Symposium contribution / Contribution à un symposium

Predicting effects of climate change on Swiss needle cast disease severity in Pacific Northwest forests[1]

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Abstract: Swiss needle cast of Douglas-fir (*Pseudotsuga menziesii*) is caused by the ascomycete *Phaeocryptopus gaeumannii*. Symptoms are foliage chlorosis and premature needle abscission due to occlusion of stomata by the ascocarps of the pathogen, resulting in impaired needle gas exchange. Growth losses of 20%–50% due to Swiss needle cast have been reported for approximately 150 000 ha of Douglas-fir plantations in western Oregon since 1996. In the western Coast Range of Oregon and in New Zealand, winter temperature is strongly correlated with pathogen abundance. Models for predicting disease severity based on winter temperature account for 77% and 78% of the variation in 1- and 2-year-old needles, respectively, for western Oregon sites and approximately 80% for New Zealand. A trend of temperatures increasing by 0.2–0.4 °C during the winter months and spring precipitation increasing by 0.7–1.5 cm/decade since 1970 suggests that regional climate trends are influencing the current distribution and severity of Swiss needle cast disease. Continuing winter temperature increases predicted for the Pacific Northwest of approximately 0.4 °C/decade through 2050 suggest that the severity and distribution of Swiss needle cast is likely to increase in the coming decades as a result of climate change, with significant consequences for Pacific Northwest forests.

Key words: Douglas-fir, *Mycosphaerella*, *Phaeocryptopus*, *Pseudotsuga.*

Résumé : La rouille suisse des aiguilles du Douglas taxifolié (*Pseudotsuga menziesii*) est causée par l'ascomycète *Phraeocryptopus gaeumannii*. Ses symptômes sont la chlorose foliaire et l'abscission prématurée des aiguilles causée par l'occlusion des stomates de ces dernières par les ascocarpes de l'agent pathogène, ce qui entrave les échanges gazeux. Depuis 1996, on estime que, sur environ 150 000 ha de plantations de Douglas taxifolié dans l'ouest de l'Oregon, la rouille suisse est responsable de retards de croissance variant de 20 % à 50 %. Dans la partie occidentale de la chaîne littorale de l'Oregon et en Nouvelle-Zélande, la température hivernale est fortement corrélée à la présence massive de l'agent pathogène. Les modèles utilizés pour prévoir la gravité de la maladie, basés sur la température hivernale, expliquent 77 % et 78 % de la variation chez les aiguilles de un et de deux ans, respectivement, dans l'ouest de l'Oregon, et environ 80 % en Nouvelle-Zélande. Une tendance qu'ont les températures à s'élever de 0,2 °C à 0,4 °C durant les mois d'hiver et les précipitations printanières à augmenter de 0,7 cm à 1,5 cm par décennie depuis 1970 suggère que les tendances climatiques régionales influencent la distribution actuelle et la gravité de la rouille suisse des aiguilles. Une augmentation constante d'environ 0,4 °C de la température hivernale par décennie dans le nord-ouest du Pacifique jusqu'en 2050 suggère que la gravité et la distribution de la rouille suisse des aiguilles sont appelées à croître en raison du changement climatique, ce qui aura de fâcheuses conséquences pour les forêts de cette région.

Mots-clés : Douglas taxifolié, *Mycosphaerella*, *Phraeocryptopus*, *Pseudotsuga*.

Introduction

Swiss needle cast of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is caused by the ascomycete *Phaeocryptopus gaeumannii* (Rohde) Petrak. The disease, and the fungus that causes it, were first described from Douglas-fir plantations in Switzerland and Germany in 1925 and soon afterward, reported from various locations in Europe, the British Isles, and northeastern North America (Boyce 1940; Peace 1962). The causal agent, *P. gaeumannii*, was found to be abundant

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on foliage of diseased trees and was determined to be distinct from any previously described foliage-infecting fungi from coniferous hosts. Subsequent surveys of Douglas-fir in the western United States found the pathogen was widespread throughout the Pacific Northwest region, where it had escaped notice because of its inconspicuous habit and negligible effect on its host. Boyce (1940) considered *P. gaeumannii* widespread but harmless on Douglas-fir in western North America and probably indigenous to the Pacific Northwest, where "… the fungus has been found at such widely separated localities in British Columbia, Washington, and Oregon that it must be considered generally distributed, although harmless, in the Douglas-fir region of the Pacific Coast." Molecular phylogenetic studies have shown that the fungus that causes Swiss needle cast is unrelated to the type of the genus *Phaeocryptopus* and should instead be classified in the genus *Mycosphaerella* (Winton et al. 2007). Although a nomenclatural change based on these findings is anticipated, the name *P. gaeumannii*, which is well established in the literature, will be used herein for the causal agent of Swiss needle cast.

Since around 1990, unusually severe and persistent symptoms of Swiss needle cast have been observed in Douglas-fir forest plantations in western Oregon, particularly near the town of Tillamook (Hansen et al. 2000). Approximately 150 000 ha of forest land in western Oregon is currently affected by the disease (Oregon Department of Forestry 2007). Unlike Boyce's (1940) characterization of the pathogen on native Douglas-fir as being inconspicuous and harmless, the fungus is abundant, trees frequently are defoliated of all but current-year needles, and attached foliage is often severely chlorotic (Fig. 1). Growth reductions of 20%–50% due to Swiss needle cast have been measured in the affected area (Maguire et al. 2002). The severity of the problem in Oregon has brought renewed interest in understanding the biology of the pathogen and epidemiology of Swiss needle cast disease. In particular, research has focused on understanding why an inconspicuous, insignificant native pathogen has become a significant forest health problem. The effects of local climate factors influencing pathogen abundance and disease severity over the past 11 years has been a major focus of this research.

Aerial surveys for Swiss needle cast conducted by the Oregon Department of Forestry have classified patches of Swiss needle cast severity based on foliage discoloration, characterizing the discoloration as being "severe" or "moderate" (Fig. 2). The affected area as determined by the aerial survey lies along the entire length of the Oregon coast, extending inland approximately 40 km, with most symptoms occurring within 30 km of the coast. The crest of the Coast Range forms the approximate eastern edge of the affected area. The aerial survey covers approximately 1.2×10^6 ha of coastal forest, with the symptomatic area comprising between 50 000 and 160 000 ha (Fig. 2).

Infection cycle and mechanism of pathogenicity

Ascospores of *P. gaeumannii* mature and are released during early May through late July, coinciding with bud break and shoot elongation of Douglas-fir. Ascospores are the only infective propagule, and there is no conidial anamorph. Infections occur on newly emerged needles shortly after bud break (Hood and Kershaw 1975; Stone et al. 2008). Ascocarp (pseudothecia) primordia begin to form in substomatal chambers at 4–9 months following infection. Internal colonization of needles continues as long as they remain attached, so numbers of ascocarps increase as needles age. Normally, fruiting bodies of the fungus are more abundant on needles aged 3 years or older and are sparse or absent on younger foliage (Boyce 1940; Hood 1982; Stone et al. 2008). However, in recent years, trees having abundant fruiting bodies on current-year needles have been commonly observed in forest plantations along the Oregon coast, with older foliage being prematurely abscised because of the disease (Hansen et al. 2000).

The ascocarp primordia completely occupy the substomatal space, thereby rendering the stoma nonfunctional. Occlusion of the stomata by pseudothecia of *P. gaeumannii* impedes gas exchange and regulation of transpiration, causes impaired photosynthetic activity, and is considered to be the primary mechanism of pathogenicity (Manter et al. 2000, 2003a). Estimates of the effect of *P. gaeumannii* on CO_2 assimilation indicate that occlusion of 25% of stomata results in negative needle carbon budgets, i.e., respiration exceeds assimilation, on an annual basis (Figs. 3 and 4) (Manter et al. 2003a).

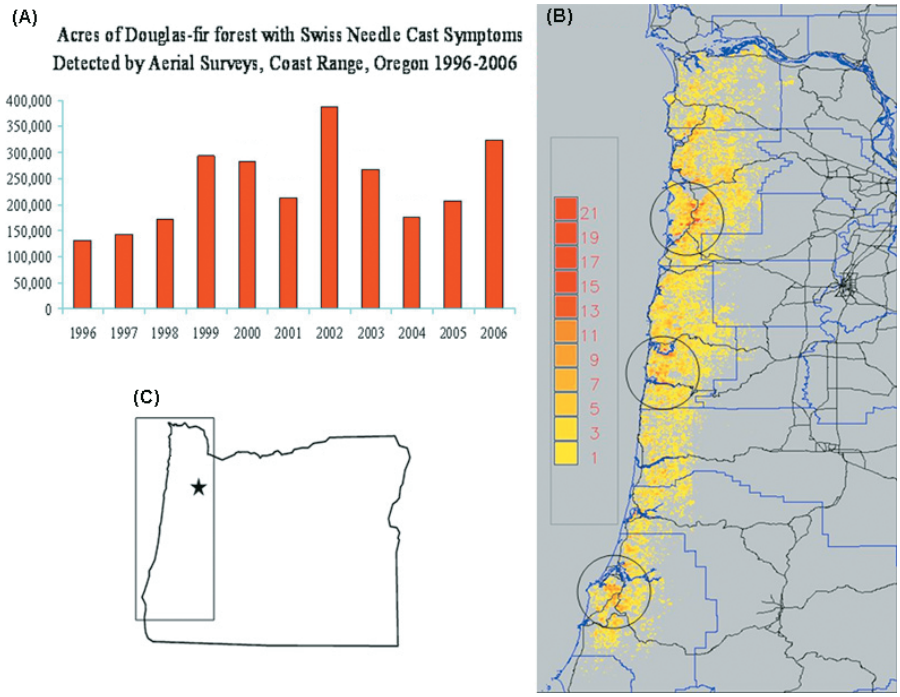
The abundance of pseudothecia is also highly correlated with needle abscission because of the effect on CO_2 assimilation. It has been suggested that foliage abscission occurs when needles switch from being carbon sources to carbon sinks (Cannell and Morgan 1990). Therefore, the mechanism of pathogenicity of *P. gaeumannii* can be accounted for by the physical blockage of the stomata and interference with photosynthetic gas exchange. The proportion of stomata occupied by pseudothecia on attached needles seldom exceeds 50%, suggesting that most needles are abscised before more than one-half of the stomata are occluded by pseudothecia, regardless of needle age (Hansen et al. 2000). Because the physiological effects of the disease (impaired CO_2 uptake and photosynthesis) are quantitatively related to the abundance of the pathogen (proportion of stomata occluded by ascocarps), pathogen ascocarp abundance is a suitable response variable for assessing effects of climatic factors on disease.

Observations on climate and disease severity

Disease severity (foliage retention, discoloration, crown sparseness, and pathogen abundance) has also been monitored annually in permanent plots in the Oregon Coast Range (Hansen et al. 2000) equipped with temperature and leaf wetness dataloggers. Foliage retention and abundance of *P. gaeumannii* ascocarps on 1- and 2-year-old needles have been monitored annually since 1996 in 9–12 Douglas-fir stands, aged 12–15 years at the beginning of the study. Study sites were selected to represent a range of elevations, distance from maritime influence, and disease severity. Within the area of severe disease, symptom severity is variable, but all Douglas-fir show some effects of the disease compared with healthy stands on the eastern slope of

Fig. 1. Symptoms of Swiss needle cast: premature defoliation and loss of older needles.

Fig. 2. (A) Annual variation in surveyed Swiss needle cast area (1 acre = 0.405 ha) in western Oregon 1996–2006, (B) location of the surveyed area in western Oregon (star indicates Salem), and (C) combined disease severity survey scores for western Oregon (severity scores for all 11 years summed and superimposed on map). Disease severities are as follows: 1, disease moderate for single year; 21, disease severe all 11 years of survey. Circled areas highlight regions where chronic Swiss needle cast has been observed. Data are from the Oregon Department of Forestry, Corvallis, Oregon.



the Coast Range and in the Cascade Range. Normal needle retention in healthy coastal form Douglas-fir is approximately 4 years. Within the epidemic area, needle retention varies from approximately 1.5 to 2.6 years (Hansen et al. 2000). Disease tends to be more severe in sites nearer the coast, at lower elevations, and on southern aspect slopes, gradually diminishing to the east (Hansen et al. 2000; Manter et al. 2003b; Rosso and Hansen 2003).

The Swiss needle cast epidemic area (Fig. 2) corresponds approximately to the Sitka spruce (*Picea sitchensis* (Bong.) Carr.) vegetation zone, a narrow strip of coastal forest characterized by elevations generally <150 m, proximity to the ocean, a moderate climate, and a distinct forest type (Franklin and Dyrness 1973). Although Douglas-fir is considered the early seral dominant in the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) vegetation zone, which borders

Fig. 3. (A) *Phaeocryptopus gaeumannii* on the underside of Douglas-fir needles with pseudothecia (fruiting bodies) emerging through stomata. (B) Pseudothecia aligned along stomatal rows. (C) Cross section through a stoma showing obstruction of the opening by the pseudothecium (p) between the guard cells (gs).

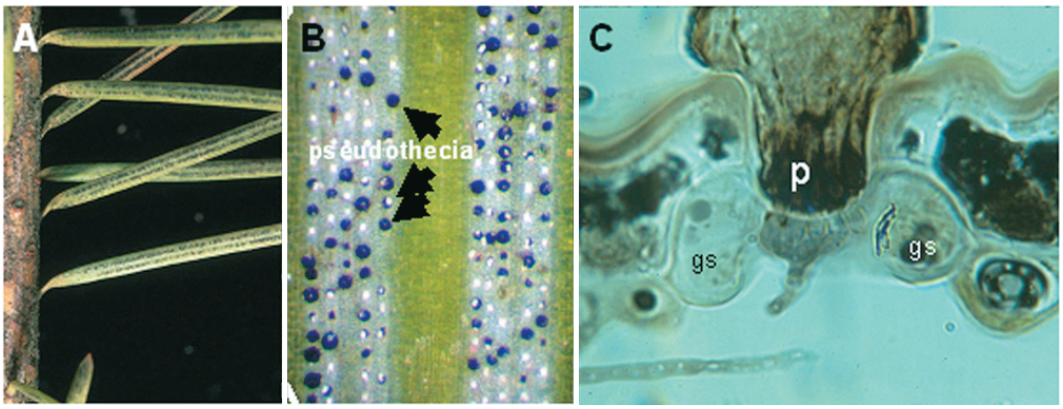
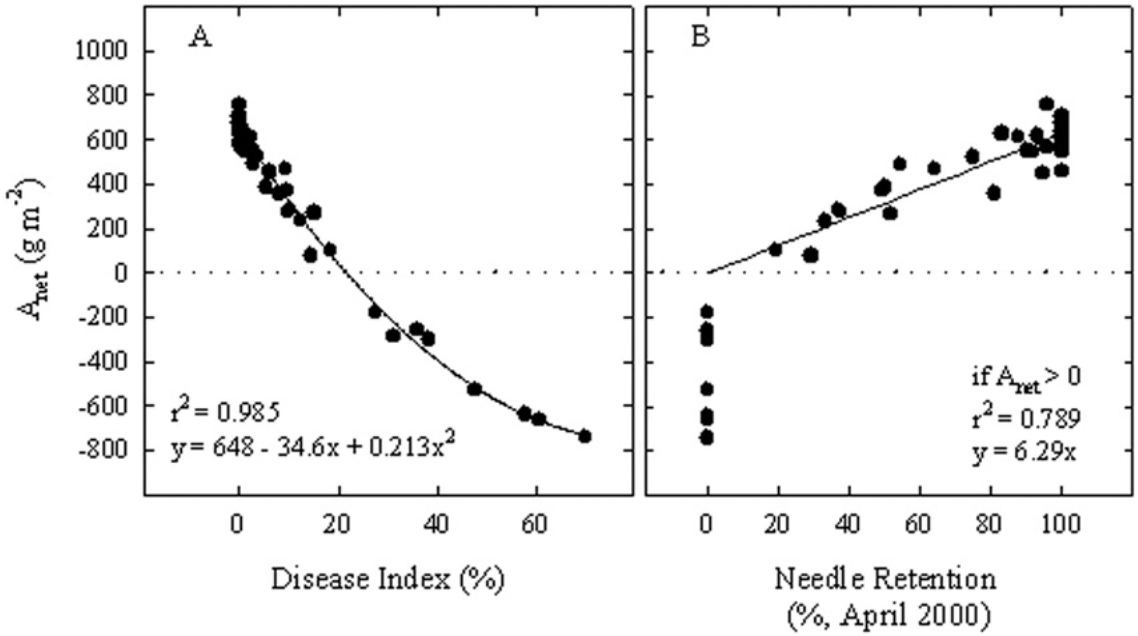


Fig. 4. Relationship of net carbon dioxide uptake (A_{net}) per unit leaf area to (A) *Phaeocryptopus gaeumannii* pseudothecia abundance (disease index, %) and (B) needle retention (%). Data are from Manter et al. (2003a).



the Sitka spruce zone to the east, its occurrence within the Sitka spruce zone is more sporadic. There, Douglas-fir occurs mainly in mixtures with Sitka spruce and western hemlock, but normally not as pure stands as is typical of early postfire succession in the western hemlock zone (Franklin and Dyrness 1973).

It has long been suspected that local climate plays a key role in the pathogenicity of *P. gaeumannii*. Boyce (1940) suggested that seasonal patterns in local climate could differentially affect fungal growth and development, and this might explain the greater virulence of *P. gaeumannii* in Europe and the eastern United States compared with the area where both *P. gaeumannii* and Douglas-fir are native. A relationship between disease severity and local climate has also been observed previously in the Pacific Northwest. Hood (1982) found more *P. gaeumannii* in southern British Columbia and western Washington in coastal forests of Vancouver Island and the Olympic Peninsula, with lower levels in the rain shadow of eastern Vancouver Island and the interior, and attributed the difference mainly to precipitation patterns. More severe disease symptoms and greater fungal colonization are commonly observed on lower elevation sites near the coast, suggesting the possible involvement of maritime fog (Rosso and Hansen 2003).

Experimental approaches to understanding climate–disease interactions

Because the most severe disease has been observed in sites within the low-elevation coastal fog zone, the presence of free water on needle surfaces during the summer has been considered a possible factor affecting disease severity (Hansen et al. 2000; Rosso and Hansen 2003). Other investigators have noted a relationship between precipitation pat-

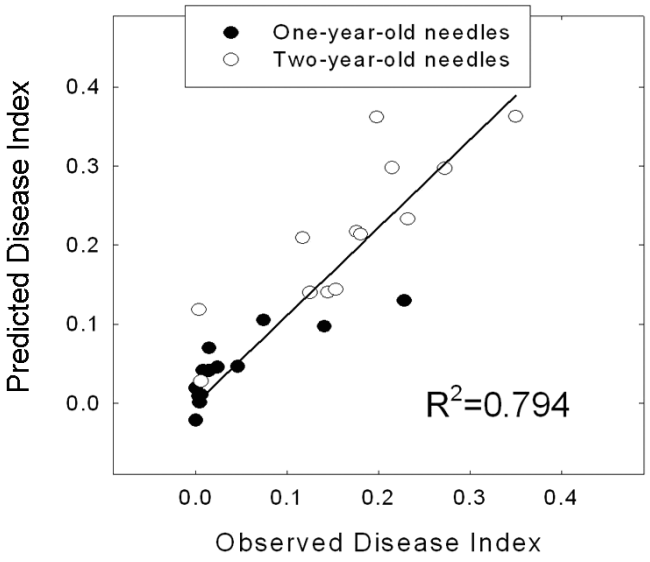
terns and Swiss needle cast severity in the Pacific Northwest (Hood 1982; McDermott and Robinson 1989). Manter et al. (2005) attempted to investigate the relative effects of individual climate factors on *P. gaeumannii* abundance experimentally. A factorial design was used to compare the effect of postinoculation incubation conditions under two levels each of drip irrigation, shade, and intermittent mist on *P. gaeumannii* colonization. Seedling trees were exposed to inoculum in a diseased forest stand, then randomized and maintained under the different postinoculation treatments. Abundance of *P. gaeumannii* ascocarps on foliage was determined monthly. The different postinoculation conditions resulted in significant differences in *P. gaeumannii* development. Contrary to the expected result, abundance of *P. gaeumanii* was negatively correlated with shade and mist, which was interpreted as being due to their indirect effects on temperature, rather than direct effect of shade or leaf wetness, whereas irrigation had no effect.

Modeling Swiss needle cast

The finding that small differences in temperature could affect rates of needle colonization and fungal development over the 11 month incubation period of *P. gaeumannii* prompted us to examine the relationship between temperature and *P. gaeumannii* abundance data from field sites in western Oregon. Mean daily temperature and cumulative leaf wetness hours were separated into 3 month groups corresponding to major phases in the infection cycle and subjected to stepwise regression against *P. gaeumannii* distribution data to identify climate factors for use in a disease prediction model. Consistently strong correlations were found between winter (December–February) mean daily temperature and infection in both 1- and 2-year-old needles (R^2 = 0.75–0.92), and this was the only climate variable with R^2 values >0.5. The best-fit climate model included winter mean daily temperature and cumulative spring leaf wetness hours (R^2 = 0.78 and 0.77 for 1- and 2-year-old needles, respectively). When this model was tested against infection data for different sites in different years, a significant 1:1 relationship was found (R^2 = 0.79; Fig. 5).

A more general model was sought that could be used to predict geographic variation in Swiss needle cast severity with the aid of spatial climate models. However, because leaf wetness is not readily available in public meteorological databases, alternative models were tried. Winter temperature was the best single predictor of *P. gaeumannii* abundance in the western Coast Range, but its relationship with infection level varied by year. The abundance of *P. gauemannii* and severity of Swiss needle cast for a particular site in a given year are not independent of previous-year disease severity for the site. Abundance of *P. gaeumannii* in 1-year-old needles is partly determined by the amount of inoculum present and the number of ascospores that initiate infection on a needle. Because ascospore infection of needles in their second year is negligible (Hood and Kershaw 1975; Stone et al. 2008), abundance of *P. gaeumannii* on 2-year-old needles is partly determined by the degree of colonization present in needles at the beginning of their second year. Therefore, two disease components, the amount of *P. gaeumannii* in 1- and 2-year-old needles for the previous year, were added to the temperature model to predict *P. gaeumannii* abundance in 1- and 2-year-old needles for the year of interest. Disease predictions generated by this model had a significant 1:1 relationship (R^2 = 0.812) when compared with observed values in the validation data set (Manter et al. 2005).

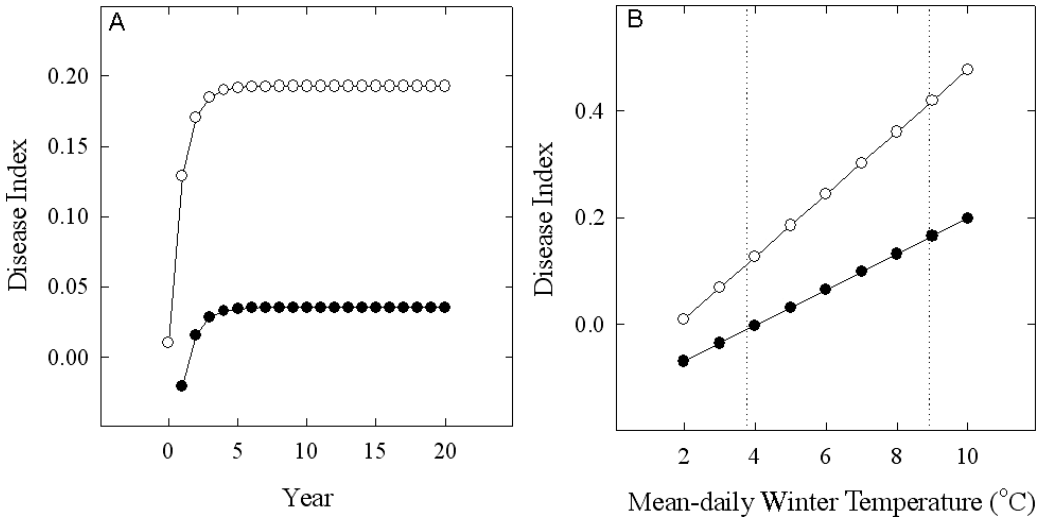
Fig. 5. Best-fit model for predicting *Phaeocryptopus gaeumannii* abundance using only climate variables (winter temperature and spring leaf wetness), predicted versus observed values. Data are from Manter et al. (2005).



The temperature–infection model described above was then run over several iterations with temperature held constant over a range of values (2–10 °C). After five iterations, the infection level reaches a stable asymptote for any value of winter temperature. The maximum infection value is a function of winter temperature, regardless of initial infection level, and represents the point of equilibrium among temperature, colonization, and inoculum production. A plot of the equilibrium infection level against temperature shows that between 3.77 and 8.90 °C, the range of mean winter temperatures measured at coastal study sites, infection levels vary from zero to approximately 15% in 1-year-old needles and from 10% to approximately 40% in 2-year-old needles (Fig. 6).

This model also was accurate for predicting disease levels for sites in the western Coast Range (R^2 = 0.85) but was less accurate when infection data from sites from the eastern slope of the Coast Range and Willamette Valley were included (R^2 = 0.70). Observed infection levels for the inland sites were less than predicted by the equilibrium temperature model, and this is likely due to the comparative dryness of the inland sites. The model that included a term for spring leaf wetness was more accurate in predicting infection levels for the inland sites than the equilibrium temperature model, illustrating that the relative importance of different climate factors can vary spatially. The simple equilibrium temperature model appears to be suitable for predicting disease levels in the western Coast Range, where spring surface moisture on foliage is probably rarely limit-

Fig. 6. (A) Simulation of *Phaeocryptopus gaeumannii* infection index over time as predicted by the combined winter temperature-infection model, with temperature held constant (5.13 °C) and initial infection index of 1% and (B) relationship between final equilibrium infection level and winter temperature for 1- (solid circles) and 2-year-old (open circles) needles.



ing, but additional parameters are necessary for disease prediction on more inland sites.

The distribution of *P. gaeumannii* also was investigated in New Zealand in 2005 (Stone et al. 2007). Foliage was collected, and abundance of *P. gaeumannii* pseudothecia was determined for 1- and 2-year-old foliage from 16 Douglas-fir plantations in the North and South Islands. *Phaeocryptopus gaeumannii* was first reported in New Zealand in 1959 and is now considered established throughout the country (Hood et al. 1990). The study was undertaken to characterize the spatial variation in disease severity and *P. gaeumannii* abundance in New Zealand and to determine whether climate factors correlated with variation in disease severity in western North America are also are correlated with disease distribution in New Zealand. Winter temperature was the best explanatory variable for predicting the abundance of *P. gaeumannii* throughout New Zealand. Univariate models using August minimum temperature or June mean temperature both had similar predictive values ($R^2 = 0.81$, $P = 0.0001$). Both variables were positively correlated with *P. gaeumannii* abundance. These results suggest that variation in Swiss needle cast severity in New Zealand is being influenced by climate factors similar to those identified for the disease in western Oregon and reinforce the conclusion that winter temperature is a key factor influencing spatial variation in disease severity. When the New Zealand *P. gaeumannii* distribution data were plotted using mean winter temperature to compare directly to the western Oregon model of Manter et al. (2005), there was no discernable difference (Stone et al. 2007).

The sensitivity of *P. gaeumannii* to relatively small temperature differences helps to explain patterns of spatial variation in Swiss needle cast severity and suggests that recent increases in Swiss needle cast severity have been influenced by regional climate trends. Over the past century, mean temperatures in the Pacific Northwest region have increased by approximately 0.8 °C, with more warming occurring during winter months (Mote et al. 2003). Mean temperatures for the period January–March have increased by approximately 0.2–0.4 °C/decade since 1966 in coastal Oregon and Washington (NOAA 2005). An increase in mean winter temperature of 1 °C corresponds to an increase in infection index (proportion of stomata occluded) of 3% for 1-year-old needles and 6% for 2-year-old needles, based on the equilibrium temperature model of Manter et al. (2005, Fig. 6). Spring precipitation in the affected area of western Oregon and Washington has also increased on average by approximately 1.6–2.6 cm/decade since 1966 (NOAA 2005).

These regional climate trends suggest that, over the past few decades, conditions have become more favorable for growth of *P. gaeumannii* and have contributed to increasing Swiss needle cast severity. Predictions for continued regional warming of approximately 0.4 °C/decade to 2050, together with increasing (2%–4%) spring precipitation (Mote et al. 2003), suggest that conditions in the region will continue to be favorable for Swiss needle cast development and could result in expansion of the area affected by the disease beyond the western Coast Range of Oregon. A goal of ongoing research is to develop an improved disease-prediction model to investigate the interactions between climate and Swiss needle cast. An expanded disease-prediction model will be designed to incorporate long-term climate trend forecasts to enable site-specific short- and long-term disease risk predictions, growth impact predictions, and the addition of various climate change model datasets to allow examination of disease development trends under different climate scenarios.

Conclusions

Improved understanding of the effects of climate factors on *P. gaeumannii* abundance now helps to clarify the underlying causes for recently observed increases in Swiss needle cast in the western Coast Range. Previous observations on the regional distribution of *P. gaeumannii* in the Pacific Northwest have suggested a connection between *P. gaeumannii* abun-

dance and spring rainfall (Hood 1982). In the western Coast Range of Oregon, where spring precipitation is abundant, winter temperature has been found to be a highly reproducible predictor of the spatial variation in abundance of *P. gauemannii* and resulting Swiss needle cast severity, presumably because of its effect on fungal growth. Winter temperature alone is not a satisfactory predictor of *P. gauemannii* abundance regionwide or in areas where spring precipitation is not as abundant, such as the Willamette Valley or Oregon Cascade Range, as shown by Manter et al. (2005). Therefore, the predictive disease model described here is applicable for predicting spatial variation in *P. gaeumannii* abundance and Swiss needle cast severity only for the western slope of the Oregon Coast Range. Within this area, there have been few historical reports of Swiss needle cast, and the disease has been considered an insignificant forest health issue. The natural distribution of Douglas-fir in the western Coast Range has undoubtedly been influenced by *P. gaeumannii* and Swiss needle cast, along with other disturbance agents. The effect of chronic, profuse *P. gaeumannii* colonization of Douglas-fir foliage is to reduce growth rates of affected trees relative to competing species, such as spruce and hemlock. Generally faster growing than western hemlock, Douglas-fir is an inferior competitor where Swiss needle cast disease pressure is high. In the coastal lowlands and interior valleys of the western Coast Range, seasonal climatic conditions are the most favorable for *P. gaeumannii* growth and reproduction. In these areas, a distinct natural forest type has historically been dominated by western hemlock and Sitka spruce, with Douglas-fir occurring only sporadically. Douglas-fir gradually becomes more abundant in natural forests at higher elevations and further inland, as the Sitka spruce zone gradually merges into the western hemlock vegetation zone, where Douglas-fir is a successional dominant and where climatic conditions are less favorable for *P. gaeumannii* growth. This leads to the conclusion that the Sitka spruce vegetation zone occurs as a consequence not only of favorable habitat for Sitka spruce and western hemlock, but also because of the inhibition of their main competitor, Douglas-fir, as a result of Swiss needle cast disease. This scenario also suggests that the severity of Swiss needle cast in the region may be the result of recent forest management practices in the western Coast Range, where Douglas-fir has been strongly favored in forest plantations because of its greater economic value, increasing the abundance of the host species in the area most favorable for growth and reproduction of the pathogen. However, as noted above recent climate trends also are likely to have contributed to current Swiss needle cast severity. Furthermore, forecasts of future climate trends for the Pacific Northwest suggest a probable expansion of the area affected by severe Swiss needle cast beyond the western Coast Range as winter temperatures and spring precipitation continue to increase, resulting in greater disease pressure on Douglas-fir stands further inland.

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