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Pests and fungal pathogens associated with Douglas fir stands showing crown defoliation and vitality loss

Schädlinge und pilzliche Krankheitserreger in Douglasienbeständen mit Kronenverlichtung und Vitalitätsverlust

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Abstract

Over the past decade, and particularly since the drought years 2018–2022, significant vitality losses have been observed in German Douglas fir stands. The epicentre of this damage was in Central and South-West Germany. To determine the cause of the observed loss of vitality, this study examined Douglas firs in twelve 37–70 years old forest stands of varying vigour. Crown condition was assessed using the terrestrial forest damage inventory (TWI) method. Sampled trees were assessed on site for abiotic and biotic damage. Needle, branch and stem samples were analysed using culture- and DNA-based methods to identify the associated fungal endophytes and pathogens. In the 48 Douglas firs studied, needle loss ranged from 0% to 90%. *Contarinia* spp*., Nothophaeocryptopus gaeumannii* and *Heterobasidion annosum* were observed in all the stands studied and were identified as the main biotic damaging factors along with the shoot dieback pathogens, which were detected in 38.9% of the trees.

Keywords

Douglas fir, vitality loss, causal agents, fungal pathogens, Douglas fir needle midges, swiss needle cast

Zusammenfassung

In den letzten zehn Jahren und insbesondere seit den Trockenjahren 2018–2022 sind in Douglasienbeständen in Deutschland erhebliche Vitalitätsverluste zu beobachten. Der Schwerpunkt dieser Schäden liegt in Mittel- und Südwestdeutschland. Um den Ursachen der beobachteten Kronenverlichtungen und Vitalitätsverluste auf den Grund zu gehen, wurden in der vorliegenden Studie 48 Douglasien in zwölf 37–70 jährigen Waldbeständen unterschiedlicher Vitalität untersucht. Der Kronenzustand wurde mit der Methode der terrestrischen Waldschadensinventur (TWI) bewertet. Die beprobten Bäume wurden vor Ort auf abiotische und biotische Schäden untersucht. Nadel-, Ast- und Stammproben wurden mit kultur- und DNA-basierten Methoden analysiert, um die zugehörigen pilzlichen Endophyten und Pathogene zu identifizieren. Bei den 48 untersuchten Douglasien schwankte der Nadelverlust zwischen 0 % und 95 %. *Contarinia* spp*., Nothophaeocryptopus gaeumannii* und *Heterobasidion annosum* wurden in allen untersuchten Beständen diagnostiziert und neben Erregern von Triebsterben, die bei 38,9 % der Bäume nachgewiesen wurden, als wichtigste biotische Schadfaktoren identifiziert.

Stichwörter

Douglasie, Vitalitätsverluste, Schadfaktoren, pilzliche Pathogene, Douglasien-Gallmücken, Rußige Douglasienschütte

Introduction

Over the past decade, and particularly since the drought years of 2018–2022, significant vitality losses have been observed in German Douglas fir stands. The focus of this damage has been in middle and South-West Germany, with reports of "unusually sparse crowns" and even dying Douglas firs (Langer et al., 2023). Swiss needle cast (SNC) and infections by other fungal pathogens, e.g. shoot dieback pathogens, as well as infestation by invasive Douglas fir needle midges (*Contarinia* spp., DFNMs) were suspected as the main causes. DFNMs are considered as alien and invasive species in Germany. They were first observed in Baden-Württemberg, Rhineland-Palatinate and Saarland in 2016 (Delb et al., 2017a; 2017b; Schumacher, 2017) and are now widely distributed in Germany.

Submitted/accepted for publication: 13 June 2024/4 September 2024

Following its introduction to Europe in the 19th century, Douglas fir (*Pseudotsuga menziesii*, *Pinaceae*) is the most commonly cultivated non-native tree species in Germany (van Loo & Dobrowolska, 2019). Although classified as an invasive species from a conservation perspective, from a forestry perspective it is discussed as a potential tree species of the future in the face of climate change (de Avila et al., 2017; Dubach et al., 2020). However, according to Vor et al. (2015), Douglas fir is not considered an invasive tree species in Germany. This contradicts the assessment made by the German Federal Agency for Nature Conservation (BFN, https://www.bfn.de/gebietsfremde-baumarteninvasivitaet). Bauhus et al. (2017) demonstrated that only a few protected forest biotopes are currently endangered by the non-native Douglas fir regeneration. A joint paper was published following expert discussions between forestry science and nature conservation, containing joint recommendations for the cultivation of Douglas fir in Germany (Ammer et al., 2016). The consensus is that, according to current knowledge, the cultivation of Douglas fir in Germany is not considered a significant threat to biodiversity and the associated ecosystem services. However, on certain special sites, such as rocky or boulder seas that were originally tree-free or tree-poor, it is generally recommended not to cultivate Douglas fir in order to preserve the habitat for specialised native species.

Due to the importance of Douglas fir for forestry in its native North American and introduced range, much work has been done on the needle endophytes and pathogens of this species (Gervers et al., 2022; Sherwood & Carroll, 1974). According to Petrini (1991), Saikkonen et al. (1998), Arnold & Lutzoni (2007) and Sieber (2007), we consider those fungi to be endophytes, which spend a significant part of their life cycle in the tissues of the host plant without causing any symptoms there. A change in environmental conditions can cause the fungus to change its lifestyle from endophytic to pathogenic (Sieber, 2007) or to saprotrophic if the host tissue dies (Sun et al., 2011). Factors that may trigger this lifestyle change include stress in the host tree and high summer temperatures (Ragazzi et al., 2003; Hyde & Soytong, 2008).

In Germany, according to Henning (1951), the SNC (pathogen: *Nothophaeocryptopus gaeumannii*) has been the only serious pathogen of the green or coastal Douglas fir (*P. menziesii* var. *menziesii*) since the introduction of the pathogen specifically associated with Douglas fir in 1925. *Nothophaeocryptopus gaeumannii* occurs subliminally in all Douglas fir stands in Germany. Since then, there have been repeated outbreaks of the disease at intervals of several years, depending on the weather. SNC is common in young and dense stands and results in yellowing, reddening of needles and intensive needle cast of older needle years, with buds usually remaining intact (Langer et al., 2023). Unlike Swiss needle cast, Rhabdocline needle cast (caused by *Rhabdocline pseudotsugae*) can lead to the death of the tree if severe. However, Rhabdocline needle cast plays no or only a minor role in large parts of Germany. This is due to the fact that green Douglas fir, which is less susceptible to this needle cast, is the dominant species in the study area (Dubach et al., 2020). Langer et al. (2023) showed, that other damaging factors such as extraordinary weather conditions, insects, and fungal root, shoot and needle pathogens play also a significant role in the dieback and loss of vitality of Douglas fir in Germany. An example of weather as a triggering factor for a disease is the physiological needle reddening of the Douglas fir as a result of frost-drought (Dubach et al., 2020). Douglas fir root and stem rot in Germany is often caused by *Armillaria* spp., *Fomitopsis pinicola*, *Heterobasidion annosum* s. s., and *Phaeolus schweinitzii*. Douglas fir shoot dieback can be caused by a variety of fungi. These are often latent pathogens such as *Diplodia sapinea*, *Sirococcus conigenus*, or *Botrytis cinerea* (Langer et al., 2023). *Diplodia sapinea*, a typical endophyte of pine shoots that causes Diplodia tip blight of pine and other conifers (Bußkamp et al., 2020), has been associated with shoot dieback in Douglas-fir when the host trees were replanted on former pine plantations or in the vicinity of pines. However, *Sirococcus conigenus*, the causal agent of Conifer shoot blight and Spruce twig blight, was isolated from dying Douglas fir shoots when the host trees were replanted on former spruce plantations or in the vicinity of spruce (Langer et al., 2023).

The DFNMs originates from North America, where the Douglas fir is native. In Europe, it was first detected in 2015 in France, Belgium and the Netherlands (Departement de la sante des forets, 2016; Leroy et al., 2015; NPPO, 2016). The first records in Germany were found in 2016 in Baden-Württemberg, Rhineland-Palatinate and Saarland (Delb et al., 2017a; 2017b; Schumacher, 2017). Condrashoff (1961) described three distinct species. As the morphology is very difficult to distinguish, it is not yet clear which of the species is present in Germany and Europe. The imagines of the Douglas fir needle midge usually hatch between April and May, depending on weather conditions, and live for only a few days. After laying their eggs, the larvae of the Douglas fir needle midge bore into the needle and cause gall formation by feeding on it. Usually, only needles from the current year are affected. The infested needles are shed in the following winter (DeAngelis, 1994; Washington state University extension & Washington state Department of Natural resources, 2015). The impact of the infestation in Europe cannot yet be estimated due to the rapid spread and sometimes high levels of infestation.

In order to clarify the cause of the observed crown thinning and loss of vitality (Fig. 1), this study examined Douglas firs in twelve forest stands of different vigour in Germany. To this end, the Douglas firs examined were assessed for 1) crown vitality and 2) infection with Swiss needle cast, 3) fungal shoot dieback pathogens, 4) root rot or other fungal pathogens, and 5) infection with Douglas fir needle midge or other insects.

Material and methods

Sampled trees and stands

Samples of 48 Douglas fir trees aged between 32 and 70 years (as of 2022) were collected in twelve different forest stands in Germany (Table 1, Fig. 2). For the selection of the study stands, extensive preliminary excursions were made to Douglas fir stands in the study area Baden-Wuerttemberg (BW), Hesse (HE) and Rhineland-Palatinate (RLP) that were proposed by

| Fig. 1: Severe crown thinning on Douglas fir trees with only needles from the current year (pictures: FVA, Jenny Wietschorke).

forestry organisations and were typical sites where Douglas fir cultivation was recommended. The aim was to find spatially close, comparison pair Douglas fir stands with the same location and environmental conditions, but which differed in their vitality. The two stands of each comparison pair (stand 1 and 2 as well as stand 3 and 4) were comparable in terms of location and site condition and included a Douglas fir stand with sparse, non-vital crowns (categorised as 'worse') and a stand with vital crowns (categorised as 'better'). The vitality of the stands was assessed visually by crown thinning of Douglas fir. All sampled forest sites in Baden-Wuerttemberg, Hesse) and Rhineland-Palatinate are mesotrophic, except from HE3 (weak mesotrophic), BW1 (oligo-mesotroph), and RLP1 (oligotrophic). To cover the full vital range of a stand, a U-shaped survey line or diagonal transect was established in each stand. To represent the entire stand, 13 to 20 of the dominant trees were selected as sample trees on these transects at regular intervals. Prior to sampling, crown thinning was recorded as a measure of vitality. Twice in 2022, in spring before bud burst (April–May) and in autumn before sampling (July–September), crown thinning was assessed ocularly using the internationally recognised TWI method. The needle loss of each sample tree was assessed in 5% increments.

For this purpose, 48 sample trees (4 trees per stand) were felled. These trees were selected to reflect the overall vitality of the stand as far as possible (one tree with poor crown vitality, one tree with better crown vitality and two trees with medium crown vitality). The felled trees were examined on site for abiotic and biotic damage. They were examined for resin flow, fungal fruiting bodies, necrosis, shoot dieback and insect infestation (Douglas fir needle midge, mealybugs and bark beetles). Needle and branch samples were taken and analysed in the laboratory for symptoms of infestation by the Douglas fir needle midge and Swiss needle cast. For the pathological examination, needles, branches, basal stem discs and, if available, samples of necrotic tree tissue were taken from three trees per stand and analysed in the laboratory for further examination. Needle and branch samples were analysed in the laboratory for the presence of the Douglas fir needle midge and *N. gaeumannii*. Infestation with the Douglas fir needle midge was detected and recorded on the basis of needle galls. A total of 1200 shoots were examined for the presence of Douglas fir needle midge. Four hundred shoots were analysed for the proportion of infested needles per shoot. The presence of fruiting bodies on the underside of the needles was used to determine the infection with *N. gaeumannii*. Needles from the last three years (2019, 2020, 2021) were visually inspected using a stereo microscope. A total of 432 shoots were examined for Swiss needle cast.

Table 1: Sampling plots and site information; all forest sites in Baden-Wuerttemberg (BW), Hesse (HE), and Rhineland-Palatinate (RLP) are mesotrophic, except from HE3 (weak mesotrophic), BW1 (oligo-mesotroph), and RLP1 (oligotrophic)

Plot-ID	Plot name	Coordinates UTM	Stand size (ha)	Meters above sea level	Exposition	Bed rock	Soil water supply	Cron vitality[a]	Douglas fir age
HE01	Biebertal	32 U 0470363 5612264	9.9	330–360	northwest	slate/graywacke with loess clay and pumice	moderately fresh	better	52–70
HE02	Wolferode	32 U 0502296 5637531	12.5	300–350	east	Buntsandstein with loess clay	fresh/emphasized fresh	worse	44–51
HE03	Beerfelden,	32 U 499323 5487713	1	500–540	west/ northwest	Middle Buntsandstein. silty sand over sand	moderately fresh-fresh	better	70
HE04	Gammelsbach Ost,	32 U 497981 5484435	1.6	330–345	south/ southwest	Buntsandstein, with boulders, clay-silitstone	moderately fresh-moderately dry	worse	43–63
BW01	Häfenschlag	32 U 450575 5420559	7.4	122	planar	Weakly loamy sands, gravelly-based weakly loamy sands, gravelly-based loamy sands	moderately fresh	worse	37–45/41
BW02	Am Birkenacker	32 U 451530 5419508	4.2	126	planar	gravelly-based loamy sands, gravelly-based weakly loamy sands, weakly loamy sands. sandy-based silty loams	moderately fresh	better	53–63/57
BW03	Hardtgraben	32U 436355.069 5404810.767	3.2	134	planar	Sand. deep sand, sand	moderately dry – moderately fresh	better	54–65/62
BW04	Hügelsheimer-wegschl,	32U 438035.490 5404853.487		127	planar	Sand, gravel sand	moderately fresh	worse	ca. 50
RLP01	Langtal Heldenstein	32 U 426591 5461284	6.1	475-510	northwest	Buntsandstein	moderately dry – moderately fresh	better	48–54
RLP02	Hölzernes Brückel,	32 U 427016 5464166	0.8	240-305	east	Upper Permian (Zechstein)	very fresh	worse	48–54
RLP03	Traben-Trarbach Longkamp	32U 365306.706 5529721.373	5	250–340	northwest	Hunsrück slate; clay and siltstone	pretty fresh	better	46
RLP04	Traben-Trarbach	32U 365306.706 5529721.373	3.8	250–300	northwest	Hunsrück slate; clay and siltstone	fresh	worse	45–50

[a] Douglas fir stand with mainly sparse, non-vital crowns were classified as “worse”; Douglas fir stand with mainly vital crowns were classified as “better”

Crown analysis based on methods of the Terrestrial Forest Damage Inventory

Based on the Terrestrial Forest Damage Inventory (TWI) method, the crown condition of the standing sample trees was determined. Needle loss and needle discolouration were assessed visually in 5% increments. The needle loss is calculated as the percentage difference to the imaginary full needling of the tree. Completely brown or red discoloured needles are dead and are therefore also counted as needle loss.

Detection, Isolation and Identification of fungal pathogens

Detection of *Heterobasidion annosum* was performed using the incubation method of Langer & Bressem (2017), and microscopic evaluation of fungal conidiophore produced on infected woody tissue. Other wood decay fungi were isolated from surface sterilized woody chips sampled from the basal stem discs or from necrotic tissue according the method of Peters et al. (2023). Dieback pathogens were isolated according the method of Bußkamp et al. (2020). Therefore, affected twigs were defoliated, washed and surface disinfested by treatment for 1 min in 70% EtOH, 5 min in 3% NaOCl, and 1 min in 70% EtOH. From each sampled tree per available needle year (2022, 2021, 2020 and 2019 if available), five green needles were defoliated, washed and surface disinfested by treating for 1 min in 70% EtOH, 1 min in a 3% NaOCl, and 1 min in 70% EtOH. Thereafter, twigs were cut into six segments in the size of 5-mm length and needles were cut into three segments and plated on malt yeast peptone agar (MYP). Emerging mycelia were subcultured separately on MYP medium. Isolated strains were first assigned to mycelial morphotypes (MTs), which were further characterised based on micromorphological characteristics and DNA sequence analysis. Representative strains were stored at the fungal culture collection of the Northwest German Forest Research Institute (NW-FVA). The DNA and morphology-based identifi-

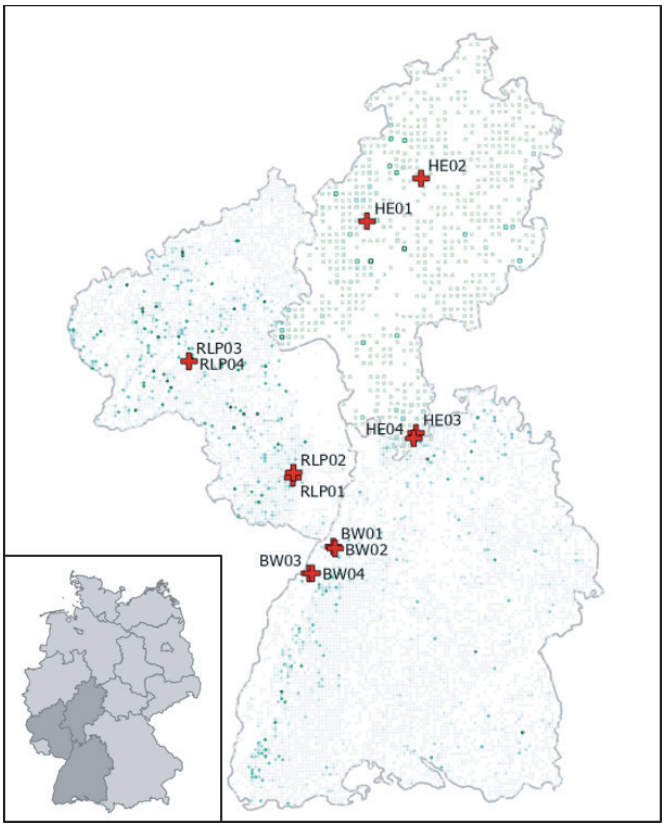

Fig. 2: Location of the study plots in Hesse (HE 1-4), Rhineland-Palatinate (RLP 1-4) and Baden-Württemberg (BW 1-4). The coloured green filling of the federal states shows the forest distribution in the project area, the intensity of the colour shows the proportion of Douglas fir (data basis: Thünen-Institut, BWI-2012 Punktkarten zum Zustand (3) – Baumgattungen (rechnerischer Reinbestand). The small map at the bottom left shows Germany with its federal states (data basis: Bundesamt für Kartographie und Geodäsie, Frankfurt am Main, 2011).

cation was carried out according to Peters et al. (2023) using ITS region or in the case of *Armillaria* spp. additionally a partial sequence of the translation elongation factor 1α (EF-1α) as barcode. Therefore, the 5.8S nuclear ribosomal gene with the two flanking internal transcribed spacers ITS-1 and ITS-2 (ITS region) was amplified for all isolated strains using the primer pair ITS-1F (Gardes & Bruns, 1993) and ITS-4 (White et al., 1990). For EF-1α, extracted DNA was amplified using the primer pair EF595F + EF1160R (Kauserud & Schumacher, 2001).

Results

Crown analysis and forest pathological assessment

Crown thinning varied considerably between stands. The mean needle loss of the examined Douglas fir stands ranges from 7.8% to 81.8% in May 2022 and from 10.0% to 73.5% in July–September 2022 (Fig. 3). The arithmetic mean of the needle loss of the "better" stands was 28.8% in May and 27.68% in July–September 2022. The "worse" stands showed an arithmetic mean needle loss of 66.5% in May and 61.7% in July–September (Table 2). All trees analysed showed defoliation between 0% and 95%. In general, there was no major difference in crown thinning between spring and autumn. Overall, the average crown thinning in 2022 was between 9% and 49% in the better stands and between 50% and 78% in the worse stands. This indicates a clear difference in crown thinning between stands. However, different crown thinning rates were also observed within a stand.

After visual inspection in the stand, 44.4% of the felled Douglas firs (subset of n = 36 trees) had old or fresh visible resin flow on the stems, 16.7% respectively shield-like necrosis on

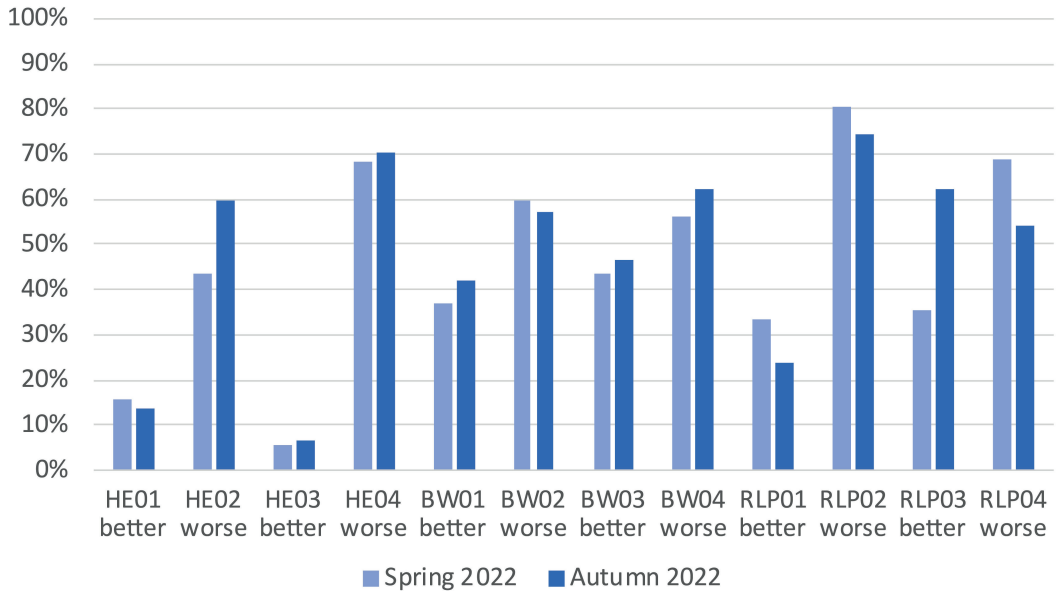

Fig. 3: Mean needle losses were recorded in 12 mature Douglas fir stands in South-West Germany in spring and autumn 2022. Stands 01 and 02 as well as 03 and 04 each form a comparison pair with different degrees of crown thinning, but are spatially comparable. Douglas fir stands with predominantly sparse, non-vital crowns were classified as "worse". Douglas fir stands with predominantly vital crowns were classified as "better".

stems or branches, 11.1% other bark necrosis on stems or branches, 44.4% wood discolouration in the basal stem disc, 8.3% wood root in the basal stem disc, and 19.4% other damages on the trunk such as old felling damages, cracks, mechanical impact damage, dark spots on the bark, or a dead tree top. No fruiting bodies of wood-decaying fungi were found on the trees. Galls of *Contarinia* species were observed on Douglas fir needles in all the twelve stands analysed, indicating an infestation with DFNMs. Infestation with *Contarinia* spp. affected the current needle age class. In total, needle galls were detected on 864 of the 1255 shoots examined by the FVA-BW. On average, 67% of the shoots per branch were affected. The number of infected needles per shoot varied between 0 and 78%. Infestation of shoots averaged 13% of needles per shoot. However, in six of the sample branches collected by the NW-FVA no galls were present. Aphids or adelgids, which were not further determined, were observed on all analysed needle samples except from site RLP04 (Traben-Trarbach, Rhineland-Palatinate). Feeding symptoms or infestation with beetles were present in 13.9% of the sampled trees, but not examined in detail.

Associated fungal pathogens

Three potential needle pathogens were associated with studied green needles without symptoms sampled from the subset of 36 trees (Table 2). *N. gaeumannii* and *Rhabdocline parkeri* (anamorph: *Meria parkeri*) could be detected in all studies stands and in all studies 36 trees. *Botrytis cinerea* was only isolated from a single stand (RLP01, better, Table 2). *Rhabdocline pseudotsugae* and *Dothistroma* spp. were not isolated.

Shoot dieback was observed in all studied stands and in 69% of the 36 Douglas fir trees surveyed. In the "better" trees, 33% (n = 12) of the trees examined showed shoot dieback and in the "worse" trees, 88% (n = 24) showed shoot dieback. *Diplodia sapinea* was associated with shoot dieback in seven of the studied stands but not isolated from the samples collected in HE04 (worse), RLP01 (better), and RLP02 (worse). *Sirococcus conigenus* was found to be associated with shoot dieback only in the forest stand HE04 (worse). *Diaporthe* species were associated with shoot dieback in eight stands, HE01 (better), HE02 (worse), HE04 (worse), BW02 (worse), BW03 (worse), BW04 (worse), RLP01 (better), and RLP02(worse) (Table 2).

Table 2: Fungi associated with sampled Douglas firs felled (subset of 36 trees) in twelve stands with different degrees of needles losses in Hesse (HE), Baden-Wuerttemberg (BW), and Rhineland-Palatinate (RLP)

	HE01	HE02	HE03	HE04	BW01	BW02	BW03	BW04	RLP01	RLP02	RLP03	RLP04
Mean needle loss of the stand in May 2022 in %	15.5	43.8	7.8	67.0	61.7	38.2	43.9	54.4	31.0	81.8	36.5	66.5
Mean needle loss of the stand in July–September 2022 in %	14.3	57.0	10.0	66.3	58.5	43.1	47.0	60.6	24.0	73.5	60.8	54.0
Species **NW-FVA ID, Accession no**	**Fungal needle cast pathogens associated with green needles[a]**											
Botrytis cinerea, 8784, PP874685	0	0	0	0	0	0	0	0	1	0	0	0
Nothophaeocryptopus gaeumannii, 9973, PP874688	1	1	1	1	1	1	1	1	1	1	1	1
Rhabdocline parkeri, 8435, PP874684	1	1	1	1	1	1	1	1	1	1	1	1
Species **NW-FVA ID, Accession no**	**Potential pathogens associated with shoot dieback[b]**											
Diplodia sapinea, 8397, PP874683	1	1	1	0	1	1	1	1	0	0	1	1
Sirococcus conigenus, 11490, PP874689	0	0	0	1	0	0	0	0	0	0	0	0
Diaporthe spp.	1	1	0	1	0	1	1	1	1	1	0	0
Species **NW-FVA ID, Accession no**	**Wood decay fungi associated with wood rot or discolouration of the basal stem discs**											
Heterobasidion annosum s.s.[c], 9610, PP874687	1	1	1	1	1	1	1	1	1	1	1	1
Phaeolus schweinitzii[d], 9074, PP874686	0	0	0	0	1	0	0	0	0	0	0	0

[a] Isolated from surface sterilised green Douglas fir needles
[b] Isolated from the transition area between living and dead tissue of a dying Douglas fir shoot
[c] Microscopic detection after incubation of the stem disks in a moist chamber according to the incubation method of Langer & Bressem (2017)
[d] Isolated from the necrotic and discoloured woody tissue of the basal stem disc

Heterobasidion annosum was detected in all studied Douglas fir stands (Table 2) and in the basal stem disc of 98% of the studied trees, regardless of whether wood rot was visible or not. Additionally, *Phaeolus schweinitzii* was isolated from brown-rotted woody tissue from a single tree in BW01 (better).

Discussion

The results of these investigations, which lead to the presumption that the loss of vitality and crown thinning Douglas fir is caused by the simultaneous occurrence of various pests, coincides with the observations of Ligot et al. (2020) and Blaser et al. (2023). Ligot et al. (2020) showed that the crown defoliation and shoot dieback were associated with DFNMs and several fungal pathogens such as *N. gaeumannii*, *S. conigenus*, *B. cinerea*. In addition, Douglas fir stands were often infested with *Adelges cooleyi* (Blaser et al., 2023). In our study, a momentary observation of crown thinning and infestation of DFNMs and *N. gaeumannii* was made in 2022. However, it should be noted that infestation and infection levels recorded for both damaging factors describe the situation from different years. In the case of *Contarina* spp., only the infestation of the current year could be recorded, as the infested needles are shed in the following winter (DeAngelis, 1994). In contrast, the survey on *N. gaeumannii* did not record the infection of the current year, but rather the infections of the three previous years (2021, 2020, 2019 (Boyce, 1940; Hansen et al., 2000)). This is because pseudothecia are not fully developed until the following spring, and therefore this year's infestation cannot be recorded. In addition, SNC leads to the shedding of older needle age classes. Due to the temporal shift of the needle loss caused by different pests, the observed crown thinning cannot be directly related to a single causal agent. It is not possible to conclude from this snapshot how strong the influence of each pathogen is on needle loss.

Contarinia

Apart from Christmas tree plantations, there is no evidence of serious damage to North American forests (West et al., 1991; Wilson et al., 2020). The results of this study confirm the general assessment of DFNMs as a non-mortality-inducing factor. This is because recovery of heavily infested trees may take several years (EPPO, 2019; West et al., 1991). Furthermore, only severe attacks by DFNMs combined with other pests and pathogens – such as *B. cinerea*, *Diaporthe* spp., *D. sapinea, H. annosum, N. gaeumannii, P. schweinitzii*, S*. conigenus*, and *R. parkeri* in the surveyed area – can cause significant defoliation (Wilson et al., 2020). The observed widespread distribution of *Contarinia* spp. in the study area supports the assumption that this species is rapidly spreading in Europe since its first observation in Western Europe in 2015 (e.g. Leroy et al. 2015). One year later, the species was registered in South-West Germany (Delb et al., 2017a, 2017b; Schumacher, 2017) and was then recorded in other German federal states (e.g. Langer et al., 2023; Lindenkreuz & Schulz, 2024) and Switzerland (Blaser et al., 2023). It is also conceivable that the needle midges arrived in Europe years before the first record and were only discovered after initial establishment. The observation that the infestation with *Contarinia* spp. affects the current needle age class confirmed the results by DeAngelis (1994). Affected needles are usually shed in the following autumn or winter after the larvae left the damaged needles (Ligot et al., 2020). One possible explanation for the observed decline in vigor in Douglas firs is the reduction of needle surface area, as well as the premature shedding of needles infested with *Contarinia* spp., which may negatively impact the photosynthesis potential and growth of affected Douglas firs (Condrashoff, 1962; Ligot et al., 2020).

Swiss Needle Cast

The detection of a wide distribution of *N. gaeumannii* in middle and South-West Germany was not unexpected, as SNC was first discovered in Switzerland and Germany almost 100 years ago in 1925 and subsequently spread throughout Central Europe (Boyce, 1940). In comparison, *N. gaeumannii* spread to all major forests in entire New Zealand in about 30 years (Kimberley et al., 2011). It is evident that the infection of needles with *N. gaeumannii* plays a significant role in the observed vitality losses. The growth of the fungus continues over the years, so that older needle age classes are often more severely affected by the disease. Its fruiting bodies (pseudothecia) clog the stomata and inhibit gas exchange and CO_2 assimilation, which ultimately results in premature needle shed (Boyce, 1940; Hansen et al., 2000). Premature defoliation impairs carbon uptake and reduces photosynthetic rates of the affected Douglas firs (Manter, 2000), resulting in up to 50% loss in volume growth compared to healthy trees (Maguire et al., 2002). Although *N. gaeumannii* was present at all of the surveyed sites, some of the studied stands exhibited a more pronounced manifestation of SNC, as evidenced by the formation of pseudothecia. The varying degree of infection with *N. gaeumannii* indicates that other factors can lead to a disease outbreak. For example, climate factors play an important role in influencing the geographical distribution of plant pathogens as well as their hosts and can lead to changes in host-pathogen dynamics (Sturrock et al., 2011). This was evident in the *N. gaeumannii*-Douglas fir pathosystem in the western Coast Ranges of Oregon and Washington, where relationships between site-specific climatic factors and severity of SNC have been identified (Hansen et al., 2000; Lee et al., 2017; Manter et al., 2005; Zhao et al., 2012). This suggests that regional or even local differences in climatic factors may already account for the variation in infestation severity between the stands examined in our study. Winter temperature has been found to correlate strongly with the occurrence of *N. gaeumannii* and thus with the severity of SNC (Manter et al., 2005). For example, in north-western Germany a severe disease outbreak was observed in the years 2018 (Langer et al., 2023) and 2024 (unpublished observation), where a black frost (ca. ≤ -10 °C) was recorded. In addition, leaf wetness and free moisture in spring to early summer are crucial for spore dispersal and successful infection (Manter et al., 2005).

Associated fungal pathogens

The detection of *R. parkeri* in green needles from all sites analysed was anticipated, as this fungus is the dominant needle endophyte with strict host specificity to *P. menziesii*

(McCutcheon & Carroll, 1993; Stone, 1987; Sieber, 2007). *Rhabdocline parkeri* infects individual epidermal needle cells and persists as a multicellular thallus without growing further, leading to cell death (Krabel et al., 2013; Sherwood-Pike et al., 1986). Following the onset of needle senescence, *R. parkeri* resumes its active and rapid colonisation of the needle, producing haustoria in cells adjacent to the first infected cell. The process of sporulation of *R. parkeri* occurs simultaneously with the abscission of needles. It has been observed that the infection rate increases with the age of the needles (Stone, 1987), while no correlation was found between the infection rate and the levels of infestation by *Contarinia* spp. no other non-native *Rhabdocline* species that cause needle cast in Douglas fir have been found in this study. Neither *R. pseudotsugae*, which was discovered in Germany in 1930 (Geyr, 1930) and causes one of the most economically important diseases of Douglas fir (Catal et al., 2010; Wilhelmi et al., 2021), nor the four other described species *R. epiphylla*, *R. oblonga*, *R. obovata* and *R. weirii*. *Botrytis cinerea*, the causal agent of grey mould, is usually saprotrophic but can also parasitically infect young Douglas fir tissue under conditions of high humidity and low temperatures. Usually, only needles and immature may shoots (shoot dieback) are damaged (Dubach et al., 2020; Dubach & Queloz, 2017).

The shoot dieback observed in the surveyed Douglas fir stands was mainly associated with *Diplodia sapinea*, regardless of whether pines were present in the stand or not. This result is consistent with the observations of Langer et al. (2023) and LFE (2023). It can be assumed that *S. conigenus* is the cause of the shoot dieback at site HE4, as this harmful fungus has been associated with shoot dieback on Douglas fir in several cases of the disease (Dubach et al., 2020; Langer et al., 2023; LFE, 2023). *Sirococcus conigenus* has been native to Germany for over 200 years (Butin et al., 2015) and primarily causes damage to spruce trees such as Sirococcus Shoot Blight (Blaschke et al., 2009). The disease is named for its ability to cause dieback of annual shoots, but it can also spread back along the twigs into the stem, causing small, elongated, and sunken cankers. Dieback of Douglas fir shoot associated with *S. conigenus* was observed in Belgium, France, and Germany (Dubach & Queloz, 2017; Langer et al., 2023). Climate influences the occurrence of infections and disease outbreaks. Cold and humid conditions during the growing season cause dieback of young shoots, resulting in the loss of needles and the bending of shoot tips into a hook shape (Dubach & Queloz, 2017). The genus *Diaporthe* comprises of plant endophytes, pathogens, and saprobes. Its species are recognised as causing plant diseases such as dieback, canker, and leaf spots (Hongsanan et al., 2023; Dissanayake et al., 2024). As the majority of isolates in this genus could not be identified to the species level in this study and no pathogenicity tests were conducted, it cannot be definitively concluded whether they were the primary cause of shoot dieback in the cases investigated. *Allantophomopsiella pseudotsugae* (≡ *Phomopsis pseudotsugae* = *Phacidium coniferarum* = *Phomopsis strobi*) was not found to be associated with the examined symptoms, despite being one of the most important fungi causing shoot dieback and necrosis in Douglas fir (Dubach et al., 2020; LFE, 2023).

The fact that almost all the trees examined are infected with *H. annosum* is consistent with the findings by Langer et al. (2023), who reported infection rates of 100% in German Douglas fir stands. The white rot and brown rot caused by *H. annosum* and *P. schweinitzii*, respectively, significantly contribute to the deterioration of the water supply and loss of growth in affected trees.

Conclusion

The results of the study show the complexity of the current damage situation on Douglas fir in Germany. The observed loss of vitality and crown defoliation in the studied Douglas fir stands cannot be directly attributed to a single causal agent. Several pests and pathogens found on Douglas fir include those from other tree species that have extended their host range to Douglas fir such as the native *H. annosum* and *P. schweinitzii*, as well as those from the native range of Douglas fir that have been introduced into Europe, including DFNMs, *N. gaeumannii*, and *R. parkeri*.

While the widespread presence of *N. gaeumannii* was to be expected, the presence of DFNMs on each of the sample trees was surprising and shows the rapid spread of this pathogen. The combined attack by these two harmful organisms can lead to considerable needle loss, affecting the vitality of the tree, at least in the midterm. However, the biology of the two pathogens necessitates a period of several years of investigation on the same sample trees in order to ascertain their impact on needle loss. Even though it is already known that weather conditions can benefit infection by SNC in early summer, the influence of weather parameters on the complex disease pattern is not yet foreseeable and must be investigated in detail. In addition, factors such as site, silvicultural treatment and provenance must be taken into account when analysing the influence of infestation on vigour.

Since the incidence of the various harmful factors analysed did not differ significantly in the better and worse stands of the comparison pairs in respect to the crown thinning, it can be assumed that abiotic factors (e.g. weather conditions), forest management or the provenance of the Douglas firs are likely to be predisposing or inciting factors. As the selection of stands analysed represents only a small part of the known damaged stands in single regions, the present study should be extended to a larger number of stands in different regions. It seems probable that Douglas fir will have to cope with the combined occurrence of pests and pathogens in the future and that the factors of increasing drought and rising temperatures may also lead to increased devitalisation.

Conflicts of interest

The authors declare that they do not have any conflicts of interest.

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