et al. (2019), who found that the age effect primarily determined the general level of defoliation whereas weather conditions were the main drivers of spatiotemporal defoliation trends.

The total defoliation increased between 2002 and 2019. Reasons for the defoliation increase could not be identified from the two separate assessments. However, two factors are very likely important drivers: the aging of stands (see above) and subnormal precipitation in three out of the last four years (Figure 2) together with the accompanying damage.

Precipitation and precipitation deficit (of the current and previous years) were the factors that were mainly correlated with defoliation in France ICP Forests Level II plots (Ferreti et al. 2014) and in Romania ICP level I network (Popa et al. 2017). Dry summers were also among the main causes of increased Norway spruce defoliation during 1986–2000 in southeastern Norway (Solberg et al. 2015).

We found that Norway spruce defoliation increased more in the stands with a lower proportion of broadleaf trees during the research period characterized by repeated droughts. The result is consistent with Iacopetti et al. (2019) findings. They found that the crown condition worsened in the Norway spruce monocultures but remained relatively stable in mixed plots of Alpine areas during the period with lower precipitation from 2008 to 2012. Iacopetti et al. (2019) also underlined that different events or conditions can differently change the sign of the relationship between tree diversity and defoliation. In relatively favourable years the defoliation was higher in mixed stands. They observed negative correlations only between defoliation and tree diversity (Shannon index) in the years when the overall defoliation of Norway spruce was highest (> 25%). Conversely, a slight but significant positive correlation between local tree diversity and Norway spruce defoliation was observed in stands at higher elevations in the Alps, i.e. in optimal climatic conditions for spruce and in climax forests which are often monospecific or with low diversity (Bussotti et al. 2018). We did not identify any statistically significant relationship between diversity (Simpson's index) and defoliations in our study area (Table 2). We suppose that an important reason can be a high variability in the species composition of particular evaluated stands. The stands with identical or very similar diversity had different species composition. Crown defoliation of individual Norway spruce trees can be more affected by species identity than diversity of their neighbouring trees (Bussotti et al. 2018). Every species has different competitiveness, aboveground and root system architectures or evapotranspira-

tion needs and these characteristics influence its effect on nearby spruces.

In our research, a positive correlation between broadleaf abundance and total defoliation was found in 2002 (when the Norway spruce total defoliation was lower than in 2019), but no such a relationship was observed in 2019. The reasons have not been identified. However, we suppose that some of the benefits provided by broadleaf trees may have disappeared in the recent multiannual drought period. Like for example at night, through deeply extending root systems (for example of beech roots), some tree species can release water into the surface-near soil horizons where it is available also for Norway spruce. The "hydraulic lift" can be functional only in situations when the water deficit is only in the upper layer of soil and not in the whole soil profile.

Specialised fungal pathogens can reduce their virulence in mixed forest stands or when the proportion of host trees is lower (Thor et al. 2005). However, *Armillaria* spp. have a huge host range. The generalist pathogens such as *Armillaria* spp. may spread from one host species to another and thereby the incidence of diseases can be increased (Parker et al. 2015). Possible effects of tree diversity on the pathogen occurrence or pathogenicity are therefore less predictable. Mixed stands may provide more suitable microclimates (e.g., higher humidity) for fungi than monocultures (Jules et al. 2014). On the other hand, a disease impact might be lowered by admixture of disease-tolerant tree species (Morrison et al. 2014).

Morrison et al. (2014) observed decreased mortality of susceptible conifers by *Armillaria* root rot in mixed conifer and broadleaf stands rather than in mixed conifer stands compared with pure conifer stands. Conversely, Dálya et al. (2019) identified no significant effects of tree species composition, soil type and altitudinal zones on *Armillaria* spp. distribution in the forest of Vallombrosa (Apennine Mountains, Italy). We found a significant effect of Norway spruce abundance and altitudinal zones on the occurrence of symptoms caused by *Armillaria* spp. in 2002, but not in 2019.

The age of the stand had a significant effect on the occurrence of symptoms caused by *Armillaria* spp. in both years (Table 2). *Armillaria* spp. generally attacked mainly Norway spruce trees in the study area, both at their young and middle age. In the case of other hosts, *Armillaria* spp. mainly

colonized strongly stressed or dying old trees. A partial number of spruces disappeared from the stands because of mortality, salvage and intermediate felling during 2002–2019. The same forestry measures were also implemented in the period before the study period, but salvage fellings were intensified during the last five years as a consequence of drought and accompanying damage.

These fellings can be a reason for the absence of the effects of Norway spruce abundance and altitudinal zones in 2019. The significance of the stand age for the distribution of *Armillaria* spp. was already identified by Dálya et al. (2019). Different *Armillaria* species dominated in different age classes; the majority of *A. cepistipes* was found in the age class of 61–80 years, while the occurrences of *A. gallica* and *A. ostoyae* were detected in the oldest stands.

CONCLUSION

We found that the forest altitudinal zone and Norway spruce abundance influenced the occurrence of symptoms caused by *Armillaria* spp. in our study area in 2002, but these relationships were not observed in 2019. The total defoliation and defoliation of primary structure of Norway spruce increased between 2002 and 2019. The broadleaf abundance affected the total defoliation of Norway spruce in 2002, but the effect was not present in 2019. Moreover, we identified a significant positive effect of broadleaf abundance in 2019 on the change in the total defoliation of Norway spruce between 2002 and 2019 – most of the stands without increase of defoliation between 2002 and 2019 had a 15% share of broadleaf trees and more in 2019. The instability of the observed relationships can be caused by many factors; we supposed that important factors were subnormal precipitation in three out of the last four years and the related increase in salvage felling. Our outputs show that the benefits for Norway spruce in mixed stands are influenced by climate and forest management.

REFERENCES

Bielak K., Dudzinska M., Pretzsch H. (2014): Mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce [*Picea abies* (L.) Karst] can be more productive than monocultures. Evidence from over 100 years of observation of long-term experiments. Forest Systems, 23: 573–589.

Bussotti F., Feducci M., Iacopetti G., Maggino F., Pollastrini M., Selvi F. (2018): Linking forest diversity and tree health: preliminary insights from a large-scale survey in Italy. Forest Ecosystems: 5, article number: 1212.

Caldwell M.M., Dawson T.E., Richards J.H. (1998): Hydraulic lift: consequences of water efflux from the roots to plants. Oecologia, 113: 151–161.

Cudlín P., Novotný R., Chmelíková E. (1999): Recognition of Stages of Montane Norway Spruce Response to Multiple Stress Impact Using Crown and Branch Structure Transformation Analysis. Phyton (Austria), Special issue: Plant Physiology, 39: 149–153.

Cudlín P., Novotný R., Chmelíková E. (2000): Crown Structure Transformation and Response of Norway Spruce Forests to Multiple Stress Impact In: Klimo E., Hager H., Kulhavý J. (eds.): Spruce Monocultures in Central Europe – Problems and Prospects. EFI Proceedings No. 33: 103–112.

Cudlín P., Novotný R., Moravec I., Chmelíková E. (2001): Retrospective evaluation of the response of montane forest ecosystems to multiple stress. Ekológia, 20: 108–124.

Čermák P., Rybníček M., Žid T., Steffenrem A., Kolář T. (2019): Site and age-dependent responses of *Picea abies* growth to climate variability. European Journal of Forest Research, 138: 445–460.

Dálya L.B., Capretti P., Ghelardini L., Jankovský L. (2019): Assessment of presence and distribution of *Armillaria* and *Heterobasidion* root rot fungi in the forest of Vallombrosa (Apennines Mountains, Italy) after severe windstorm damage. iForest - Biogeosciences and Forestry, 12: 118–124.

de Vries W., Dobbertin M.H., Solberg S., van Dobben H.F., Schaub M. (2014): Impacts of acid deposition, ozone exposure and weather conditions on forest ecosystems in Europe: an overview. Plant and Soil, 380: 1–45.

Eichhorn J., Roskams P., Ferretti M., Mues V., Szepesi A., Durrant D. (2010): Visual Assessment of Crown Condition and Damaging Agents. Manual Part IV. In: Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests. UNECE ICP Forests Programme Co-ordinating Centre, Hamburg. [cited 2017 November 20] Available from: http://www.icp-forests.org/Manual.htm

Eickenscheidt N., Augustin N.H., Wellbrock N. (2019): Spatio-temporal modelling of forest monitoring data: modelling German tree defoliation data collected between 1989 and 2015 for trend estimation and survey grid examination using GAMMs. iForest, 12: 338–348.

Felton A., Lindbladh M., Brunet J., Fritz Ö. (2010): Replacing coniferous monocultures with mixed-species production stands: An assessment of the potential benefits for forest biodiversity in northern Europe. Forest Ecology and Management, 260: 939–947.

Harris I., Jones P.D., Osborn T.J., Lister D.H. (2014): Updated high-resolution grids of monthly climatic observations–the CRU TS3.10 dataset. International Journal of Climatology, 34: 623–642.

Iacopetti G., Bussotti F., Selvi F., Maggino F., Pollastrini M. (2019): Forest ecological heterogeneity determines contrasting relationships between crown defoliation and tree diversity. Forest Ecology and Management, 448: 321–329.

Jactel H., Brockerhoff, E.G. (2007): Tree diversity reduces herbivory by forest insects. Ecology Letters, 10: 835–848.

Jules E. S., Carroll A. L., Garcia A. M., Steenbock C. M., Kauffman M. J. (2014): Host heterogeneity influences the impact of a non-native disease invasion on populations of a foundation tree species. Ecosphere, 5: 1–17.

Kambach S., Kühn I., Castagneyrol B., Bruelheide H. (2016): The Impact of Tree Diversity on Different Aspects of Insect Herbivory along a Global Temperature Gradient - A Meta-Analysis. PLoS ONE, 11: e0165815.

Kozlowski T.T. (1971): Growth and Development of Trees. New York, Academic Pres:443.

Lafond V., Lagarrigues G., Cordonnier T., Courbaud B. (2014): Uneven-aged management options to promote forest resilience for climate change adaptation: effects of group selection and harvesting intensity. Annals of Forest Science, 71: 173–186.

Modrzyński J. (2003): Defoliation of older Norway spruce (*Picea abies* /L./ Karst.) stands in the Polish Sudety and Carpathian mountains. Forest Ecology and Management, 181: 289–299.

Morrison D., Cruickshank M., Lalumière A. (2014): Control of laminated and *Armillaria* root diseases by stump removal and tree species mixtures: amount and cause of mortality and impact on yield after 40 years. Forest Ecology and Management, 319: 75–98.

Parker I., Saunders M., Bontrager M., Weitz A.P., Hendricks R., Magarey R., Suiter K., Gilbert G. S. (2015): Phylogenetic structure and host abundance drive disease pressure in communities. Nature, 520: 542–544.

Pettersson M., Stenlid J., Sténs A., Wallertz K. (2016): Replacing monocultures with mixed-species stands: Ecosystem service implications of two production forest alternatives in Sweden. Ambio, 45 (Suppl 2): 124–139.

Popa I., Badea O., Silaghi D. (2017): Influence of climate on tree health evaluated by defoliation in the ICP level I network (Romania). iForest - Biogeosciences and Forestry, 10: 554–560.

Pretzsch H., Block J., Dieler J., Hoang Dong P., Kohnle U., Nagel J., Spellmann H., Zingg A., (2010): Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Annals of Forest Science, 67: 712.

Pretzsch H., Forrester D.I., Bauhus J. (eds.) (2017): Mixed-Species Forests. Ecology and Management. Springer: 653.

Pretzsch H., Rötzer T., Matyssek R., Grams T. E. E., Häberle K.H., Pritsch K., Kerner R., Munch J.C. (2014): Mixed Norway spruce (*Picea abies* [L.] Karst) and European beech (*Fagus sylvatica* [L.]) stands under drought: from reaction pattern to mechanism. Trees, 28: 1305–1321.

Schuler L.J., Bugmann H., Snell R.S. (2017): From mono-cultures to mixed-species forests: is tree diversity key for providing ecosystem services at the landscape scale? Landscape Ecology, 32: 1499–1516.

Simpson E. (1949): Measurement of Diversity. Nature, 163: 688.

Solberg S., Aamlid D., Tveito O. E., Lystad S. (2015): Increased needlefall and defoliation in Norway spruce induced by warm and dry weather. Boreal Environment Research, 20: 335–349.

Thor M.G., Ståhl J., Stenlid J. (2005): Modelling root rot incidence in Sweden using tree, site and stand variables. Scandinavian Journal of Forest Research, 20: 165–176.

Vitale M., Proietti C., Cionni I., Fischer R., De Marco A. (2014): Random Forests analysis: a useful tool for defining the relative importance of environmental conditions on crown defoliation. Water, Air & Soil Pollution, 225: 1992.

Zhang Y., Chen H.Y.H., Reich P.B. (2012): Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. Journal of Ecology, 100: 742–749.

Žemaitis P., Stakenas V. (2016): Ecological factors influencing frequency of Norway spruce butt rot in mature stands in Lithuania. Russian Journal of Ecology, 47: 355–363.