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Prediction of the severity of Dothistroma needle blight in radiata pine using plant based traits and narrow band indices derived from UAV hyperspectral imagery

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ABSTRACT

Dothistroma needle blight, caused by the fungi *Dothistroma septosporum* and *D. pini* is globally one of the most damaging diseases of pine species. Infection from the pathogen, which is initiated in the lower crown, causes needle chlorosis, loss of cellular integrity, necrosis and premature needle loss with this developmental sequence impacting key plant functional traits such as chlorophyll content and leaf area index. This study uses data collected from four year old field grown radiata pine (*Pinus radiata* D. Don) exhibiting a wide range in disease severity (0 - 58%). Hyperspectral data collected from a UAV was used to determine how plant functional traits inverted from a 3D radiative transfer model (PRO4SAIL), can be used by random forests to improve predictions of disease severity, relative to a model with only narrowband hyperspectral indices. Model precision was assessed on a test dataset that was not used for model fitting and this cross validation process was repeated 50 times to ensure reported results were robust, with the mean precision reported from these repeats.

The model of disease severity using narrow band hyperspectral indices was moderately precise ($R^2 = 0.52$). Addition of the inverted plant functional traits markedly improved model precision and this final model strongly predicted disease severity with R^2 of 0.85. Analyses of variable importance in the final model showed significant interchange in variable importance as the disease progressed. Early stages of the disease were most readily distinguished from asymptomatic trees (severity = 0%) using variables that predominantly describe changes in photosynthesis (Photochemical Reflectance Index), chlorophyll degradation (Normalized Phaeophytinization Index) and chlorophyll content. In contrast, the more severe impacts of the disease were most well characterised by traits associated with an extreme reduction in transpiration (carotenoid content) and loss of foliage.

1. Introduction

Dothistroma needle blight (DNB), also known as red band needle blight, is globally one of the most damaging foliage diseases of plantations and natural stands of pine (Bradshaw, 2004). Although the causal agents have undergone a number of taxonomic revisions the most recent phylogenetic understanding of causation is two divergent lineages of fungi, *Dothistroma septosporum* (Dorog.) M. Morelet and *D. pini* Hulbary (Barnes et al., 2004). These fungi have been shown to infect 109 Pinaceae host taxa within six genera (*Abies, Cedrus, Larix, Picea, Pinus, Psuedotsuga*) of which the majority are *Pinus* spp. accounting for 95 of the host taxa (Drenkhan et al., 2016). The disease has a very cosmopolitan distribution and occurs in 76 countries with climates ranging from sub-arctic to tropical (Drenkhan et al., 2016; Watt et al., 2009). Although DNB is widespread the disease is most strongly expressed during warm conditions with high humidity and rainfall (Bulman et al., 2013b; Fabre et al., 2012; Murray and Batko, 1962; Peterson, 1973; Rodas et al., 2016; Woods et al., 2005) and recent outbreaks over the last

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Fig. 1. The displayed panels show (a) the location of the study site, (b) high resolution RGB orthophotograph of the study area (taken prior to the hyperspectral capture on the 13th November) showing the 13 plots that were sampled for this study, (c) an enlargement of plot 48 showing individual tree numbers and the masks that were applied to the hyperspectral data (transparent blue and red shapes). The selected trees in this plot have blue masks. Canopy reflectance for the circled trees is shown in (d) for trees 22 (purple line), 40 (orange line) and 46 (yellow line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

two decades in northern Europe and west Canada are thought to result from warmer, wetter conditions (Welsh et al., 2014; Woods et al., 2016).

The developmental stages and symptoms of the disease have been well characterised. Rain-splashed conidia most commonly infect needles through the stomata (Gibson, 1972) which leads to development of yellow spots, that later encircle the needle and widen to a necrotic band which often leads to tip death (Bradshaw, 2004; Gadgil, 1967; Shain and Franich, 1981). Red bands develop within the necrotic lesions as a result of the accumulation of the toxin dothistromin (Bassett and Buchanan, 1970; Shain and Franich, 1981). Desiccation of tissue that is distal to the lesion then occurs and the needle progressively changes colour from pale green to brown or tan (Franich et al., 1986). The sequence of symptoms that usually occurs includes initial chlorosis, production of red and brown metabolites, loss of cellular integrity, cellular necrosis and premature needle loss (Edwards and Walker, 1978), which is accompanied by a reduction in growth and in severe cases tree mortality (Brown and Clayden, 2012; Brown and Webber, 2008). Infection is initiated in the lower crown within older foliage and spreads upwards (Macdonald, 2011).

The development of methods that can characterise disease severity for individual trees would be very useful for characterising the disease within genetic trials, where clones are often randomly distributed. At the tree level Dothistroma spp. can be identified using DNA techniques (Barnes et al., 2004; Barnes et al., 2016), real-time PCR (Ioos et al., 2010) and from morphology characteristics (Barnes et al., 2004) while the disease itself can be identified from visual observation based on the distinctive symptoms (Bulman et al., 2004). However, all these methods are time consuming. Plant health and the response of plants to environmental and biotic stressors is closely linked to plant functional traits (PT) such as biochemical composition, chlorophyll fluorescence, dry matter and water content, crown temperature and vegetation structure (Gonzalez-Dugo et al., 2014; Hernández-Clemente et al., 2019; Hernández-Clemente et al., 2011; Iordache et al., 2020; Mohammed et al., 2019; Sapes et al., 2021; Sims and Gamon, 2002; Zarco-Tejada et al., 2018; Zarco-Tejada et al., 2012). Fine scale hyperspectral and thermal imagery obtained from a UAV can be used to characterise many of these traits at the tree level and a recent review describes strategies to quantify PTs in natural forestry canopies (Hernández-Clemente et al., 2019).

The use of hyperspectral imagery to detect disease within forests and tree crops is complex as canopy heterogeneity has a strong impact on the effects caused by soil background, shadows and understory, which affects the spectral signature of pure crowns (Hernández-Clemente et al., 2019; Liu et al., 2020; Pisek et al., 2015). Despite these challenges, there are a number of recent examples of successful disease detection and characterisation at scale in the field when hyperspectral imagery is used in combination with 3-D radiative transfer models (3D-RTM) and machine learning data analysis methods. Using this approach, Holm oak decline, caused by Phytophthora cinnamomi, was detected with an accuracy of 82% and pre-symptomatic trees were detected up to 2 years before visual identification (Hornero et al., 2021). The infection of olive trees by Xylella fastidiosa has been accurately detected using PT derived from 3D RTM with an accuracy of 80% and key PT in the model retrieved from hyperspectral and thermal imagery could reveal symptoms before they were visible (Zarco-Tejada et al., 2018).

A number of studies have used remotely sensed data to detect and characterise the severity of DNB. Hyperspectral imagery from a fixed wing aircraft (CASI-2) was used to predict three levels of disease severity in radiata pine (Pinus radiata D. Don) plantations in Australia with an accuracy of over 70% (Coops et al., 2003). A combination of aerially acquired LiDAR and hyperspectral imagery was used to predict DNB severity on lodgepole pine (Pinus contorta Douglas) within central Scotland (Smigaj et al., 2019b). The LiDAR metrics were found to be more important than hyperspectral indices. However, the authors noted that that spatial resolution of the airborne hyperspectral imagery (2 m) was a major limiting factor and recommended further research should use UAV acquired hyperspectral imagery to facilitate tree level analysis (Smigaj et al., 2019b). In a study undertaken in the same area, six thermal captures made over the course of a day from a diseased stand of Scots pine (Pinus sylvestris L.), found significant correlations between canopy temperature depression (CTD) and DNB severity (Smigaj et al., 2019a). The relationship between disease severity and CTD was strongest ($R^2 = 0.41$) when imagery was obtained during the time of highest solar radiation and maximum photosynthetic activity. In contrast to the previous study, the inclusion of structural metrics obtained from LiDAR only slightly improved predictions of disease severity (Smigaj et al., 2019a).

Although hyperspectral imagery has been used for prediction of DNB severity, further research is required to understand how utilisation of PT acquired from fine scale data can advance prediction accuracy. Hyper-spectral imagery can also be used to identify the role of specific plant traits in DNB detection and to improve the understanding of the physiological changes experienced by trees infected with *Dothistroma* spp. This study uses high spatial resolution UAV hyperspectral imagery acquired from a field trial of radiata pine with wide variation in DNB severity. Using PT extracted from RTM, the objectives were to use machine learning methods to (i) predict DNB severity using narrow-band hyperspectral indices (NBHI) and (ii) compare these predictions to a

model that combines both functional PT and key NBHI indices and (iii) identify the key NBHI and PT associated with different levels of DNB severity.

2. Methods

2.1. Experimental design and tree selection

Data was obtained from a four-year old field trial located near Rangipo in the central North Island, New Zealand (Fig. 1a). The selected site had a grass understorey with very few weeds and the trees had not closed canopy at the time of measurement. The site was established with 12 genotypes, that were selected to cover a range of attributes that included disease resistance and water use efficiency. The genotypes comprised one hybrid cross (*Pinus radiata x attenuata*), 10 clones of radiata pine, and a standard unselected radiata pine stock (GF19). These genotypes were laid out, as single genotype plots, in 144 square plots across the site that included 49 trees/plot. At the plot level each genotype was subjected to two ripping treatments (no ripping and 300 mm deep ripping) and two stand density treatments (planting density of 833 and 1282 stems ha⁻¹) and these randomly allocated plots were replicated across the sites in three blocks. Thus, the 144 plots comprised 12 genotypes x four treatments x three blocks.

We selected 13 plots of radiata pine within the trial that covered a range in foliage nutrition and DNB severity (Fig. 1b). These 13 plots included 6 clones and one plot that was established with GF 19 stock. Nutrition measurements from a previous sampling of the entire trial in February 2020, that pooled samples at the plot level, were used to identify plots covering the range in foliage N and P content. Preliminary measurements of disease severity undertaken during mid-late October 2020 were used to identify plots and trees that expressed a range in DNB severity. Within the 13 plots, 126 trees were selected to cover a range in DNB severity and all the measurements described below were taken from these trees.

2.2. Dothistroma needle blight severity

Recent research, that utilised national survey data, shows peak disease severity for DNB within New Zealand to be reached in December (Watt et al., 2021). Consequently, we scheduled our data collection as close to this month as possible. Measurements of DNB severity that were used in this study were assessed on November 13 and December 2^{nd} 2020.

Following the method described and illustrated within Smigaj et al. (2019a), severity was determined from the following equation:

$$Sev = 100 \frac{H_{\rm inf} - H_{base}}{H_{lop} - H_{base}}$$
(1)

where H_{inf} , H_{base} and H_{top} are, respectively, the maximum height of the infection, base of the crown and top of the tree. The disease progresses in a uniform way from the ground towards the crown and the height of infection was taken as the uppermost height of the diseased needles on the tree. The base of the crown was defined as the base height of the lowest branch with needles. As these were young trees with relatively high needle retention the crown base was close to ground level for almost all trees and averaged 43 cm. These heights were measured by a single observer using a height pole for trees < 6 m and a Vertex 4 hypsometer (Haglof, Langsele, Sweden) for trees \geq 6m. It is worth noting that the method we used differs slightly from previous methodologies such as those described in Bulman et al. (2004) and Kershaw et al. (1982).

2.3. Hyperspectral imagery

2.3.1. Data acquisition

Hyperspectral imagery was captured from the trial on the 17th December 2020 using a Resonon Pika XC2 hyperspectral imager (Resonon Inc., Bozeman, MT, USA) that was mounted to a DJI Matrice 600 (M600) Pro UAV (DJI Ltd., Shenzen, China). Data collection was scheduled for December, as sun angles are high and disease severity reaches a peak during this month (Watt et al., 2021). The Pika XC2 is a push-broom sensor that captures 447 bands with wavelengths ranging from 400-1000 nm with a spectral full width at half maximum (FWHM) of 1.9 nm and a spectral bandwidth of 1.3 nm.

The flight planning used UgCS software (SPH Engineering, Riga, Latvia) to optimise the acquisition. Data was acquired between the hours of 11am and 12pm under completely clear sky conditions to minimise the effects of shadow. The camera was set to a frame rate of 145 fps to ensure that square pixels were captured. Data was captured from an altitude of 70 m at a speed of 3.5 m s^{-1} and consistent with previous research we used a line spacing of 25 m, which resulted in a 35% overlap (Angel et al., 2019; Sankey et al., 2017). The resulting imagery had a GSD of 5 cm/pxl.

A network of five ground control points (GCPs) was established across the area of interest, prior to data capture, to ensure the accurate geolocation of the imagery. Each GCP comprised a \sim 1 m square plastic target with high contrast black and white quarters. The GCPs were surveyed using a Trimble Geo7X handheld GPS unit (Trimble Inc., Sunnyvale, CA, USA) with a Trimble Zephyr Model 2 external aerial and each point was averaged for approximately 5 minutes to achieve 300 point fixes. The resulting RMSE per point ranged from 0.05–0.15 m.

A single 3 by 3 m grey calibration tarp (Type 822) with a reflectivity level of 24% (Group 8 Technology, Provo, Utah, USA) was laid out within the area of interest and later used in the data processing pipeline for spectral calibration. The Resonon Pika XC2 system also comprises a Flame-S VIS-NIR 350-1000 nm downwelling irradiance sensor (Ocean Optics Inc., Dunedin, FL, USA), which was mounted to the top of the UAV. Data from this sensor was used for measuring the irradiance and subsequent calculation of hyperspectral reflectance.

2.3.2. Data processing

The Spectronon Pro version 3.1.1 software (Resonon Inc., Bozeman, MT, USA) was used to process the hyperspectral data. To derive surface reflectance, the raw hyperspectral data cubes were converted to radiance using radiometric calibration coefficients derived in the laboratory. The radiance-converted data cubes were then geo-rectified within the same software package utilising terrain data derived from a LiDAR Digital Elevation Model (DEM) that was collected over the site for a previous project (Hartley et al., 2020). This process involved calibrating the angular offset of roll, pitch and yaw from the imager to correct visual distortions in the imagery and produce calibrated and geolocated data cubes. To extract reflectance data, the radiance data were converted to reflectance using the mean reflectance of the calibration tarp within the image and the dark noise of the sensor.

Regions of interest (ROIs) were manually drawn for each crown (Fig. 1c), and mean reflectance spectra for the crowns were extracted from the hyperspectral images (Fig. 1d).

2.4. Modelling methods

Reflectance was utilised for the calculation of narrowband hyperspectral indices (NBHI) and to retrieve leaf and canopy attributes via inversion of a Radiative Transfer Model (RTM).

2.4.1. Calculation of narrowband hyperspectral indices

Following Zarco-Tejada et al. (2018), NBHI that were related to structural traits, chlorophyll fluorescence, disease and concentration of plant pigments such as chlorophyll a+b, carotenoids, anthocyanins, and

Table 1

Ranges of parameters used to perform simulations with the PRO4SAIL radiativ	e
transfer model.	

Parameter	Abbreviation	Units	Range
Chlorophyll content	C_{a+b}	[µg/cm ²]	[4,70]
Carotenoid content	C_{x+c}	[µg/cm ²]	[1,15]
Anthocyanin content	Anth.	[µg/cm ²]	[1,12]
Dry matter content	Cm	[g/cm ²]	[0.005,0.04]
Water content	Cw	[g/cm ²]	[0.004,0.08]
Mesophyll struct. coeff.	Ν	-	[1.2,1.6]
Leaf area index	LAI	$[m^2/m^2]$	[1,7]
Average leaf angle	LIDFa	[deg.]	[1,90]
Hot spot parameter	hot	-	0.01
Observer angle	tto	[deg.]	0
Sun zenith angle	tts	[deg.]	[45]
Relative azimuth angle	psi	[deg.]	0

xanthophylls were calculated. These indices were determined from spectral bands in the VNIR spectral region and equations for these indices are given in Appendix 1.

2.4.2. Retrieval of plant traits using machine learning to invert parameters from Radiative Transfer Models (RTM)

The inversion of RTM involves the identification of the simulated reflectance that best matches with the measured reflectance in order to identify the optimal set of estimated parameters. The PRO4SAIL radiative transfer model, which combines the leaf radiative transfer model PROSPECT-D (Féret et al., 2017), with the canopy radiative transfer model 4SAIL (Verhoef et al., 2007) was used to model leaf biochemical components and canopy structural features from vegetation pixels, as has been undertaken previously (Poblete et al., 2021; Zarco-Tejada et al., 2018; Zarco-Tejada et al., 2021). This model was used to simulate the concentration of leaf pigments such as chlorophyll a+b (C_{a+b}), anthocyanins (Anth.) and carotenoids (C_{x+c}), and structural features such as the leaf inclination distribution function (LIDF_a) and the leaf area index (LAI).

A look-up table of 200,000 simulations was built in forward mode by running the PRO4SAIL model using as inputs the parameters and their ranges shown in Table 1, which were varied randomly using continuous uniform distributions. The ranges used in Table 1 were based on previously published values for radiata pine and other tree species (Verrelst et al., 2010; Watt et al., 2020a; Zarco-Tejada et al., 2019). Although the initial range for anthocyanins was set wider than that typically used, the maximum inverted value of $3.65 \ \mu g/cm^2$ was consistent with previous studies focussed on disease detection (Hornero et al., 2021; Zarco-Tejada et al., 2021). The remaining settings were set to their default values. Data resampling was undertaken to match the spectral resolution of the hyperspectral sensor utilised in this research since simulated reflectance from PRO4SAIL spans the 400-2500-nm spectral region with an FWHM of 1 nm. This spectral resampling was performed using a Gaussian response function.

The plant attributes resulting from model simulations were inverted using support vector machine (SVM) techniques. SVM models are nonparametric models that are based on statistical learning theory (Vapnik, 1999). These models have been widely used in remote sensing studies (Mantero et al., 2005) and are trained to locate the hyperplane that maximises the margin between classes while minimising misclassification error. When used for regression Support Vector Regression (SVR) algorithms aim to discover the function with the greatest variance between the observed responses for all instances of observation. SVR models were trained in parallel with MATLAB (MATLAB; Statistics and Machine Learning toolbox, parallel computing toolbox, and Deep Learning toolbox; Mathworks Inc., Natick, MA, USA) and used as inputs the resampled reflectance and outputted the biochemical and structural traits described above. The SVR algorithms were trained using a radial basis function as the kernel and the remainder of the hyperparameters were optimised during training. Although we did not validate the



Fig. 2. Biochemical and structural parameters obtained by Support Vector Regression (SVR) algorithms trained using reflectance from PROSAIL simulations as inputs: (a) chlorophyll content, (b) carotenoid content, (c) anthocyanin content, (d) leaf area index, and (e) average leaf angle.

predictions from the model inversion this method is widely accepted and has been used in many recently published papers to detect diseases and abiotic stresses (Longmire et al., 2022; Poblete et al., 2020; Poblete et al., 2021; Zarco-Tejada et al., 2018; Zarco-Tejada et al., 2021)

2.4.3. Disease severity prediction using random forest algorithms

Several studies have focused on the detection of the disease incidence by using classification algorithms to detect asymptomatic vs. symptomatic trees (Hornero et al., 2021; Poblete et al., 2020; Poblete et al., 2021; Zarco-Tejada et al., 2018; Zarco-Tejada et al., 2021). As the severity of DNB was quantified in this study as a continuous variable, based on the methodology proposed by Smigaj et al. (2019a), machine learning algorithms for regression were trained to predict the severity percentage. Random forest (RF) algorithms for regression were trained in parallel using MATLAB (MATLAB; Statistics and Machine Learning toolbox, parallel computing toolbox, and Deep Learning toolbox; Mathworks Inc., Natick, MA, USA).

Disease severity was predicted by training two different models using as inputs i) a subset of non-collinear indices obtained from the full set of NBHI, and ii) the five plant traits retrieved from the inversion of RTM that were supplemented with non-collinear NBHI indices selected through a recursive feature elimination strategy. In i) the subset of indices was extracted by a dimensionality reduction applied over the NBHI pool. This reduction was undertaken using variance inflation factor (VIF) analysis (James et al., 2013), where indices with a VIF > 5(Akinwande et al., 2015) were excluded from the dataset. Within ii) the set of biochemical (Ca+b, Anth., Cx+c) and structural plant traits (LAI and LIDF_a) were supplemented with a smaller variable subset derived from i). Using a recursive feature elimination strategy, the indices that did not contribute to the prediction precision, as assessed by the coefficient of determination (R^2) and the root mean square error (RMSE), were omitted from the models and the retained indices were included for the severity prediction.

Determination of fit and precision for both models was undertaken through randomly splitting the 126 observations into a training dataset that comprised 80% of observations while the remaining 20% of the observations were reserved for model testing. This process was repeated 50 times using a different training; test split to ensure the reported results were robust. During each iteration the hyperparameters were optimised using Bayesian optimization (Statistics and Machine Learning toolbox; MathWorks Inc., Natick, MA, USA). The reported results for both models were a representative prediction that had the mean precision obtained from the 50 model runs.

2.4.4. Contribution of plant traits within prediction models

The contribution of plant traits to prediction of DNB severity was performed at two levels. First, the importance of each trait was evaluated when predicting severity as a continuous variable in order to determine the relative importance of plant traits across the range of infection levels, including asymptomatic infection (i.e. severity = 0). This analysis was performed by training random forest (RF) algorithms for regression and the importance of each predictor was quantified using the permutation of the out-of-bag method (OOB) (Thomas et al., 2021).

In the second analysis, plant trait importance was determined on three severity categories to examine if there was interchange in variable importance as severity increased. The three severity levels that were used for this analysis follow a previous categorisation (Bulman et al., 2016) where trees with disease DNB severities of 1-10, 10-25 and >25%were classed as being of minor, low, and medium/major severity (hereafter termed major severity), respectively. Classification was undertaken using RF algorithms that were trained by classifying asymptomatic (disease severity=0) vs. infected trees at the three different severity levels. During each classification training stage, the disease severity was progressively increased by cumulatively adding trees with minor, low and then major severity to the analysis with the three classes including minor severity (1-10%); minor and low severity (1-25%); minor, low, and major severity (1-58%). The importance of the plant trait to the classification processes was assessed using the OOB methodology. All the RF algorithms were trained in parallel and the hyperparameters were optimized using a Bayesian optimization method in MATLAB (Statistics and Machine Learning toolbox; MathWorks Inc., Natick, MA, USA).

The functional form between DNB severity and important predictor variables (NBHI and PT) was explored through the use of boxplots and analysis of variance (ANOVA). The ANOVA was undertaken on each of these traits using four severity classes, that included trees that were



Fig. 3. Prediction of tree level dothistroma needle blight severity made on the test dataset using random forest models. Shown is measured dothistroma severity against model predictions that use (a) non-collinear indices obtained from the set of Narrowband Hyperspectral Indices (NBHI), and (b) plant traits obtained by inversions of PRO4SAIL simulations and non-collinear NBHI selected by the recursive feature elimination method.

asymptomatic (0%), or symptomatic with minor severity (1–10%), low severity (10–25%) and major severity (25 – 58%). The analysis included all seven NBHI identified in step (i) and the five PT used in step (ii). For variables that exhibited significant differences between severity classes Dunnett's test was used to identify which of the three symptomatic classes were significantly different (at $\alpha < 0.05$) from the asymptomatic trees.

3. Results

3.1. Range in pigments and structural parameters

The concentrations of pigments and structural parameters were retrieved using SVR models that were trained using the simulated reflectance obtained from PRO4SAIL simulations (Fig. 2). The distribution of chlorophyll and carotenoid contents were slightly left skewed while the anthocyanin content was slightly right skewed and more uniform than the other two pigments. Mean values for chlorophyll, carotenoid and anthocyanin contents were, respectively, 40.5, 10.7, and 1.82 µg/cm². The distribution of leaf area index was left skewed with a mean value of 3.76 m²/m² and most values ranged between 3.5 – 4.0 m²/m². In contrast, the average leaf angle was right skewed with a mean value of 44.5 degrees.

3.2. Model predictions of disease severity

The model with NBHI was moderately precise and had an R^2 of 0.52 with RMSE of 9.41% (Fig. 3a). The NBHI included in this model were TVI, NPQI, PRI_n, LIC₃, B, BF₁ and CUR. Across the four severity categories there was significant variation between the major and the asymptomatic category for PRI_n, LIC₃ and B (Fig. 4). There were significant differences between asymptomatic and the higher two severity classes for NPQI. No significant differences between asymptomatic trees and the three severity classes were noted for BF₁, TVI and CUR (Fig. 4).

Addition of the inverted variables to a subset of these seven NBHI markedly improved model precision and this final model strongly predicted disease severity with R^2 of 0.85 and RMSE of 4.5% (Fig. 3b). The five PT in this final model (C_{a+b} , Anth., C_{x+c} , LAI and LIDF_a) were supplemented with four NBHI that included NPQI, PRI_n, LIC₃ and B. For the inverted variables, C_{a+b} in trees within the two highest severity categories significantly differed from the asymptomatic trees (Fig. 4). Values of C_{x+c} for trees in the highest severity category significantly differed from the asymptomatic trees. The C_{x+c}/C_{a+b} ratio increased from 0.249 for the asymptomatic trees to 0.273 and 0.270, respectively, for the two highest severity categories. No significant differences between asymptomatic trees and symptomatic trees were noted for Anth., LAI or LIDF_a (Fig. 4).

3.3. Variable importance of the final model

Analysis of variable importance for the final model that was based on continuous severity values is shown in Fig. 5a. Carotenoid content was the most important variable, followed by PRI_n , B, LAI and then C_{a+b} . The two least important variables within this model were Anth. and NPQI.

The second analysis investigated variable importance for three models that classified symptomatic and asymptomatic trees (i.e. severity = 0). This analysis clearly showed significant interchange in variable importance for the model that included trees with minor severity and the model that included all three categories (minor, low, and major severity). This interchange in variable importance with increasing disease severity was most pronounced for NPQI, LAI, C_{x+c} , and LIC₃ (Fig. 5b).

For the model that included the contrast of minor severity vs. asymptomatic trees, the variables that were the most important included, NPQI, PRI_n, C_{a+b} and LIC₃, with B and C_{x+c} being the least important (Fig. 5b). In contrast, for the model that included all categories, the most important variables were LAI, followed by PRI_n, C_{x+c} , and LIDF_a, with LIC₃ and NPQI the least important. Importance values of most variables for the intermediate model, that included minor and low severity trees, were between the values for models that included minor severity or all three categories of symptomatic trees (Fig. 5b).

4. Discussion

The observed DNB severity levels within our study covered a very wide range. Average disease severity within the dataset was 17.6% and ranged from 0 to 57.9%. The impacts of DNB have been classed, based on the percentage of affected foliage, as ranging from minor (0 - 10%) to major (51 - 75%) with our data covering this entire range. Among the 26 countries with reports, most have minor and low severity with only New Zealand and Britain reporting major levels of DNB severity (Bulman et al., 2016). The upper values of severity reported here were also similar to maximum values observed within New Zealand from national monitoring undertaken from 1973 – 2010 in radiata pine plantations (Watt et al., 2011; Watt et al., 2021).

A large part of the reported range in our data was attributable to variation in DNB severity between genotypes in different plots, with plot level averages ranging from 2.8 - 39.3%. Percentage reductions in annual volume growth for radiata pine trees that are infected with DNB over a three year period has been shown to be similar to the DNB severity percentage (van der Pas, 1981). Assuming that our trees are infected at a similar rate over three years this equates to average and maximum annual volume growth reductions of, respectively, ca. 18% and 58%. These impacts highlight the damaging nature of DNB and the need for a reliable method of characterising severity.



Fig. 4. Boxplots for plant traits obtained from the Radiative Transfer Model inversions and a subset of sensitive NBHI indices used for the prediction of DNB severity. Black lines inside the boxes represent medians, and the top and bottom line in each box represent the 75th and 25th quartiles, respectively. Whiskers represent $\pm 1.5 \times$ the interquartile range and black crosses represent outliers. Red asterisks denote severity classes with significant differences from the asymptomatic trees according to Dunnett's test at $\alpha < 0.05$. The disease severity for trees associated with the displayed four classes were 0% for asymptomatic, 1–10% for minor severity, 10–25% for low severity and 25 – 58% for major severity. Full names for acronyms are as follows: PRI_n, Photochemical Reflectance Index; NPQI, Normalized Phaeophytinization Index; LIC₃, Lichtenthaler Index; B, blue index; TVI, Triangular Vegetation Index; CUR, Reflectance Curvature Index. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The methodology developed here provided a robust means of predicting DNB and extends previous research through use of PT extracted from radiative transfer modelling. The high importance of chlorophyll and carotenoid contents that was shown in the sensitivity analysis is consistent with fundamental leaf-level physiological processes. Consistent with the disease induced decline in chlorophyll observed here, the infection of radiata pine with *Dothistroma* spp. has been previously shown to markedly reduce chlorophyll concentration within all elements of infected foliage and it is thought that the toxin dothistromin may target chloroplasts and/or chlorophyll (Kabir et al., 2015). Within a wide range of tree species the carotenoid: chlorophyll ratio has been found to increase in response to a variety of environmental stresses (Baquedano and Castillo, 2007; Ensminger et al., 2004; Gamon et al., 2016) and this ratio provides an indicator of reduced photosynthetic activity (Gamon et al., 2016; Stylinski et al., 2002). Consistent with this research we found an increase in the carotenoid: chlorophyll ratio with increasing disease severity as reductions in carotenoid content were less sensitive and proportionally lower than those of chlorophyll content.

Leaf area index is strongly affected by DNB, particularly during more advanced stages during which time there is premature needle loss and significant defoliation (Bradshaw, 2004; Stone et al., 2003). In contrast to other needle diseases, dead needles that are infected by DNB are held



Fig. 5. Variable importance for models that (a) predicted DNB severity as a continuous variable and (b) predicted DNB severity using classification models that categorised the diseased trees against those that were asymptomatic (i.e. severity = 0). Three classes were used that included minor severity (1-10%); minor and low severity (1-25%); minor, low, and major severity (1-58%). Full names for acronyms given in the figure are as follows: NPQI, Normalized Phaeophytinization Index; PRIn, Photochemical Reflectance Index; Ca+b, total chlorophyll content; LAI, leaf area index; LIC₃, Lichtenthaler Index; Anth, anthocyanin content; LIDF_a, average leaf angle; C_{x+c}, carotenoid content; B, blue index. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

onto the tree for some time before dropping (Bulman et al., 2013a). This previous finding is consistent with our field observations that show needle loss was not a strong visual feature of the trees, at the time of measurement, and the tree crowns with needles, in almost all cases, reached the lowest branch. Consistent with these observations, values of LAI predicted from the model inversions did not significantly differ between asymptomatic trees and the three symptomatic severity classes and these inverted values were within normal ranges of measured LAI for radiata pine (Pearse et al., 2017). The importance of LAI in the RF model increased as trees with higher severity were added to the model (Fig. 5b) which does suggest that as the disease severity increases, reductions in LAI will become a stronger feature of the symptoms.

The four NBHI included in the final model have been widely used in detection of disease and plant stress and significantly differed between DNB severity levels providing confidence in the robustness of the predictive model. Photochemical reflectance index (PRI) was an important NBHI predictor across all stages of disease severity and has been previously identified as the most important NBHI for detection of DNB (Smigaj et al., 2019b). Many studies show that PRI is an indicator of pre-visual stress (Nichol et al., 2006; Peguero-Pina et al., 2008; Zarco-Tejada et al., 2009) and an effective proxy for photosynthetic traits (Hernández-Clemente et al., 2019). The changes in PRI that occurred with increasing disease levels are likely to reflect reductions in assimilation and stomatal conductance and these linkages have been previously reported in diseased trees (Calderón et al., 2013; López-López et al., 2016) and more generally in stressed trees (Scholten et al., 2019; Watt et al., 2020b). Both NPQI and the blue index (B) are indices derived from the blue region of the spectrum and NPQI has been proposed to predict the impacts of pests and diseases on a variety of plants (Penuelas et al., 1995b; Zarco-Tejada et al., 2018; Zarco-Tejada et al., 2021) as this index accounts for the degradation of chlorophyll under stress (Barnes et al., 1992; Penuelas et al., 1995b). The observed reductions in the Lichtenthaler index with increasing disease severity characterise the extent of the leftwards shift in the red edge that occurs as stress increases and chlorophyll content diminishes (Lichtenthaler, 1996; Lichtenthaler et al., 1996).

There was significant interchange in variable importance as the severity of DNB increased with structural variables assuming greater importance in more severely diseased trees. Analyses clearly showed that early stages were most readily distinguished from asymptomatic trees using NPQI, PRI_n, C_{a+b} and LIC₃ which predominantly describe changes in key photosynthetic traits such as xanthophylls (PRI_n), chlorophyll degradation (NPQI) and chlorophyll content (C_{a+b} , LIC₃). The more severe impacts of DNB were characterised most well by traits associated with an extreme reduction in transpiration (C_{x+c}) and loss of foliage (LAI) that occurs when DNB reaches an advanced stage. This progression in trait importance is generally consistent with previous

research for other diseases that demonstrates the importance of NPQI as an early indicator of disease (Zarco-Tejada et al., 2018) while structural indices such as LAI have been found to be important for predicting moderate to advanced disease damage (Hornero et al., 2021).

Accurate prediction of disease severity is often more difficult to achieve than two class discrimination of healthy and damaged foliage (Hornero et al., 2021) and few studies have demonstrated the accuracy reported in this study. Using a combination of PT and NBHI allowed prediction of disease severity with very high precision on an independent dataset ($R^2 = 0.85$; RMSE = 4.5 %) that exceeds the accuracy of previous models describing DNB severity. In a comparable study, indices derived from airborne hyperspectral imagery were used to predict three classes of DNB severity in radiata pine with an accuracy of ca. 70% (Coops et al., 2003). Predictions of DNB severity in lodgepole pine that were made using UAV thermal imagery had an RMSE of 11% (Smigaj et al., 2019a). Our results were also more accurate than predictions of tree stress symptoms resulting from other pests or diseases that were characterised using high resolution spectral imagery acquired from either airborne or UAV platforms (Leckie et al., 2004; Lehmann et al., 2015; Näsi et al., 2015; Pietrzykowski et al., 2007; Yu et al., 2021). The accurate predictions made within this study may be partially attributable to the high spatial resolution of the imagery and the clear crown delineation that was possible in young trees with discontinuous canopies which contrasts previous studies undertaken in closed canopy stands (e. g. Coops et al., 2003). However, as shown in the results, a large proportion of these gains resulted from use of radiative transfer modelling and PT estimation by inversion methods, rather than more conventional indices that do not fully account for the influence of canopy heterogeneity on spectra and that are calculated from a limited number of spectral bands.

Thermal data was not collected in this study and further research should investigate if the fusion of thermal and spectral data improves the predictive precision of the developed model. Normalised canopy temperature $(T_c - T_a)$ and derived indices (Maes and Steppe, 2012) have been extensively utilised to characterise spatial variation in stomatal conductance (g_s) and drought stress in orchard crops (Agam et al., 2014; Andrews et al., 1992; Ben-Gal et al., 2009; García-Tejero et al., 2011; Gonzalez-Dugo et al., 2012; Sepulcre-Cantó et al., 2006; Virlet et al., 2014; Wang and Gartung, 2010; Zarco-Tejada et al., 2012) and to a lesser extent forests (Buddenbaum et al., 2015; Ludovisi et al., 2017; Scherrer et al., 2011; Seidel et al., 2016). Thermal data has also been successfully used to characterise disease in mainly agricultural and orchard crops (Calderón et al., 2013; Calderón et al., 2015; López-López et al., 2016; Mengistu et al., 1987; Nilsson, 1995; Nilsson, 1991; Zarco-Tejada et al., 2018) with fewer studies on forest species (Hornero et al., 2021). A study on olive trees showed the increases in canopy temperature that were associated with increased disease severity were

Table A1

Hyperspectral indices	Equation	Reference
Structural indices Normalized Difference Veg. Index	$NDVI = (R_{800} - R_{670})/(R_{800} + R_{670})$	Device et al. (1074)
Renormalized Difference Veg. Index	$RDVI = (R_{800} - R_{670}) / \sqrt{(R_{800} + R_{670})}$	Rouse et al. (1974)
Optimized Soil-Adjusted Veg. Index	$OSAVI = ((1 + 0.16) \cdot (R_{800} - R_{670}) / (R_{800} + R_{670} + 0.16))$	Roujean and Breon (1995)
Modified Soil-Adjusted Vegetation Index	$MSAUT = \frac{2 \cdot R_{800} + 1 - \sqrt{\left(2 \cdot R_{800} + 1\right)^2 - 8(R_{800} - R_{670})}$	Qi et al. (1994)
Triangular Vegetation Index	$TVI = 0.5[120(R_{750} - R_{550}) - 200(R_{670} - R_{550})]$	Progo and Lablana (2001)
Modified Triangular Veg. Index 1	$\textit{MTVI1} = 1.2[1.2(R_{800} - R_{550}) - 2.5(R_{670} - R_{550})]$	Haboudane et al. (2004)
Modified Triangular Veg. Index 2	$MTVI2 = \frac{1.5[1.2(R_{800} - R_{550}) - 2.5(R_{670} - R_{550})]}{(/(2R_{570} + 1)^2 - (6R_{570} - 5/(R_{570}) - 0.5))}$	Haboudane et al. (2004)
Modified Chlorophyll Abs. Index	$MCARI = [(R_{700} - R_{670}) - 0.2(R_{700} - R_{550})] \cdot (R_{700} / R_{670})$	Haboudane et al. (2004)
Modified Chlorophyll Abs. Index 1	$\textit{MCARI1} = 1.2[2.5(R_{800} - R_{670}) - 1.3(R_{800} - R_{550})]$	Haboudane et al. (2004)
Modified Chlorophyll Abs. Index 2	$MCARI2 = \frac{1.5[2.5(R_{800} - R_{670}) - 1.3(R_{800} - R_{550})]}{\sqrt{(2R_{800} + 1)^2 - (6R_{800} - 5\sqrt{R_{670}}) - 0.5}}$	Haboudane et al. (2004)
Simple Ratio	$SR = R_{800}/R_{670}$	Jordan (1969)
Modified Simple Ratio	$MSR = \frac{R_{800}/R_{670} - 1}{R_{670} - 1}$	Chen (1996)
Enhanced Vegetation Index	$\frac{(R_{800}/R_{670})^{0.5} + 1}{EVI} = 2.5 \cdot (R_{800} - R_{670}) / (R_{800} + 6 \cdot R_{670} - 7.5 \cdot R_{800} + 1)$	Liu and Huete (1995)
Pigment indices Vogelmann indices	$VOG1 = R_{740}/R_{720}$	Vogelmann (1993)
	$VOG2 = (R_{734} - R_{747})/(R_{715} + R_{726})$	Vogelmann (1993)
	$VOG3 = (R_{734} - R_{747})/(R_{715} + R_{720})$	Vogelmann (1993)
Gitelson & Merzlyak indices	$GM1 = R_{750}/R_{550}$	Gitelson and Merzlyak (1996)
	$GM2 = R_{750}/R_{700}$	Gitelson and Merzlyak (1996)
Transformed Chlorophyll Absorption in Reflectance Index	$TCARI = 3 \cdot \left[(R_{700} - R_{670}) - 0.2 \cdot (R_{700} - R_{550}) \cdot \left(\frac{R_{700}}{R} \right) \right]$	Haboudane et al. (2002)
TCARI/OSAVI	TCARI	Haboudane et al. (2002)
Chlorophyll Index Red Edge	$\frac{OSAVI}{CI} = R_{750}/R_{710}$	Haboudane et al. (2002)
Simple Ratio Pigment Index	$SRPI = R_{430}/R_{680}$	Penuelas et al. (1995a) Barnes et al. (1992)
Normalized Phaeophytinization Index	$NPQI = (R_{415} - R_{435})/(R_{415} + R_{435})$	Penuelas et al. (1995a) Barnes et al. (1992
Normalized Pigments Index	$\textit{NPCI} = (R_{680} - R_{430}) / (R_{680} + R_{430})$	Penuelas et al. (1995a)
Carter indices	$CTRI1 = R_{695}/R_{420}$	Carter (1994)
	$CAR = R_{695}/R_{760}$	Carter et al. (1996)
Reflectance band ratio indices	$DCabCxc = R_{672}/(R_{550} \cdot 3R_{708})$	Datt (1998)
	$DNIRCabCxc = R_{860}/(R_{550} \cdot R_{708})$	Datt (1998)
Structure-Intensive Pigment Index	$SIPI = (R_{800} - R_{445})/(R_{800} + R_{680})$	Penuelas et al. (1995a)
Carotenoid Reflectance Indices	$CRI_{550} = (1 / R_{510}) - (1 / R_{550})$	Gitelson et al. (2003, 2006)
	$CRI_{700} = (1 / R_{510}) - (1 / R_{700})$	Gitelson et al. (2006)
	$CRI_{550_515} = (1 / R_{515}) - (1 / R_{550})$	Gitelson et al. (2006)
	$CRI_{700_{515}} = (1 / R_{515}) - (1 / R_{700})$	Gitelson et al. (2006)
	$\textit{RNIR} \cdot \textit{CRI}_{550} \ = \ ((1 / R_{510}) - (1 / R_{550})) \cdot \textit{R}_{770}$	Gitelson et al. (2003, 2006)
	$\textit{RNIR} \cdot \textit{CRI}_{700} \ = \ ((1 \ / \textit{R}_{510}) \ - \ (1 \ / \textit{R}_{700})) \cdot \textit{R}_{770}$	Gitelson et al. (2003, 2006)
Plant Senescing Reflectance Index	$PSRI = (R_{680} - R_{500})/R_{750}$	Merzlvak et al. (1999)

P Pigment Specific Simple Ratio Chlorophyll a Pigment Spec. Simple Ratio Chl. b Pigment Specific Simple Ratio Carot. Pigment Specific Normalized Difference

9

 $\textit{PSNDc} = (\textit{R}_{800} - \textit{R}_{470}) / (\textit{R}_{800} + \textit{R}_{470})$

 $PSSRa = R_{800}/R_{675}$

 $PSSRb = R_{800}/R_{650}$

 $PSSRc = R_{800}/R_{500}$

(continued on next page)

Blackburn (1998)

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Table A1 (continued)

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Hyperspectral indices	Equation	Reference
Xanthophyll indices Photochemical Refl. Index (570)	$\textit{PRI}_{\rm 570} = (\textit{R}_{\rm 570} - \textit{R}_{\rm 531}) / (\textit{R}_{\rm 570} + \textit{R}_{\rm 531})$	Gamon et al. (1992)
Photochemical Refl. Index (515)	$PRI_{515} = (R_{515} - R_{531})/(R_{515} + R_{531})$	Horméndez Clemente et al. (2011)
Photochemical Refl. Index (512)	$PRI_{m1} = (R_{512} - R_{531})/(R_{512} + R_{531})$	Hernández-Clemente et al. (2011)
Photochemical Refl. Index (600)	$PRI_{m2} = (R_{600} - R_{531})/(R_{600} + R_{531})$	Gamon et al. (1992)
Photochemical Refl. Index (670)	$PRI_{m3} = (R_{670} - R_{531})/(R_{670} + R_{531})$	Gamon et al. (1992)
Photochemical Refl. Index (670 and 570)	$\textit{PRI}_{\textit{m4}} = (\textit{R}_{570} - \textit{R}_{531} - \textit{R}_{670}) / (\textit{R}_{570} + \textit{R}_{531} + \textit{R}_{670})$	Hernández-Clemente et al. (2011)
Normalized Photoch. Refl. Index	$PRI_n = PRI_{570} / [RDVI \cdot (R_{700} / R_{670})]$	Zarco-Tejada et al. (2013)
Carotenoid/Chlorophyll Ratio Index	$\textit{PRI-CI} = (\textit{R}_{570} - \textit{R}_{530}) / (\textit{R}_{570} + \textit{R}_{530}) \cdot ((\textit{R}_{760} / \textit{R}_{700}) - 1))$	Garrity et al. (2011)
R/G/B indices Redness Index	$R = R_{700}/R_{670}$	Gitelson et al. (2000)
Greenness Index	$G = R_{570}/R_{670}$	
Blue Index	$B = R_{450}/R_{490}$	
Blue/green indices	$BGI1 = R_{400}/R_{550}$	Calderon et al. (2013)
	$BGI2 = R_{AEO}/R_{EEO}$	Zarco-Tejada et al. (2005)
Rlue/red indices	$BR11 - R_{100}/R_{100}$	Zarco-Tejada et al. (2005)
blue, red indices	$BRT = R_{400}/R_{690}$	Zarco-Tejada et al. (2012)
	$BRIZ = R_{450}/R_{690}$	Zarco-Tejada et al. (2012)
BF1	$BF1 = R_{400}/R_{410}$	Zarco-Tejada et al. (2018)
BF2	$BF2 = R_{400}/R_{420}$	Zarco-Tejada et al. (2018)
BF3	$BF3 = R_{400}/R_{430}$	Zarco-Tejada et al. (2018)
BF4	$BF4 = R_{400}/R_{440}$	Zarco-Tejada et al. (2018)
BF5	$BF5 = R_{400}/R_{450}$	Zarco-Tejada et al. (2018)
Red/green indices	$RGI = R_{690}/R_{550}$	Zarco-Tejada et al. (2005)
Ratio Analysis of Reflectance Spectra	$RARS = R_{746}/R_{513}$	Chappelle et al. (1992)
Lichtenthaler Index	$LIC1 = (R_{800} - R_{680}) / (R_{800} + R_{680})]$	Lichtenthaler (1996)
	$LIC2 = R_{440}/R_{690}$	Lichtenthaler (1996)
	$LIC3 = R_{440}/R_{740}$	Lichtenthaler (1996)
Chlorophyll fluorescence Reflectance Curvature Index	$CUR = (R_{675} \cdot R_{690}) / R_{683}^2$	Zarco-Tejada et al. (2000)
Plant disease index Healthy-index	$HI = rac{R_{534} - R_{698}}{R_{534} + R_{698}} - rac{1}{2} \cdot R_{704}$	Mahlein et al. (2013)

related to reductions in g_s (Calderón et al., 2013) demonstrating reductions in crown transpiration from vascular disease are similar to the impacts of water stress. Consistent with these findings, weak to moderate positive correlations have been found between DNB severity in Scots pine and both $T_c - T_a$ and the standard deviation (SD) of $T_c - T_a$ (Smigaj et al., 2019a). A model including both of these terms was very sensitive to the time of data collection, reaching a peak at midday (R^2 range of 0.07 – 0.41). Further research will be required to determine if addition of $T_c - T_a$ improves the results presented here, but even without this variable, the developed model was able to account for 85% of the variation in the data.

The methodology described here could be useful for characterising phenotypic variation in disease severity within genetic trials. Previous research shows that variation in susceptibility to *Dothistroma* spp. exists within and between pine species (Bulman et al., 2016), and this trait has moderate heritability in radiata pine (Ivković et al., 2010; Kennedy et al., 2014). These findings agree with our results that clearly show a considerable range in DNB severity between genotypes. The accurate characterisation of DNB achieved in this study is very promising and suggests that a robust methodology can be developed. Application of this method to field trials could be used to alleviate the phenotyping bottleneck associated with traditional methods and accelerate the breeding process. New Zealand has a large number of field based genetic trials that span the entire environmental range of radiata pine. The phenotyping of these trials using such methods will facilitate rapid identification of DNB resistant genotypes and allow accurate characterisation of Genotype x Environmental interactions (G x E) for this trait.

5. Conclusions

The wide range in tree level DNB severity exhibited within the measured field trial (0-58%) was predicted with moderate precision by random forests using NBHI ($R^2 = 0.52$; RMSE = 9.41%). Addition of five inverted PT to the set of predictive variables considerably improved precision and the final model strongly predicted DNB severity with R^2 of 0.85 and RMSE of 4.5%. Analyses demonstrate interchange in variable importance as DNB severity increased. Variables associated with key photosynthetic traits, chlorophyll content and degradation were most

important for distinguishing asymptomatic trees from those with minor severity. In contrast variables that described extreme reductions in transpiration and foliage loss were most important for characterising more advanced stages of DNB. Further research should investigate whether variables derived from thermal data can improve model precision and provide further insight into how radiata pine responds to infection from *Dothistroma* spp.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

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Appendix 1

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Agricultural and Forest Meteorology 330 (2023) 109294

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