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First Report of *Sydowia polyspora* Causing Current Season Needle Necrosis on *Abies grandis* in Sweden

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Received: 10 September 2025 | **Revised:** 31 October 2025 | **Accepted:** 1 December 2025

ABSTRACT

Current season needle necrosis (CSNN) is a conifer foliar disease and a particular problem for Christmas tree plantations, as it causes necrosis and premature foliage shedding, resulting in significant economic and aesthetic devaluation. In September 2022, CSNN symptoms were detected on 10-year-old *Abies grandis* trees at a plantation located in Southern Sweden. Field surveys were employed to assess the extent of damage, and the causal agent of damage was identified via isolation and tissue culturing, microscopy, molecular diagnostics and pathogenicity testing. DNA sequencing and phylogenetic analysis of obtained cultures identified *Sydowia polyspora* as the potential causal agent of the observed CSNN symptoms. The pathogenicity of *S. polyspora* was confirmed through seedling inoculation and successful re-isolation from induced necroses. Field surveys indicated a high incidence (98%) of CSNN, with severity levels typically affecting up to 50% of the crown. To our knowledge, this is the first documented occurrence of CSNN *on A. grandis* in Sweden. Extreme weather conditions, that is, drought and high precipitation, may exacerbate CSNN development, increasing tree susceptibility to *S. polyspora* infections. These findings underscore the increasing threat of weak or latent pathogens like *S. polyspora* to trees under changing climatic conditions, emphasising the need for proactive management strategies, including shielding and resistance breeding.

1 | Introduction

Sydowia polyspora (Bref.) E. Müll. is a cosmopolitan ascomycete fungus, well adapted to endophytic, saprophytic and pathogenic lifestyles. It is mainly associated with conifer damage and has a wide geographical distribution, commonly occurring in North America, Asia and Europe. Because of its plasticity to transition between lifestyles, from endophytism to saprophytism, *S. polyspora* is regularly isolated from asymptomatic and symptomatic conifer needles (Talgø et al. 2010; Pan et al. 2018).

Under varying pathological conditions, the fungus can infect branches, shoots, needles and even seeds (Cleary et al. 2019; Jankowiak et al. 2024). Often the fungus causes chlorosis and scorching of pine needles, but has also been reported in spruce, larch, cedar and hemlock (Pan et al. 2018). *Sydowia polyspora* is linked to current season needle necrosis (CSNN) commonly reported from noble fir (*Abies procera* Rehder) and grand fir (*A. grandis* (D. Don) Lindl.) plantations across Europe and North America. The disease has been increasingly reported since the 1980s following the increased production of *Abies* spp. for Christmas trees (Talgø et al. 2010) and can significantly reduce the economic and aesthetic value of fir trees as a result of needle necrosis and premature needle shedding. Typically, symptoms of CSNN appear as spotty discolorations or bands on needles, usually within 2–4 weeks following the infection, turning red-brick or brown during late summer (Talgø et al. 2010). Entire needles can become necrotic and prematurely shed as the infection progresses. *Sydowia polyspora* can also infect the phloem of pine branches. *Pinus pinea* L. and *P. yunnanensis* Franch. artificially infected by *S. polyspora* can develop necrotic lesions (Pan et al. 2018) and characteristic CSNN chlorotic and/or discoloured needle symptoms. A recent study in the Polish Tatra mountains suggests *S. polyspora* to be one of the main causative

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agents of shoot dieback of *Pinus mugo* Turra subsp. *mugo*, and that it's likely a species complex containing at least four cryptic species (Jankowiak et al. 2024).

This pine tip dieback was historically often referred to by its two anamorphs—*Hormonema dematioides* Lagerb. & Melin, and *Sclerophoma pithyophila* (Corda) Höhn. (synanamorph). The former (*H. dematioides*) has been frequently associated with certain species of pine bark beetles such as *Tomicus piniperda*, *T. minor* and *Pityogenes bidentatus*, suggesting a possible insect-vector dissemination of this fungus (Pan et al. 2018; Jankowiak and Bilański 2007; Jankowiak and Rossa 2008). *Sydowia polyspora* has been noted to potentially influence the severity of pine needle diseases such as Dothistroma needle blight, potentially acting as a pathogen enabler (Ridout and Newcombe 2015). This fungus can affect seedling performance by postponing or reducing seedling emergence by as much as 30% (Ridout and Newcombe 2018).

During autumn 2022, necrotic needles randomly scattered on branches were found in a 10-year-old *Abies grandis* plantation in southern Sweden, resembling symptoms of CSNN. As grand fir is an economically important species for the regional forestry economy, we aimed to (i) confirm whether *S. polyspora* was the causal agent of the observed symptoms and (ii) determine the incidence and severity of damage.

2 | Materials and Methods

2.1 | Field Sampling and Isolation

In September 2022, branches showing necrotic and healthy needles (Figure 1a) were collected from a 9-year-old plantation of *Abies grandis* located in Svedala municipality, southern Sweden (55°32′42.0″N 13°12′23.0″E). Collected material from five trees was sealed in paper envelopes, marked and placed in cold storage at 4°C. Before isolations, all needles were surface sterilised by washing in 70% ethanol for 30 s, then in 2% sodium hypochlorite for 2 min and again in 70% ethanol for 30 s. Subsequently, the needles were rinsed in sterile water several times and air-dried on sterile filter paper under a laminar flow hood. Under aseptic conditions, both healthy and symptomatic needles were cut into 0.5–1.0 cm long slices and plated onto Petri dishes containing Malt Extract agar (MEA: 20 g of malt extract, 20 g bacterial agar, distilled H_2O up to 1000 mL) and incubated at 21°C in the dark.

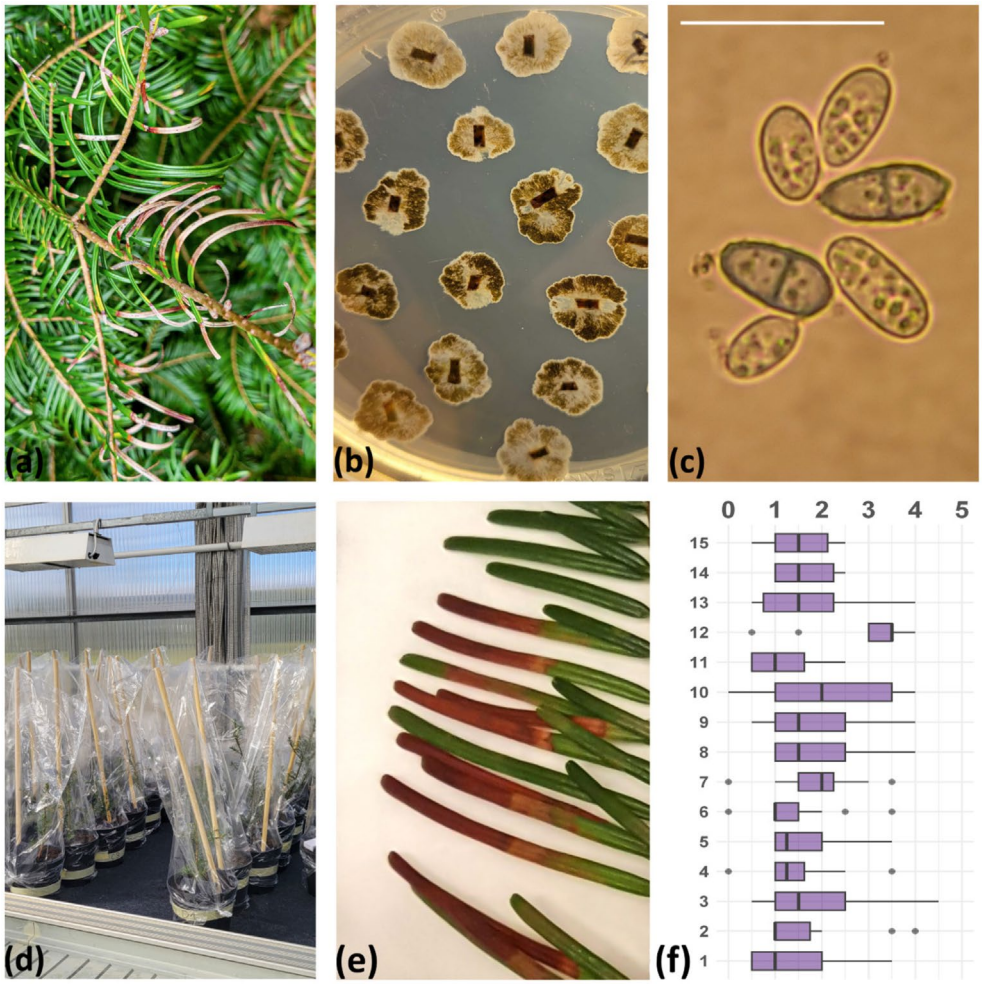

FIGURE 1 | Symptoms and damage levels observed on *Abies grandis*, and morphological characters of *Sydowia polyspora* isolates. (a) Symptomatic *A. grandis* branches showing necrotic needles; (b) Fungal colonies grown on PDA after 10 days at 21°C in the dark; (c) Conidia of *S. polyspora* observed under light microscopy, Scale bar = 10 μm; (d) Inoculated *A. grandis* seedlings under glasshouse conditions; (e) CSNN symptoms on inoculated *A. grandis* seedlings; (f) Distribution of CSNN damage severity among *A. grandis* trees across sample plots.

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After 10 days of incubation, fungal growth was observed around symptomatic needle parts and transferred to clean MEA plates for purification. The fungal colony most consistently isolated from necrotic needles was chosen for molecular identification, described below. After 10 days, the cultures had a mucilaginous surface, with an ivory-white colour turning dark green to black. Five isolates representing five different trees were made and deposited at the culture collection (MCCC28–MCCC32) of the Southern Swedish Forest Research Centre, SLU, Alnarp. Fungal morphology was assessed after 15 days of incubation on MEA at 21°C in the dark. Propagules were observed using Olympus BX43 (Olympus Co, Tokyo, Japan).

2.2 | Molecular Identification

Genomic DNA was extracted using the DNeasy Plant Pro Kit (Qiagen, Valencia, California, USA) according to the manufacturer's recommendations, evaluated for concentration and purity using a NanoDropND-1000 spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA), then diluted to approximately 30 ng/μL working stock. The internal transcribed spacer (ITS) rDNA region (ITS1-5.8S-ITS2) was amplified using ITS1 and ITS4 primer pairs. Amplifications were achieved in a 25 μL reaction volume, using 12.5 μL GoTaq G2 Green Master Mix (Promega, USA), 9.5 μL of molecular grade H_2O, 1 μL of 10 mM primer pairs, and 2 μL of genomic DNA. PCR reactions were performed under the following conditions: 5 min at 95°C followed by 35 cycles of denaturation at 95°C for 30 s, annealing at 62°C for 30 s and extension at 72°C for 1 min, with a final extension step at 72°C for 8 min. The PCR amplicons were separated by gel electrophoresis on a 1% agarose gel stained with GelRed (Biotium, Hayward, CA, USA), and verified under UV light. Sequence analysis was performed by Macrogen Europe, Amsterdam. Raw sequences were edited and identified by comparing them with those in the GenBank database using the BLAST program (NCBI-BLAST, www.ncbi.nlm.nih.gov/BLAST) with a 99% sequence identity threshold. The obtained sequences are available at GenBank under accession numbers: PP294684, PP294685, PP294686, PP294687 and PP294688.

Analysis of maximum parsimony was conducted in PAUP 4.0a. Parsimony-based heuristic search with tree bisection reconnection as the tree-perturbation algorithm and a random stepwise addition of 1000 replicates was used for constructing the phylogenetic trees. Gaps were considered as an additional character with equal value. The confidence levels of the branching points were estimated using 1000 bootstrap replicates. Maximum Likelihood analysis was performed using MEGA X, with Kimura 2-parameter with rate variation among sites (K2 + G) selected as the most suitable substitutional model. Branch support was evaluated with 1000 bootstrap replicates.

2.3 | Pathogenicity Testing

To prove microbial causality between the isolated fungi and the observed symptoms, pathogenicity tests were performed on 40 2-year-old *A. grandis* seedlings. Six seedlings were inoculated with each fungal isolate, and 10 seedlings were used as negative controls. The inoculation material originating from five isolates obtained directly from the infected *A. grandis* needles (MCCC28–MCCC32) was subcultured on MEA at 21°C for 2 weeks to provide sufficient inoculum. Conidial suspensions were made by adding 20 mL of sterilised water into 3-week-old cultures and gently rubbing the colony surface to release conidia. Conidial suspension concentrations were measured using a haemocytometer and ranged from 7.6×10^5 to 4.6×10^6 spores/mL. Each seedling was sprayed with approximately 15–20 mL of the suspension, whereas the control line of seedlings was sprayed with sterilised water. Seedlings were enclosed in nylon bags to maintain high relative humidity (> 80%), promoting fungal growth and infection. After 5 days, the seedlings were unwrapped to allow air circulation. Seedlings were then maintained under glasshouse conditions with natural light and temperatures ranging from 20°C to 28°C until symptoms started to appear. To confirm pathogenicity, symptomatic seedling needles were sampled, surface sterilised, plated and incubated under the same protocol as the initial isolations. In addition, needles from control seedlings were also sterilised and plated under the same conditions to exclude cross-contamination.

2.4 | Field Survey

A virtual grid of approximately 100 m^2 cells was superimposed over a 5.7-ha infected *Abies grandis* stand to guide sampling. From this grid, 10% of the cell centers ($n = 15$) were selected as plot centers, each corresponding to a circular sample plot with a radius of 5.65 m, within which all trees were assessed for CSNN incidence and severity. The plantation also contained *Picea abies* (L.) H. Karst., *Larix decidua* Mill. and *Betula pendula* Roth. trees. In each selected plot, *A. grandis* trees were measured for height and diameter at breast height (DBH) and scored for the presence or absence of CSNN symptoms in both the upper and lower crown sections. Disease severity was determined by visual estimation of the proportion of affected crown area and by assigning each tree a damage score on a six-point scale, whereby 0 = no symptoms, 1 = 25% of the branches symptomatic, 2 = 50% of the branches symptomatic, 3 = 75% of the branches symptomatic, 4 = 100% of the branches symptomatic, and 5 = dead. A linear mixed-effects model was used to assess whether crown section, DBH and height influenced damage severity, accounting for plot-level variability. One-way ANOVA and Tukey's HSD post hoc tests were performed to evaluate if crown damage differed significantly between plots. All descriptive statistics, mixed-effects modelling, and ANOVA were performed using R Studio (v. 12) and the 'lme4', 'ggplot2', 'dplyr' packages.

3 | Results and Discussion

Dark colonies isolated from symptomatic needles grew well on MEA, reaching diameters of approximately 5–8 cm and achieving peak conidial production in 10–14 days. The colonies appeared slightly irregular, raised and mildly umbonate with filiform margins (Figure 1b). Conidia were produced intercalary and were ovoid to ellipsoid in shape, non-septate and septate, hyaline, and measured 8.5 μm (range: 6.85–9.50) × 4.5 μm (range: 4.05–4.90) ($n = 50$) (Figure 1c). BLAST analysis of the ITS region identified all five isolates as *Sydowia polyspora* with > 99% similarity. These molecular and morphological findings

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are consistent with previous descriptions of *S. polyspora* (Talgø et al. 2010; Pan et al. 2018; Jankowiak et al. 2024).

Phylogenies generated during ML and MP analyses displayed similar topologies; the MP tree was selected for presentation (Figure 2). In the MP analysis, tree length (TL) was 170, with a consistency index (CI) of 0.79, a retention index (RI) of 0.91, a rescaled consistency index (RC) of 0.80 and a homoplasy index (HI) of 0.21. All Swedish *A. grandis* isolates clustered together in a distinct clade alongside reference *S. polyspora* sequences retrieved from GenBank (Figure 2). However, in line with the recent work showing that *Sydowia polyspora* comprises a cryptic species complex (Jankowiak et al. 2024), the isolates are referred to as *S. polyspora* sensu lato.

After nearly 2 weeks of incubation, inoculated *A. grandis* seedlings (Figure 1d) began to exhibit brick-red needle discoloration, typically initiating from the middle or tip of the needle. Within 3–4 weeks, characteristic CSNN symptoms developed in 30% of seedlings (Figure 1e). Of the five isolate lines used for seedling inoculations, four successfully induced symptoms while one failed to cause infection. The failure of one isolate line to cause infections could result from the reduced pathogenic potential of that strain. In addition, the elevated temperatures, typical of summer greenhouse conditions, might have exacerbated its inability to infect. *Sydowia polyspora* s.l. was successfully re-isolated from symptomatic seedlings, fulfilling Koch's postulates and confirming its pathogenicity on *A. grandis* and the probable causal agent of the needle necrosis observed in the young plantation. This study represents, to our knowledge, the first documented occurrence of CSNN on *A. grandis* in Sweden.

Infection symptoms were present in 98% of surveyed *A. grandis* trees, with varying levels of severity. The mean damage level across plots ranged between 1 and 2, indicating that up to 50% of the crown was affected in most trees (Figure 1f). CSNN symptoms were also observed on previous years' growth in 72% ($n = 196$) of the trees examined, suggesting the disease had already been present during the previous growing season. The average tree height in plots was 352 ± 96 cm (range: 160–610 cm),

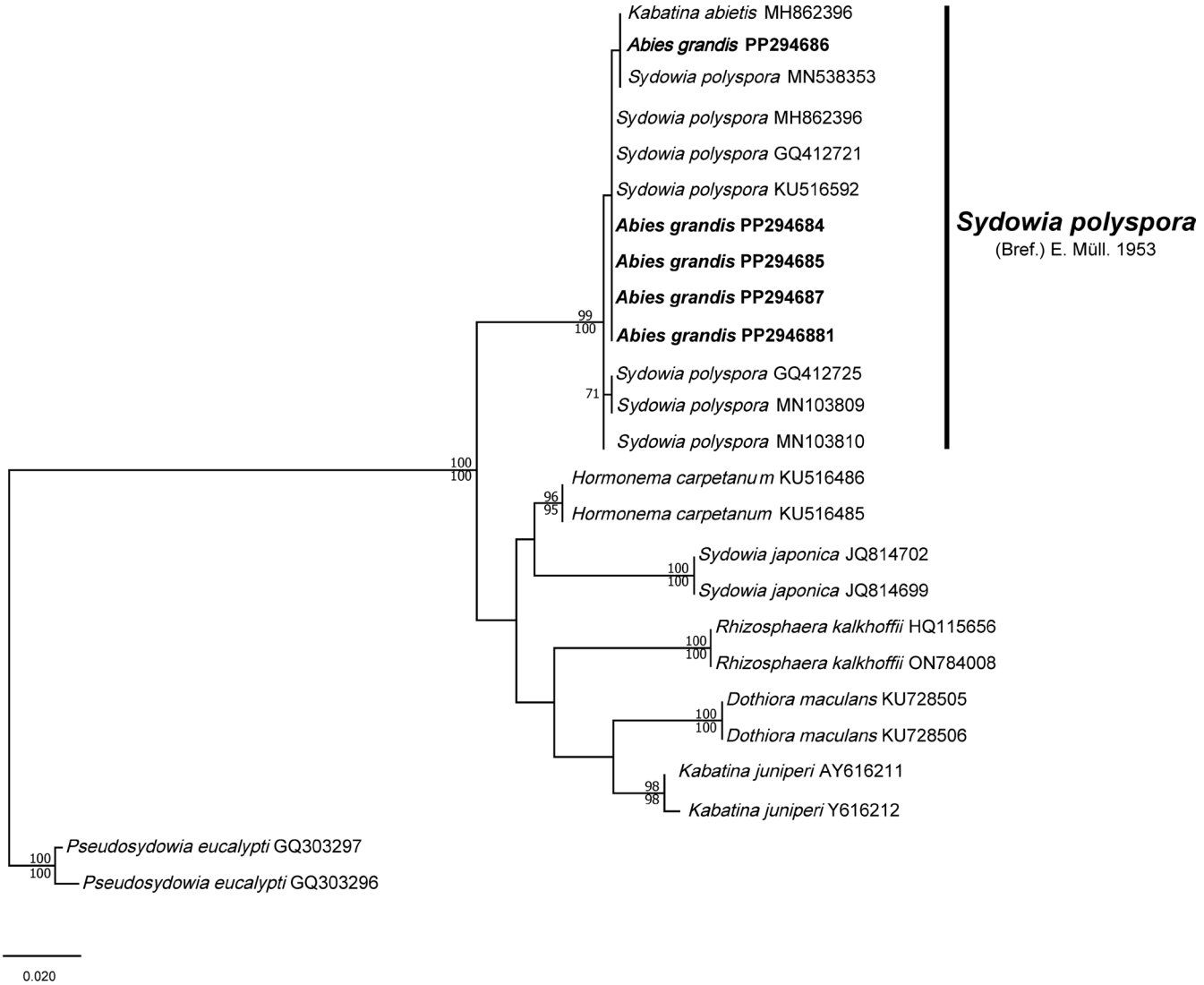

FIGURE 2 | The most parsimonious tree based on maximum parsimony analyses of a 499-base pair portion of the ITS from isolates obtained in a Swedish *Abies grandis* plantation. Phylogenies generated in both maximum likelihood and maximum parsimony analyses displayed similar topologies. Maximum likelihood bootstrap support values (> 75%) sit above, whereas maximum parsimony (> 7%) sit below the branches.

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and the average DBH was 7.3 ± 2.8 cm (range: 1.5–14.5 cm). No significant effect of tree size on disease severity was detected, nor were there significant differences in disease severity levels between the upper and lower crown sections. ANOVA analysis indicated a potential difference in disease severity between plots in both upper and lower crown sections ($p < 0.05$), yet Tukey's HSD post hoc test suggested this was likely due to severe damage in a single plot (Plot 12) (Figure 1f).

CSNN is an umbrella term associated with several pathological agents and physiological disorders (i.e., disturbed calcium uptake). Other frequent fungal taxa commonly associated with CSNN are weak or facultative pathogens mainly belonging to the genera *Alternaria*, *Aureobasidium* and *Didymella*, with *S. polyspora* being the most frequently reported. Notably, *S. polyspora* has often been isolated not only from symptomatic but also from asymptomatic *Abies* spp. and *Pinus* spp. (Talgø et al. 2010; Jankowiak et al. 2024).

Extreme weather patterns may be driving the spread and severity of CSNN. For instance, the severe drought during the summer of 2018 in Sweden may have triggered *S. polyspora* development. Some studies suggest that abiotic stress can increase trees susceptibility to *S. polyspora* infections (Lazarevic and Menkis 2022), especially when drought periods are followed by ample rainfall (Thomsen 2008). Jankowiak et al. (2024) also suggested that environmental conditions such as drought or frost weaken shoots' vitality which facilitates fungal colonisation. Higher risks of CSNN development are associated with high precipitation levels in spring, coinciding with shoot elongation (Thomsen 2008). Furthermore, fungal infection weakens fir needle cells, making them more vulnerable to desiccation under high radiation during drought, which accelerates cell collapse and necrosis (Talgø et al. 2010). Although these observations and literature suggest that extreme weather conditions exacerbate CSNN, controlled studies are needed to clarify the precise roles of drought and precipitation in facilitating *S. polyspora* infections. Naturally or artificially shaded young branches tend to develop fewer CSNN symptoms (Talgø et al. 2010), so shading young fir growth, alongside breeding for resistance, may reduce symptom development in nurseries and plantations.

Our study provides evidence of *S. polyspora* s.l. causing CSNN symptoms in *A. grandis*, highlighting how weak or facultative pathogens can become significant threats to forest and plantation health amid changing climatic conditions. This underscores the need for proactive management strategies to mitigate the impact of such pathogens on economically valuable tree species. With global climate change driving more frequent and severe weather extremes which increase trees' susceptibility to both biotic and abiotic stressors, we can expect the prevalence and impact of pathogens like *S. polyspora* to rise further.

Funding

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in GenBank at https://www.ncbi.nlm.nih.gov/genbank/, reference numbers PP294684–PP294688.

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