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Predicting the severity of *Cyclaneusma minus* on *Pinus radiata* under current climate in New Zealand

Michael S. Watt, Carol A. Rolando, David J. Palmer, and Lindsay S. Bulman

Abstract: Despite being a damaging foliar disease of *Pinus* species, little research has characterized spatial variation in disease severity of Cyclaneusma needle cast at a macroscale. Using an extensive data set describing Cyclaneusma needle cast (S_{sev}) on plantation-grown *Pinus radiata* D. Don stands distributed widely across New Zealand, the objectives of this research were to (*i*) develop a regression model describing S_{sev}, (*ii*) use this model to identify key drivers of S_{sev} and their functional form and relative importance, and (*iii*) develop spatial predictions of S_{sev} for New Zealand *P. radiata* under current climate. Using an independent validation data set, the final model accounted for 73% of the variance in S_{sev} using four significant ($P < 0.001$) explanatory variables and an isotrophic exponential model to account for the spatial covariance in the data. S_{sev} was most sensitive to elevation followed by mean winter air temperature, mean relative humidity during July, and then stand age. S_{sev} increased to a maximum at mean winter air temperatures of between 7 and 9 °C before declining. Relationships between S_{sev} and all other variables were linear and positive. Spatial predictions of S_{sev} varied widely throughout New Zealand. Values of S_{sev} were highest in moderately warm, wet, and humid high-elevation environments located in the central North Island. In contrast, relatively low values of S_{sev} were predicted in drier eastern and southern regions of New Zealand.

Résumé : Bien que le rouge des aiguilles causé par *Cyclaneusma* soit une maladie de feuilles nuisibles chez les espèces du genre *Pinus*, peu de travaux de recherche ont caractérisé la variation spatiale de la sévérité de cette maladie à grande échelle. À l'aide d'un large ensemble de données sur la sévérité de la maladie ($S_{\text{sév}}$) dans les plantations de *Pinus radiata* D. Don établies un peu partout en Nouvelle-Zélande, les objectifs de cette recherche consistaient à (*i*) élaborer un modèle de régression qui décrit $S_{\text{sév}}$, (*ii*) utiliser ce modèle pour identifier les facteurs clés qui sont responsables de $S_{\text{sév}}$ et leur forme fonctionnelle et leur importance relative et (*iii*) établir des prédictions de $S_{\text{sév}}$ sur une base spatiale pour *P. radiata* dans les conditions climatiques actuelles en Nouvelle-Zélande. À l'aide d'un jeu de données de validation indépendant, le modèle final expliquait 73 % de la variation de $S_{\text{sév}}$ en utilisant quatre variables explicatives significatives ($P < 0,001$) et un modèle exponentiel isotrope pour tenir compte de la covariance spatiale dans les données. $S_{\text{sév}}$ était surtout sensible à l'altitude, suivie par la température moyenne de l'air en hiver, l'humidité relative moyenne en juillet et l'âge du peuplement. $S_{\text{sév}}$ augmentait jusqu'à un maximum lorsque la température moyenne de l'air en hiver se situait entre 7 et 9 °C puis diminuait. La relation entre $S_{\text{sév}}$ et toutes les autres variables était linéaire et positive. Les prédictions de $S_{\text{sév}}$ dans l'espace variaient fortement à travers la Nouvelle-Zélande. Les valeurs de $S_{\text{sév}}$ étaient les plus élevées dans les milieux modérément chauds, pluvieux et humides en altitude dans le centre de l'île du Nord. Par contre, les valeurs de $S_{\text{sév}}$ prédites pour les régions plus sèches dans l'est et le sud de la Nouvelle-Zélande étaient relativement plus faibles.

[Traduit par la Rédaction]

Introduction

Cyclaneusma needle cast caused by the pathogens *Cyclaneusma minus* (Butin) DiCosmo, Peredo & Minter and *Cyclaneusma niveum* (Pers.) DiCosmo, Peredo & Minter has been reported as a serious disease of many *Pinus* species (Millar and Minter 1980) and is present on all continents where *Pinus* species are grown. The disease is characterized by yellow and brown mottling of needles that are prematurely cast (Stahl 1966; Gadgil 1984).

Significant economic losses have been associated with outbreaks of this disease in pine forests worldwide, especially where the disease is associated with exotic pine monocultures (Merrill et al. 1980; Bulman 1988; Choi and Simpson 1991). Premature needle cast caused by *C. minus* occurs widely in *Pinus radiata* D. Don plantations throughout New Zealand. Severe needle cast has been recorded there since 1952 (Bulman and Gadgil 2001). *Pinus radiata* accounts for 90% of the plantation resource in New Zealand (New Zealand Forest Owners' Association 2010), and in 2009, the total financial

Received 5 July 2011. Accepted 21 January 2012. Published at www.nrcresearchpress.com/cjfr on 14 March 2012.

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Can. J. For. Res. 42: 667–674 (2012) doi:10.1139/X2012-021 Published by NRC Research Press

loss attributable to Cyclaneusma needle cast over the *P. radiata* estate aged between 6 and 20 years was estimated at \$38 million per annum (L. Bulman, unpublished data). van der Pas et al. (1984*b*) estimated that the reduction of revenue at clearfelling of *P. radiata* stands increased by approximately \$600–\$700·ha^{-1} for each 10% increase in the proportion of diseased trees.

Cyclaneusma minus is an colonist of *P. radiata* needles (Gadgil 1984) and of other pine species (Rack and Scheidemann 1987). The infective propagules of *C. minus* are airborne ascospores that are discharged from apothecia on dead needles lying on the forest floor (Gadgil 1984). Time of development of disease symptoms and subsequent pattern and period of casting of needles are strongly influenced by environmental factors and host and vary considerably between regions worldwide (Merrill et al. 1980; Choi and Simpson 1991). In New Zealand, the main period of ascospore release is in autumn and winter and infection occurs from May to June. Although spores are produced over the entire year on needles lying on the forest floor, new *P. radiata* foliage is resistant to infection for the first 6 months. In New Zealand, *Cyclaneusma* therefore first infects healthy current needles around April to June and continues into winter if temperatures are mild. Once infected, most of the infected needles turn yellow and are cast in the following spring, but some remain green and are not cast. These needles turn yellow during a second and usually less severe period of needle cast in autumn 1 year after first becoming infected and also carry a higher number of apothecia than those shed in spring. Severity of Cyclaneusma needle cast in New Zealand has been related to weather during the infection period, with mild wet winters associated with high severity (Gilmour 1966). In autumn and winter, when needles are susceptible to infection and inoculum levels are high, wet periods of about 5 h duration and temperatures above 10 °C would provide good conditions for infection (Gadgil 1984).

Given the high impact of Cyclaneusma needle cast on plantation forests in New Zealand, and worldwide, development of a model of disease severity would be of considerable use to both managers and researchers. Such a model may provide insight into the relative importance of the key drivers of disease severity and highlight the combination of environmental conditions associated with outbreaks of the disease. Use of GIS surfaces describing driving variables for the model would allow predictions of disease risk to be spatially projected. Using such maps, managers could identify areas at risk from large growth losses that would provide an objective basis for mitigation strategies to reduce risk from this disease. Most studies indicate that factors likely to be associated with *Cyclaneusma* infection in New Zealand include autumn to winter rainfall and temperature and altitude and stand characteristics, such as stand age and density (Podger and Wardlaw 1990; van Maanen et al. 2000; Bulman and Gadgil 2001). Aerial surveys of forests throughout New Zealand during the 1980s indicated that severity was highest in 11- to 20-year-old stands and lowest in 1- to 5-year-old stands and stands over 25 years (Bulman 1988). However, research could not significantly relate severity to weather over the infection period of autumn and winter and found only weak positive relationships between severity, elevation, and autumn rainfall for the data from one region (Bulman 2009).

Application of geostatistical techniques that account for spatial correlation may provide a means of strengthening models for diseases such as Cyclaneusma needle cast where strong environmental relations have not been found. Geostatistical techniques such as kriging have been widely used to predict spatial variation in plant disease most often at plot or field scales (Lecoustre et al. 1989; Stein et al. 1994; Jaime-Garcia et al. 2001). Most studies have utilized ordinary kriging, which uses estimates of spatial covariance between measurements to predict disease severity at unvisited locations. Hybrid geostatistical procedures that account for environmental correlation have become increasingly popular in recent years (McBratney et al. 2000). Regression kriging (or universal kriging, kriging with external drift) is one of the most widely used hybrid techniques and combines ordinary kriging with regression using ancillary information. If the correlation between the dependent (disease severity in this case) and predictor variables is significant, regression kriging generally results in more accurate local predictions than generic geostatistical models such as ordinary kriging (Odeh and McBratney 2000; Hengl et al. 2004). Although regression kriging has not yet been used to model disease severity at national scales, this method is likely to gain popularity in the future, as the availability of ancillary data with large spatial coverage is rapidly increasing (Pebesma 2006).

Using an extensive data set describing severity of Cyclaneusma needle cast on *P. radiata* across New Zealand, the objectives of this research were to (*i*) develop a regression model describing disease severity of Cyclaneusma needle cast in New Zealand, (*ii*) use this model to identify key drivers of severity and their functional form and relative importance, (*iii*) investigate if regression kriging can substantially improve on predictions of severity obtained from regression modelling, and (*iv*) develop spatial predictions of disease severity across New Zealand under current climate.

Materials and methods

Severity data set

Data from ground surveys of disease severity carried out between 1972 and 2006 and aerial surveys between 2005 and 2006 were included in the analyses. In total, there were 9855 records included in the database of disease from plantations across New Zealand. For each record, the fraction of the stand affected by the disease (S_{inc}) (scale 0 to 1) and the severity of the infection (A_{sev}) (scale 0 to 1) were estimated. The product of these measurements ($S_{\mathrm{inc}} \times A_{\mathrm{sev}}$) was used to determine the severity of Cyclaneusma needle cast for each record (S_{sev}) (scale 0 to 1). For each observation, location (latitude, longitude) was recorded as well as the age of the stand on which the estimate was being made. Previous research shows that data from ground and aerial surveys are comparable (van der Pas et al. 1984*a*). Only measurements taken at a time of the year coinciding with peak disease expression (early spring with secondary expression in autumn) were used in the analysis.

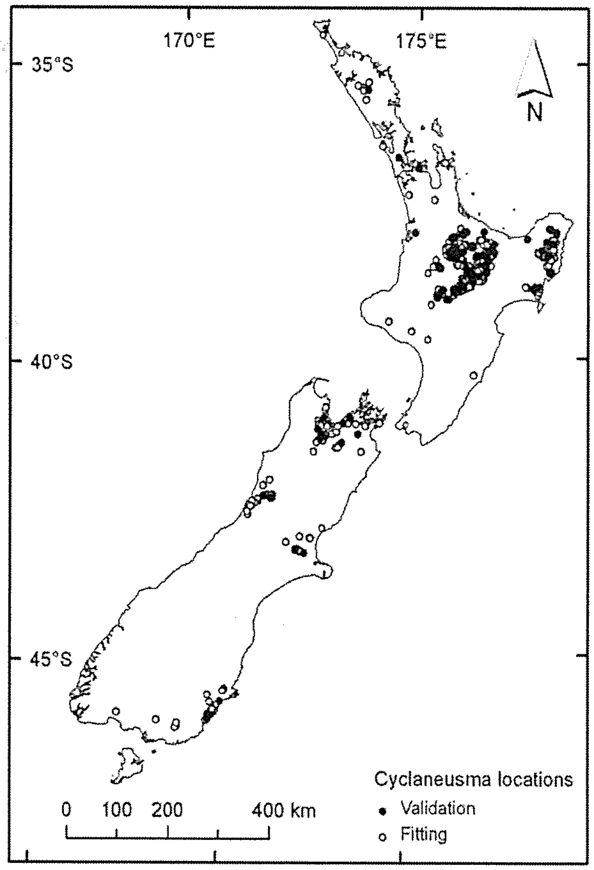
To spatially consolidate the data, the 9855 records were averaged to a 5 km^2 resolution. This averaging was undertaken so that measurements of S_{sev} included a number of temporally dispersed observations representative of the long-term average meteorological data used to model disease se-

Table 1. Climatic conditions, stand age, and disease severity for the sampled sites.

	Fitting data set (n = 309)		Validation data set (n = 78)	
Variable	Mean	Range	Mean	Range
General site variables				
Total rain (mm·year^{-1})	1669	690–3510	1730	754–3174
Mean air temperature (°C)	11.3	7.6–15.8	11.3	8.9–14.2
Mean 9 a.m. relative humidity (%)	82.6	74.0–89.0	82.7	75.9–88.6
Variables in final model				
Mean winter air temperature (°C)	6.6	3.4–12.6	6.6	4.3–10.4
Elevation (m)	403.2	43–832	71–822	403.6
Mean 9 a.m. relative humidity, July (%)	88.1	77.0–93.4	88.0	80.9–93.4
Age (years)	15.5	7–29.4	15.4	7.3–24.6
Disease				
Stand severity (%)	8.8	0.1–35.8	8.8	0.1–25.8

Note: Values shown are the mean and range for the fitting and validation data sets. All data have been averaged to a 5 km^2 resolution.

Fig. 1. Map of New Zealand showing the location of the *Cyclaneusma* severity data used for the fitting (open circles) and validation (solid circles) of the model.



verity. After undertaking this averaging, a total of 387 estimates of S_{sev} were available for the modelling. These data covered a wide environmental range (Table 1) and were located within almost all areas in which the current *P. radiata* plantation resource occurs (Fig. 1).

Predictive variables used in the modelling

From the coordinates of each of the disease measurements, data were extracted from biophysical GIS surfaces that included primary and secondary terrain attributes (Palmer 2008), fundamental soil layers, land resource information (Newsome et al. 2000), and biophysical surfaces (Leathwick et al. 2003) for New Zealand. Mean monthly meteorological data from National Institute of Water and Atmospheric Research Ltd. were used in this study. Data were estimated for the whole of New Zealand on a 500 m^2 grid using a thin-plate smoothing spline to spatially interpolate the data. This surface was derived from data collected over a 30-year period from 1971 to 2000 (mean time of 1985). Meteorological data comprised mean monthly and annual values for windspeed, solar radiation, total rainfall, relative humidity, and mean, minimum, and maximum air temperature. Physiographic data included measurements of site wetness, elevation, aspect, rooting depth, soil physical properties, site nutrition, and soil water availability.

Regression kriging model

Regression kriging enables characterization of the pattern of spatial variability observed in the data such that spatial dependence can be predicted with greater precision at unobserved locations (Littell et al. 2006). The observations of disease severity were denoted as $z(s_1)$, $z(s_2)$, ..., $z(s_n)$, where $s_i = (x_i, y_i)$ is a location, x_i and y_i are the coordinates, and n is the number of observations. Regression kriging was used to predict disease severity at a new unvisited location (s_0) by summing the predicted drift and residuals as

$$[1] \quad z(s_0) = m(s_0) + e(s_0)$$

where m represents the trend model and e the residuals. Expanding eq. 1 yields

$$[2] \quad z(s_0) = \sum_{k=0}^{p} B_k q_k(s_0) + \sum_{i=1}^{n} w_i(s_0) e(s_i)$$

where B_k are the estimated regression model coefficients, q_k (s_0) is the kth external explanatory variable or predictor at location s_0, p is the number of predictors, $w_i(s_0)$ are weights

Table 2. Summary of statistics for the regression model of Cyclaneusma needle cast severity.

Parameter	Value	Variable	Significance
β_0	–0.7306	Intercept	
β_1	0.08144	Mean winter air temperature (T_{win}) (°C)	30.9***
β_2	–0.00481	T_{win}^2	24.2***
β_3	1.60×10^{-4}	Elevation (m)	42.8***
β_4	4.259×10^{-3}	Mean relative humidity, 9 a.m., July (%)	9.1***
β_5	3.326×10^{-3}	Stand age (years)	30.5***

Note: All statistics relate to the log-transformed dependent variable (i.e., tS_{sev}), which represents a natural log transformation of S_{sev} determined as $tS_{\mathrm{sev}} = \ln(tS_{\mathrm{sev}} + 1)$. For the significance category, the F values from an F-test are shown with asterisks representing significance at $P < 0.001$.

determined by the covariance function, and $e(s_i)$ are the regression residuals.

The covariance function uses a semivariogram, which is a standard statistical measure of spatial variability as a function of the distance between two observations (Littell et al. 2006). Key features of the semivariogram are the nugget, the sill, and the range. The nugget, or intercept, is the semivariogram between two observations where distance (h) = 0, the sill corresponds to the value of the semivariogram for observations not spatially correlated, and the range is the distance at which the semivariogram reaches the sill. For distances less than the range, observations are spatially correlated.

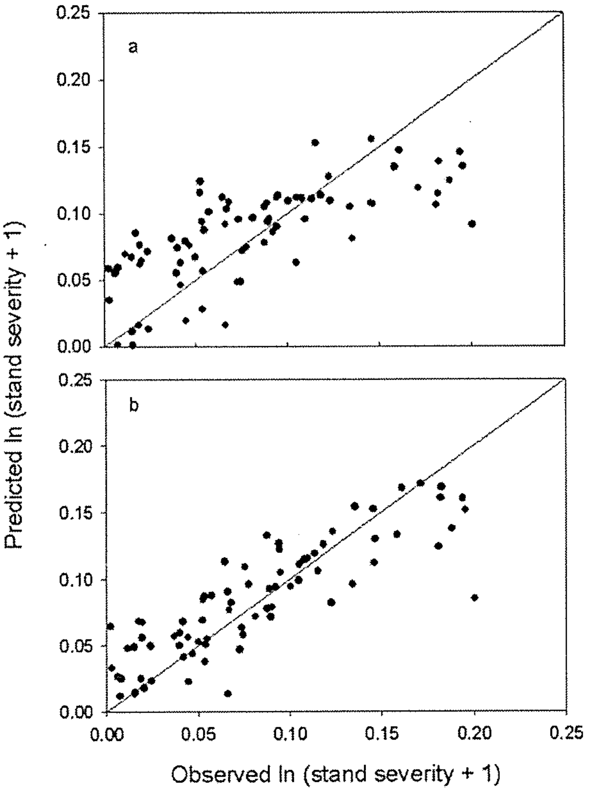
Data analysis

All analyses were undertaken using SAS (SAS Institute Inc. 2000). Current climate normals and stand age at the time of sampling were spatially intersected with S_{sev} measurements at the base resolution of the climatic surfaces and these data were then averaged to a 5 km^2 resolution for analyses. Of the 387 observations available for modelling, 20% (78) were randomly selected and withheld from the model fitting for later validation. Transformed values, tS_{sev}, were determined from S_{sev} using a natural log transformation ($tS_{\mathrm{sev}} = \ln(S_{\mathrm{sev}} + 1)$) that corrected the nonnormal distribution.

Using observations within the fitting data set, a linear mixed-effects model was used to develop a multiple regression model of tS_{sev} from environmental data. A full description of the mixed-effects model methodology with accompanying matrix notation is given in Littell et al. (2006). Briefly, linear mixed-effects models can be used to undertake regression analysis using data with spatially correlated error structures. Variables were introduced sequentially into the model starting with the variable that exhibited the strongest correlation until further additions were not significant or the mechanistic basis for influencing disease severity was not sound. Variable selection was undertaken manually, one variable at a time, and plots of residuals were examined prior to variable addition to ensure that the variable was included in the model using the least biased functional form.

Spatial covariance of residuals from the final regression model were modelled using a range of isotropic spatial covariance structures (spherical, exponential, power, Gaussian, linear, log linear), fully described in Littell et al. (2006). Comparisons among the model structures were undertaken using the –2 res log likelihood, with lower values indicating a superior fit to the data. These analyses showed that the isotrophic spherical model most accurately represented the spatial covariance in the data (–2 res log likelihood = –1070.1).

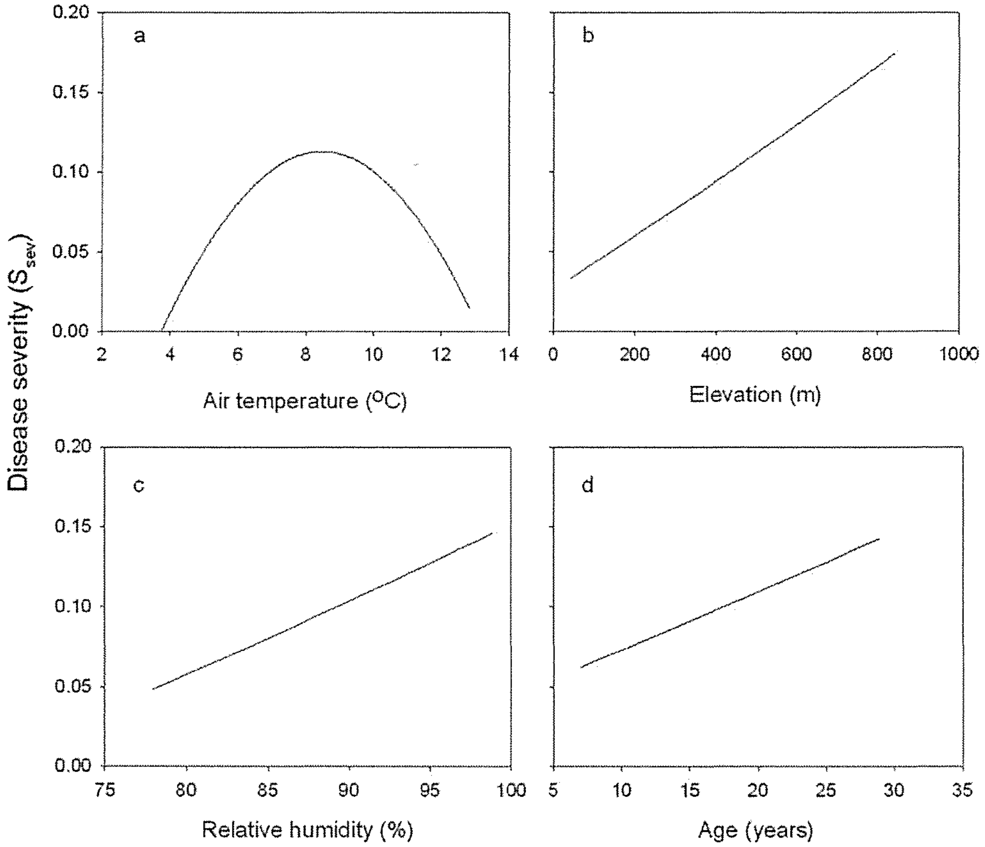
Fig. 2. Relationship between measured stand severity, S_{sev}, and predictions from the validation data sets using (*a*) regression modelling and (*b*) regression kriging. Presented values of stand severity have been transformed using a natural log ($\ln(S_{\mathrm{sev}} + 1)$) to provide consistency with analyses. The line represents the 1:1 line.



Using the isotrophic spherical model, the significance of accounting for spatial covariance was tested by the log likelihood ratio test of spatial covariance as fully described in Littell et al. (2006). The log likelihood ratio statistic between models with independent errors and spatial covariance was 88.3 (i.e., –981.8 + 1070.1). Comparison of this statistic to the χ^2 distribution with 2 degrees of freedom indicated that spatial covariance was highly significant ($P < 0.001$).

The fitted model was applied to the validation data set to assess model precision and bias. The influence of including spatial covariance on precision in predicting tS_{sev} was determined by comparing observations of tS_{sev} against predictions from two fitted models using regression model formulations

Fig. 3. Partial response curves of *Cyclaneusma* severity, S_{sev}, plotted against (*a*) mean winter air temperature, (*b*) elevation, (*c*) relative humidity in winter, and (*d*) stand age. For each partial response curve, all other variables were held at mean values when the response curve was generated.



that included (*i*) fixed effects and no spatial covariance between errors and (*ii*) both fixed effects and spatial covariance, as described by the isotrophic exponential model. Model precision was determined using the coefficient of determination (R^2).

Partial response functions and least squares means for ancillary variables

The effects of environmental variables on S_{sev} were examined through partial response functions generated by the final model. Partial response functions were generated for each continuous variable by holding other continuous variables at mean values in the fitting data set.

Model projections

Using the final model, spatial predictions of S_{sev} were made throughout New Zealand. For these predictions, the stand age was held at a constant value of 16 years, which was the mean value in the fitting data set.

Results

Final model

The regression model of tS_{sev} included mean winter air temperature (T_{win}), relative humidity (RH_{win}) in winter (July), elevation (E), and stand age (A) (Table 2). The regression model was described by the function

$$[3] \quad tS_{sev} = \beta_0 + \beta_1 T_{win} + \beta_2 T_{win}^2 + \beta_3 E + \beta_4 RH_{win} + \beta_5 A$$

Estimated covariance parameters for the partial sill, range, and nugget were 0.0014, 29 km, and 6.7×10^{-4}, respectively. The sill, which represents the sum of the partial sill and nugget, was 0.002. The effective range, the distance at which the spatial autocorrelation in the data set declined to less than 0.05, was determined as 3 × range = 87 km. For distances greater than or equal to the range (87 km), spatial correlation between observations was effectively zero.

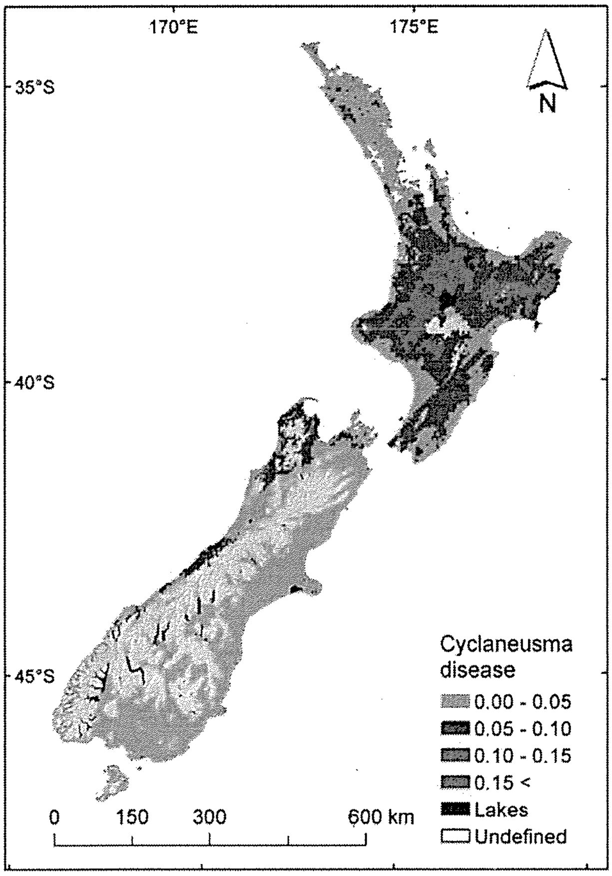
Model validation

Predictions from the regression model, without spatial covariance, accounted for 51.7% of the variance in tS_{sev} in the validation data set. The model overpredicted severity at low values of tS_{sev} and underpredicted severity at high values of tS_{sev} (Fig. 2*a*). Accounting for spatial correlation within the model reduced the bias and improved the coefficient of determination by over 20%, with the final model accounting for 72.8% of the variance in the validation data (Fig. 2*b*). Although bias was markedly improved in this final model, there was still some overprediction at low disease levels and underprediction at high disease levels (Fig. 2*b*).

Regression model partial responses

Using the final model, partial response surfaces were gen-

Fig. 4. Map of New Zealand showing spatial variation in *Cyclaneusma* severity, S_{sev}, predicted by the final model based on regression kriging.



erated to characterize the functional form of all independent variables. The effect of air temperature on disease severity was best explained by a quadratic function. Disease severity increased to a maximum at sites with an mean winter air temperature of 8.4 °C before declining at higher air temperatures (Fig. 3*a*). The effects of relative humidity, elevation, and age on severity were all fitted as positive linear functions (Figs. 3*b*, 3*c*, and 3*d*). Across the range represented within the data, disease showed the greatest sensitivity to elevation (Fig. 3*b*).

Model projections

Spatial projections of disease severity, developed using the kriged model, clearly highlighted the effect of the selected environmental variables on S_{sev} (Fig. 4). Severity was predicted to be highest around the central North Island region, with some extension to the east coast. Isolated areas of high severity were also predicted in Northland and in the Nelson region (upper west coast of the South Island). High severity in these regions is associated with higher elevations and relative humidity. Reductions in S_{sev} occurred on the east coast of the South Island where S_{sev} is likely to be limited by low relative humidity, elevation, and air temperature. Reductions in disease severity in the north of the North Island are attributable to air temperatures that exceed the optimum.

Discussion

The models and maps presented here highlight the sensitivity of Cyclaneusma needle cast to environment. The final regression model showed elevation to be the variable with the most influence. Air temperature and relative humidity were of intermediate importance, while age had somewhat lesser influence on disease severity. Regression kriging substantially improved the predictive power of the regression model, demonstrating the utility of characterizing spatial dependence when modelling disease severity. Characterization of this spatial variation is likely to be particularly important for diseases such as Cyclaneusma needle cast that only exhibit a moderate degree of correlation with environment. The good agreement between predicted and observed measurements from the validation data set show this model to be relatively robust.

Considerable research has demonstrated a moderate influence of environment on development of *Cyclaneusma* over a number of important stages in the lifecycle. In general, the incidence and severity of infection by *Cyclaneusma* have been found to depend on a combination of factors including age, temperature, and elevation. Results from this study broadly agree with these previously identified environmental drivers. Previously developed maps denoting district-level variation in severity (Bulman and Gadgil 2001) also show good general agreement with our finer scale estimates of disease severity. Our results extend this previous research by expanding the scope of the model from the regional to the national level and refining the resolution of prediction (from district to 5 km^2). Accounting for the spatial correlation evident between observations also markedly improves predictive precision over previous models of Cyclaneusma needle cast (Bulman and Gadgil 2001).

Inclusion of relative humidity and elevation in the final model is likely to describe the sensitivity of the disease to leaf wetness at the time of sporulation. *Cyclaneusma* requires moisture for ascospore release to occur. Pawsey (1967) found that peak spore concentrations occurred within 2–3 h of the onset of rain and Gadgil (1984) found that maximum spore release occurred in the fifth hour after rainfall started. Higher values of relative humidity, found with mist and low cloud associated with higher elevation, may act as a surrogate for rainfall by maintaining hydration of apothecia, allowing maximum spore release to occur. Bulman (2001) showed that in four experiments in different forests, average disease was more severe in plots established at higher altitudes compared with plots in the same experiment sited 200–350 m lower. Thus, the importance of elevation in the model can be explained because of the high relative humidity on high-elevation sites where mist and low cloud are common.

The results presented here highlight the utility of regression kriging as a method for improving spatial estimates of disease severity. Use of this method resulted in substantial gains in model precision. Spatial association between measurements within the data set extended for a reasonable distance and an effective range of 87 km was fitted by the model. Although the objective of this research was not to compare geostatistical methods, it is worth noting that regression kriging more precisely estimated S_{sev} than ordinary kriging (R^2 for validation data set = 0.72 versus 0.52). This is consistent with previous research that shows that the accuracy of regression kriging often surpasses that of ordinary kriging when there are significant relationships between the dependent variable and predictor variables (Odeh and McBratney 2000; Hengl et al. 2004).

Selected stands included those both treated and untreated with copper fungicide to control Dothistroma needle blight. Such treatment would have no effect on incidence or severity of Cyclaneusma needle cast. Six aerial applications of copper 1 month apart starting in April did not reduce disease levels (Vanner 1986). Copper is applied to control Dothistroma needle blight in spring and late summer, which does not coincide with the infection period of *Cyclaneusma*.

Data were averaged to a 5 km^2 resolution in this study to enable environmental determinants of stand severity to be identified. At a finer scale of 1 km^2, relationships between environment and stand severity were evident but not as strong as at the coarser scale used here. Averaging to the coarser scale was undertaken to mitigate against the subjective nature of the disease scoring system, as the mean value included many observations from different observers.

In conclusion, the model developed in this paper accounted for a substantial proportion of the variation in severity of Cyclaneusma needle cast within New Zealand. Partial response functions developed from this model show disease severity to be most sensitive to elevation followed by mean winter air temperature, mean relative humidity during July, and then stand age. Given the moderate sensitivity of disease severity to air temperature, further research should investigate how climate change influences the spatial distribution of severity throughout New Zealand.

Acknowledgements

We thank the Ministry of Agriculture and Forestry (contract No. C04X0901) for funding this research. The data were collected during forest health surveys funded from 1970 to 1987 by the New Zealand Forest Service and thereafter primarily by members of the New Zealand Forest Owners' Association.

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Fedoroff *Agric & Food Secur (2015) 4:11*
DOI 10.1186/s40066-015-0031-7

Agriculture & Food Security

REVIEW

Open Access

Food in a future of 10 billion

Nina V Fedoroff*

Abstract

Over the past two centuries, the human population has grown sevenfold and the experts anticipate the addition of 2–3 billion more during the twenty-first century. In the present overview, I take a historical glance at how humans supported such extraordinary population growth first through the invention of agriculture and more recently through the rapid deployment of scientific and technological advances in agriculture. I then identify future challenges posed by continued population growth and climate warming on a finite planet. I end by discussing both how we can meet such challenges and what stands in the way.

Keywords: Population growth, Agriculture, Domestication, Genetic modification, Technology

Background

Today we have enough food to meet the world's needs. Indeed, we have an extraordinary global food system that brings food from all over the planet to consumers who can afford to buy it. The food price spike of 2008 and the resurgence of high food prices in recent years have had little impact on the affluent citizens of the developed world who spend a small fraction of their income on food. By contrast, food prices have a profound impact on the world's poorest people. Many of them spend half or more of their income on food. During the food price crisis of 2008, there were food riots in more than 30 countries. Unrest in the Middle East and North Africa tracks with the price of food, as is dramatically illustrated in Fig. 1. Spiraling food prices drive the world's poorest into chronic hunger even in a world of relative plenty.

Does this mean we need worry only about poverty, not about the global food supply, as suggested in a recent editorial by the influential New York Times food commentator Mark Bittman [2]? Analyses of the most recent United Nations projections indicate that the human population will expand from roughly 7.2 billion today to 9.6 billion in 2050 and 10.9 billion by 2100 [3, 4]. Current yield growth trends are simply insufficient to keep up with growing demand [5]. As well, the rapid expansion of agriculture over the past century to feed today's population has had a devastating impact on biodiversity [6]. As a result, there is an acute need to intensify agricultural productivity, while at the same time decreasing the deleterious impact of agriculture on biodiversity and the services provided by complex ecosystems [7].

Historical perspective

For most of our evolutionary history, our numbers were small and we were mobile hunter-gatherers. We spent our time finding and capturing enough food to feed ourselves and our closest kin. Then sometime between 10 and 20,000 years ago—maybe even more—that started to change. We began to shape plants and animals to our own advantage and settled down to grow and herd them [8]. The process by which we have modified plants and animals to suit our needs, traditionally called "domestication," is a process of genetic modification [9]. Early peoples selected variant organisms—plants, animals, and microbes—with useful traits, such as seeds that adhere to plants until they are harvested and animals tame enough to herd. Domestication is a process of modification that is possible because of the genetic variation constantly arising in all living organisms.

While hunter-gatherers were quite sophisticated in their resource management, it was systematic planting and harvesting of crops that marks the origin of what we now call "agriculture" [10]. Agriculture allowed people to produce more food than they consumed; cities and civilization followed. Thus human civilization

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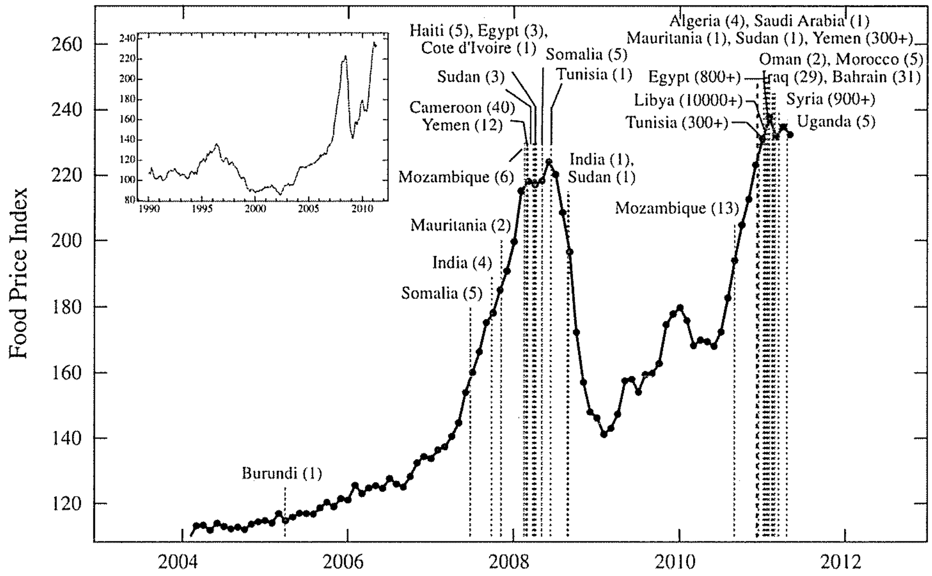

Fig. 1 Food price spikes are correlated with increases in food riots. *Red dashed vertical lines* correspond to beginning dates of "food riots" and protests associated with the major recent unrest in North Africa and the Middle East. The overall death toll is reported in *parentheses*. The *blue vertical line* indicates the date on which the authors of the cited report [1] submitted a report to the U.S. government warning of the link between food prices, social unrest, and political instability. The *inset* shows the FAO Food Price Index from 1990 to 2011. (The figure is reproduced with permission from [1]).

emerged because we figured out how to produce surplus food. We could feed artisans and scribes and warriors and kings. For the next 10 millennia, people built cities and civilizations, wore out the land, invaded their neighbors or abandoned the cities and civilizations, eventually rebuilding on fresh land [11]. It was often the fertility of the land that determined how long a civilization lasted. Plants extract nutrients from the soil and crop yields decline, making it harder and harder to produce enough food as the number of people grows [8].

Concern about access to sufficient food, today called "food security," is as old as mankind. Thomas Malthus' famous Essay on Population, published in 1798, crystallized the problem of balancing food and human population for the modern era [12]. Malthus believed that humanity was doomed to food insecurity because our numbers increased exponentially, while our ability to produce food could only increase linearly.

Curiously, Malthus penned his essay at about the time that science began to play a major role in boosting agricultural productivity. Late eighteenth century milestones were Joseph Priestley's discovery that plants emit oxygen and Nicholas-Théodore de Saussure's definition of the chemical composition of plants [13, 14]. Malthus could not have envisioned the extraordinary increases in productivity that the integration of science and technology into agricultural practice would stimulate over the ensuing two centuries.

Both organic- and mineral fertilization of plants have been practiced since ancient times. Farmers knew that certain chemicals and biological materials, ranging from fish and oyster shells to manure and bones, stimulated plant growth [15, 16]. Justus von Liebig made important contributions to the study of plant nutrient requirements, understanding that biological sources of nitrogen could be replaced with purely chemical sources. But supplying nitrogen in the forms that plants use remained a major limitation until the development of the Haber–Bosch process for fixing atmospheric nitrogen early in the twentieth century [17]. Today, agriculture in the developed world relies primarily on chemical fertilizers. Indeed, the global human population could not have grown from roughly 1 billion at the turn of the nineteenth century to today's 7.2 billion without synthetic nitrogen fertilizer.

Crop domestication

Humans practiced genetic modification long before chemistry entered agriculture, transforming inedible wild plants into crop plants, wild animals into domestic animals, and harnessing microbes to produce everything from cheese to wine and beer. Oddly, it is only our contemporary methods of bending organisms' genetic constitution to suit our needs that are today recognized as genetic modification, known in common parlance by the abbreviations "GM" (genetically modified), "GMO" (genetically modified organism) or "GE" (genetically engineered). Yet all of the useful, heritable traits nurtured by people in organisms constitute "domestication" and all are the result of genetic modifications. Each microbe, crop and animal has its own interesting history. To take just one example, a fundamental trait that distinguishes wild from domesticated plants is the retention of mature seeds on the plant. Plants have many mechanisms for dispersing their seeds, but it is much easier for people to harvest seeds that remain attached to the plant at maturity. Hence one of the earliest steps in grain crop domestication was the identification of mutations—genetic changes—that prevent seed dispersal [18].

Corn, also known as maize, remains one of our most spectacular feats of genetic modification. Its huge ears, packed with starch and oil, provide one of humanity's most important sources of food and feed. Corn bears little resemblance to its closest wild relative, teosinte. Indeed, when teosinte was first discovered in 1896, it was assigned to a different species [19]. By the 1920s, it was known that teosinte and corn readily produce fertile hybrids, but controversies about their relationship and about the origin of corn continued throughout most of the twentieth century. The key genetic changes that transformed teosinte into corn appear to have happened in the Balsas River Valley in Mexico some 9000 years ago [20]. The mutations that converted teosinte, a grass with hard, inedible seeds, into modern corn altered just a handful of genes that control plant architecture and the identity of reproductive organs. Remarkably, once these mutations had been brought together in an early corn plant, they stayed together and spread very rapidly, moving from Mexico into the American southwest by 3000 years ago [20].

Among the many other traits altered during domestication of plants are the size and shape of leaves, tubers, berries, fruits and grains, as well as their abundance, toxicity, and nutritional value. The changes are often in genes coding for proteins that regulate the expression of many other genes [9]. Differences in nutrient composition among varieties of the same crop are caused by mutations in genes coding for proteins in a number of different biosynthetic pathways. Thus, for example, sweet corn has mutations that prevent the conversion of sugar to starch in the kernel [21].

Modern crop improvement

The genetic revolutions of the twentieth century boosted crop productivity immeasurably. Austrian monk Gregor Mendel's pioneering observations on inheritance were published in 1865, but did not get wide attention until a half-century later [22]. A simple demonstration project to illustrate Mendelian inheritance led to the re-discovery of hybrid vigor, a long-known phenomenon whose incorporation into crop breeding resulted in a dramatic expansion of the corn ear and, thereby, crop yield [23].

However, when corn hybrids were first introduced in the U.S. during the 1930s, they faced resistance and criticism similar to that leveled at contemporary GM crops. The hybrids were complex to produce and agriculture experiment stations were not interested. Eventually a company was formed to produce hybrid seed. But farmers accustomed to planting seed from last year's crop saw no reason to buy it. It was only when farmers realized the yield benefits and the drought-resistance of hybrid corn during the 1934–1936 dust-bowl years that farmers began to adopt hybrid corn rapidly [24].

Techniques for accelerating mutation rates with radiation and chemicals and through tissue culture were developed and widely applied in the genetic improvement of crops during the twentieth century [25]. These methods introduce mutations rather indiscriminately and require the growth of large numbers of seeds, cuttings or regenerants to detect desirable changes. Nonetheless, all of these approaches have proved valuable in crop improvement and by the end of the twentieth century, more than 2300 different crop varieties, ranging from wheat to grapefruit, had been developed using radiation and chemical mutagenesis [25].

Mechanization of agriculture

A major development with impact Malthus could not have envisioned is the mechanization of agriculture. Human and animal labor provided the motive force for agriculture throughout most of its history and continues to do so in many less-developed countries. The invention of the internal combustion engine at the turn of the twentieth century led to the development of small, maneuverable tractors. The mechanization of plowing, seed planting, cultivation, fertilizer and pesticide distribution, and harvesting accelerated in the US, Europe, and Asia following World War II [26]. Agricultural mechanization drove major demographic changes virtually everywhere. In the U.S., 21 % of the workforce was employed in agriculture in 1900 [27]. By 1945, the fraction had declined to 16 % and by the end of the century the fraction of the population employed in agriculture had fallen to 1.9 %. At the same time, the average size of farms increased and farms increasingly specialized in fewer crops. This profound demographic shift from agrarian to urban underlies the development of today's attitudes about food and farming in developed countries. Today the vast majority of the developed world's population is urban and far removed from primary food production.

The Green Revolution

Malthus penned his essay when the human population of the world stood at less than a billion. The population tripled over the next century and a half. As the second half of the twentieth century began, there were neo-Malthusian predictions of mass famines in developing countries that had not yet experienced science- and technology-based advances in agriculture. Perhaps the best known of the mid-century catastrophists was Paul Ehrlich, author of The Population Bomb [28].

Remarkably, the extraordinary work of just a handful of scientists and their teams, principally plant breeders Norman Borlaug and Gurdev Khush, averted the widely predicted Asian famines [29]. The Green Revolution was based on the development of dwarf rice and wheat varieties that responded to fertilizer application without falling over (lodging). Subsequent breeding for increased yield continued to improve the productivity of these crops by as much as 1 % per year. Perhaps most remarkably, the Green Revolution and other technological advances reduced the fraction of the world's hungry from half to less than a sixth, even as the population doubled from 3 to 6 billion. These accomplishments earned Borlaug a well-deserved Nobel Prize. Curiously, the Green Revolution is often vilified today.

Genetic modification of crops

The equally revolutionary molecular genetic advances that began in the 1960s led to the development of new methods of crop improvement. The basic methodology lies in the construction of hybrid DNA molecules designated "recombinant DNA (R-DNA)" because they consist of a piece of bacterial or viral DNA combined with a piece of DNA from a different kind of organism, plant or animal [30]. The ability to multiply such hybrid DNA molecules in bacteria made it possible to develop the DNA sequencing techniques that underlie today's genomic revolution.

As well, techniques were developed to introduce genes into plants using either the soil bacterium *Agrobacterium tumefaciens*, which naturally transfers a segment of DNA into a plant cell, or mechanical penetration of plant cells using tiny DNA-coated particles [31]. This combination of methods and knowledge made it possible to transfer a well-understood segment of genetic material from either the same or a related plant or from a completely unrelated organism into virtually any crop plant, creating what is known as a "transgenic" plant. Because genes work the same way in all organisms, this made it possible to introduce a desirable trait, such as disease- or pest-resistance, without the extensive genetic and epigenetic disturbance attending what we now consider to be the "conventional" crop improvement techniques such as hybridization and mutagenesis [32–34]. Indeed, recent comparisons have revealed plant modification by molecular techniques has less impact on gene expression, protein, and metabolite levels than do conventional genetic crosses [35–37].

Several crop modifications achieved using these methods are now in widespread use. Perhaps the best known of these are crop plants containing a gene from the soil bacterium, *Bacillus thuringiensis*, long used as a biological pesticide. The gene encodes a protein that is toxic to the larvae of certain kinds of insects, but not to animals or humans [38]. Such a toxin gene is often called the "Bt gene," but is actually a family of related toxin genes from a group of closely related bacteria and these are increasingly used in combinations to decrease the probability of resistance developing in the target insects, an approach that has been dubbed gene "stacking."

Herbicide tolerance is another widely accepted GM crop modification. Among the most common herbicides in use today are compounds that interfere with the production of certain amino acids that plants synthesize, but animals do not [39]. Such herbicides, therefore, kill plants, but have low or no toxicity for animals or humans. Herbicide-tolerant crops make it possible to control weeds without damaging the crop and without tilling the soil. Such crops have been derived through natural mutations and induced mutations, as well as by introduction of genes from either bacterial sources or plant sources. Today, herbicide-tolerant varieties of many crops, most importantly soybeans and canola, are widely grown [40].

Papayas resistant to papaya ringspot virus (PRSV) saved the Hawaiian papaya industry and are the only such GM crop to emerge from public sector GM research. Papaya ringspot virus is a devastating insect-borne viral disease that wiped out the papaya industry on the Hawaiian island of Oahu in the 1950s, forcing its relocation to the Puna district of the big island. PRSV was first detected in the Puna district in 1992; by 1994 it was widespread and threatening the industry. A project initiated in 1987 introduced a gene from the PRSV into papayas based on reports that introducing a viral gene could make a plant resistant to the virus from which the gene came [41, 42]. Transgenic seeds were released in 1998; by 2000, the papaya industry was returning to pre-1995 levels. This remarkable achievement of disease resistance enhanced a virus protection mechanism already present in the plant, much as vaccination protects people and animals from infection by pathogens [43].

New methods are rapidly being developed that promise to further increase the specificity and precision of genetic modification. These techniques capitalize on growing knowledge of the dynamic processes underlying genome maintenance, particularly the repair of breaks in the genetic material, DNA. Known under the general rubric of "site-directed nuclease (SDN)" technology, this approach uses proteins (or protein-nucleic acid complexes) that seek out, bind to, and cut specific DNA sequences, introducing breaks in the DNA at one or a small set of sequences targeted for modification [44]. Repair of such DNA cuts by natural cellular processes results in precisely targeted genetic changes rather than the random ones introduced by older methods of mutagenesis. This method can also be used to introduce a gene at a pre-identified site in the genome or to modify a resident gene precisely, something that could not be done with pinpoint specificity and precision by R-DNA methods. As well, such genetic changes can often be made without creating a transgenic plant. The changes are the same at the molecular level as those that occur in nature or can be induced by older mutagenic techniques. What is new is that the genetic changes introduced by SDN techniques are not random, but confined precisely to the gene or genes selected by the breeder.

Adoption of GM crops

GM crops have been adopted at unprecedented rates since their commercial introduction in 1996. In 2014, GM crops were grown in 28 countries on 181.5 million hectares [45]. More importantly, more than 90 % of the 18 million farmers growing biotech crops today are smallholder, resource-poor farmers. The simple reasons that farmers migrate to GM crops are that their yields increase and their costs decrease. A recent meta-analysis of 147 crop studies conducted over a period of 20 years concluded that the use of GM crops had reduced pesticide use by 37 %, increased crop yields by 22 %, and increase farmers' profits by 68 % [46]. The vast majority of GM hectarage is devoted to the growing of GM corn, soybeans, cotton, and canola with either Bt toxin-based pest resistance or herbicide tolerance traits. The reasons for the narrow GM crop and trait base to date lie in a combination of the economic, regulatory, and legal issues, discussed below.

While some resistance to the Bt toxin has developed, it has not been as rapid as initially feared and second-generation, two-Bt gene strategies to decrease the probability of resistance are already being implemented [47]. Predicted deleterious effects on non-target organisms, such as monarch butterflies and soil microorganisms have either not been detected at all or are insignificant [48]. The better cropping practices supported by GM crops have decreased the availability of the milkweed on which monarch larvae feed [49]; hence efforts are being directed to the establishment of milkweed preserves (http://monarchjointventure.org/get-involved/create-habitat-for-monarchs/). The development of herbicide tolerance in previously susceptible weeds, while not unique to GM crops, is becoming an increasing problem because of the widespread use of glyphosate with glyphosate-tolerant GM crops [50]. Although the pace of herbicide discovery has slowed markedly since the 1980s, new combinations of herbicide-tolerant crops and older herbicides are likely to come on the market in the near future [51].

The overwhelming evidence is that the GM foods now on the market are as safe, or safer, than non-GM foods [37, 52]. Moreover, there is no evidence that the use of GM techniques to modify organisms is associated with unique hazards. The European Union alone has invested more than €300 million in GMO biosafety research. Quoting from its recent report, "The main conclusion to be drawn from the efforts of more than 130 research projects, covering a period of more than 25 years of research and involving more than 500 independent research groups, is that biotechnology, and in particular GMOs, are not per se more risky than, e.g. conventional plant breeding technologies." (http://ec.europa.eu/research/biosociety/pdf/a_decade_of_eu-funded_gmo_research.pdf). Every credible scientific body that has examined the evidence has come to the same conclusion (http://gmopundit.blogspot.com/p/450-published-safety-assessments.html).

Despite occasional one-of-a-kind, often sensationalized reports, the vast majority of feeding studies have identified no meaningful nutritional differences between GM and non-GM food and feed. Indeed, and perhaps unsurprisingly, comparative molecular analyses show that GM techniques have less impact on the genetic and molecular constitution of crop plants than conventional plant breeding techniques [37]. This is because conventional breeding mixes whole genomes comprising tens of thousands of genes that have previously existed in isolation, while GM methods generally add just a gene or two to an otherwise compatible genome. Thus the probability of introducing unexpected genetic or epigenetic changes is much smaller by GM methods than by conventional breeding methods.

Crops modified by GM techniques are also less likely to have unexpected genetic effects than crops modified by the more conventional techniques of chemical and radiation mutagenesis methods simply because of the greater precision and predictability of molecular modification. Taken together with the closer scrutiny paid during product development to the potential for toxicity and allergenicity of novel proteins expressed by GM methods, GM crops are arguably the safest new crops ever introduced into the human and animal food chains.

Indeed, to date, the only unexpected effects of GM crops have been beneficial. Many grains and nuts, including corn, are commonly contaminated by mycotoxins, which are toxic and carcinogenic compounds made by fungi that follow boring insects into the plants. Bt corn, however, shows as much as a 90 % reduction in mycotoxin levels because the fungi that follow the boring insects into the plants cannot get into the Bt plants [53]. There is also evidence that planting Bt crops reduces insect pressure in non-GM crops growing nearby. The widespread adoption of Bt corn in the U.S. Midwest has resulted in an area-wide suppression of the European corn borer [54].

Future challenges in agriculture

Since Malthus' time, the human population has expanded more than sixfold. Through science and technology, agriculture in developed nations has become far less labor-intensive and has kept pace with population growth worldwide. Today, fewer than 1 in 50 citizens of developed countries grows crops or raises animals for food. But after a half-century's progress in decreasing the fraction of humanity experiencing chronic hunger, the food price and financial crises commencing in 2008 have begun to swell the ranks of the hungry once more [1, 55]. Population experts anticipate the addition of another 2–4 billion people to the planet's population within the next 3–4 decades [4, 56, 57], but the amount of arable land has not changed appreciably in more than half a century [58]. Moreover, arable land continues to be lost to urbanization, salinization, and desertification.

Supplies of fresh water for agriculture are under pressure, as well. Today, about a third of the global population lives in arid and semi-arid areas, which cover roughly 40 % of the land area. Climate scientists predict that in coming decades, average temperatures will increase and dryland area will expand. Inhabitants of arid and semi-arid regions of all continents are extracting ground water faster than aquifers can recharge and often from fossil aquifers that do not recharge [59]. Yet the major crops that now feed the world—corn, wheat, rice, soy—require a substantial amount of water. It takes 500–2,000 L of water to produce a kilogram of wheat and the amount of water required to produce a kilogram of animal protein is 2–10 times greater [60].

Increasing average temperatures and decreasing fresh water availability present critical challenges to agricultural researchers to increase crop performance under suboptimal conditions. Rapid advances in our knowledge of plant stress responses and improving molecular knowledge and tools for plant breeding have already resulted in the introduction of new drought-tolerant crop varieties, both GM and non-GM [61]. New varieties of drought-tolerant maize produced using modern breeding approaches that employ molecular markers, but do not generate transgenic plants, have been released in the North American market by Syngenta and DuPont Pioneer, while Monsanto and BASF have jointly developed MON87460 (aka Genuity DroughtGard Hybrids), a drought-tolerant maize variety expressing a cold-shock protein from the bacterium *Bacillus subtilis*, introducing it in the U.S in 2013 (http://www.monsanto.com/products/pages/droughtgard-hybrids.aspx).

However, it should be kept in mind that suboptimal "stress" conditions necessarily move plants away from their peak ability to use sunlight to convert carbon dioxide, water, and other simple compounds into the carbohydrates and proteins that feed people and animals. Stress-tolerant varieties do not generally outperform less stress-tolerant varieties by much or at all under optimal conditions, but simply survive better under suboptimal conditions, losing less of their yield potential.

More with less

Why do we need to do more with less? The FAO has estimated that we will need to increase the amount of food produced by 70 % by 2050 [62]. We will need more food, feed, and fiber both because there will be more people and because they will be richer. Among the things that people demand as they become more affluent is more meat in their diet. Producing more meat requires growing more grain. But increasing the grain supply by expanding the land under cultivation cannot be sustained. All the best land is already under cultivation and preserving what remains of our planet's rich biological heritage by leaving more land unplowed is a growing priority. Indeed, modeling exercises reveal that within just a few decades, the planet's natural resources will be insufficient to support developed-world consumption patterns [63].

As well, the negative impact of climate change on agriculture is becoming increasingly apparent and is predicted to worsen [64, 65]. While more agriculturally suitable land may become available at greater distances from the equator as the climate warms, there is no guarantee that the productivity of these lands will compensate for productivity losses in the more populous equatorial regions. Whether our current highly productive food and feed crops can be modified and adapted to be substantially more productive at the higher temperatures expected or at more northern latitudes with shorter growing seasons is not yet known. Substantial research will be required not just on the salt, drought, and temperature tolerance of existing crop plants, but also for the domestication of plants that are not now used in agriculture, but that are capable of growing at higher temperatures and on saline water.

In today's highly productive developed-world agriculture, fertilizers and other chemicals are applied and used inefficiently, themselves becoming pollutants in our air, land, and water. As well, some of the chemicals used in both conventional and organic agriculture to control pests and diseases are toxic to people and to wildlife. Transitioning to more sustainable agricultural practices while doubling the food and feed supply, even as we must increasingly cope with the negative effects on agricultural productivity of a warming climate, is likely to be the greatest challenge of the twenty-first century [66, 67].

Impediments to sustainable intensification of agriculture

To live sustainably within planetary constraints, we must grow more on the same amount of land using less water, energy, and chemicals. The molecular genetic revolution of the late twentieth century that powered the development of precise GM methods is the most critical technology for meeting these challenges. Paradoxically, although the use of GM technology has been accepted in medicine, it has evoked an almost unprecedented level of societal controversy in the realm of food production, resulting in the proliferation of regulatory and legal constraints that threaten to cripple their use in achieving a more sustainable existence for humanity on planet Earth.

While productivity gains based on earlier scientific advances can still increase food production in many countries, particularly in Africa, such productivity gains appear to have peaked in most developed countries and recent productivity gains have been achieved largely through adoption of GM crops [68]. The knowledge and GM technology are available to address these challenges throughout the world, but there are political, cultural, and economic barriers to their widespread use in crop improvement. As noted earlier, there is a global consensus among scientific societies that GM technology is safe. However, the political systems of Japan and most European and African countries remain opposed to growing GM crops. Many countries lack GM regulatory systems or have regulations that prohibit growing and, in some countries, importing GM food and feed.

Even in countries such as the U.S. that have a GM regulatory framework [69], the process is complex, slow, and expensive. U.S. developers must often obtain the approval of three different agencies, the Environmental Protection Agency, the U.S. Department of Agriculture (USDA), and the Food and Drug Administration, to introduce a new GM crop into the food supply. Bringing a GM crop to market, including complying with the regulatory requirements, was estimated to cost $135 million in 2011 [70]. The effort, time, and cost for regulatory approval have dramatically contracted the pipeline of GM innovations that would directly benefit consumers [71].

In Europe, the regulatory framework is practically non-functional; only one GM crop is currently being grown and only two others have gained approval since 1990 when the EU first adopted a regulatory system [72]. The EU recently agreed to allow member countries decide individually whether to permit cultivation of an EU-approved GM crop (http://ec.europa.eu/food/plant/gmo/legislation/future_rules_en.htm). The impact of this decision will not be known for some time, but it is likely to further complicate trade and food aid as crops approved in one country await regulatory approval in others [73]. Moreover, the increasing politicization of risk assessment makes it unlikely that uniform global safety standards for GM crops and animals will emerge in the foreseeable future [74]. European influence has been especially detrimental in Africa, causing African leaders to be excessively precautionary in approving GM crops and even to ban the import of GM grain to alleviate famine [75].

However, it is the case of Golden Rice, genetically modified to produce the vitamin A precursor β-carotene, that provides the paradigmatic example of an opportunity foregone to use GM technology to address a major global malnutrition issue [76]. Severe vitamin A deficiency results in blindness, and half of the roughly half-million children who are blinded by it annually die within a year. Vitamin A deficiency also compromises immune system function, exacerbating many kinds of illnesses. It is a disease of poverty and poor diet, responsible for 1.9–2.8 million preventable deaths annually, mostly of children aged less than 5 years and women [77, 78].

Two scientists, Ingo Potrykus and Peter Beyer, and their teams developed a rice variety whose grains accumulate β-carotene, which our bodies convert to vitamin A. Collaborating with the International Rice Research Institute over a period of a quarter century, they developed and tested a transgenic rice variety that expresses sufficient quantities of β-carotene so that a few ounces of cooked rice can provide enough to eliminate the morbidity and mortality of vitamin A deficiency [79]. Yet, Golden Rice remains mired in controversy and has been tied up in the regulatory process for more than a decade [80]. Millions suffer and die while Golden Rice remains in test plots.

The increasing politicization of risk determination raises questions about the underlying motivations [74]. NGOs, most vocally Greenpeace and Friends of the Earth, appear to have conducted vigorous campaigns of misinformation about GMOs first in Europe, then around the world [81–85]. Greenpeace remains adamantly against even the most benign and beneficial uses of GM technology in agriculture, such as the development and distribution of Golden Rice. Given the weight of scientific evidence to the contrary, it is difficult to avoid the conjecture that its continued opposition to a harmless and beneficial technology has more to do with preserving its funding base than benefitting humanity [84, 85].

Perhaps the most counterproductive development is the increasing vilification of GM foods as a marketing tool by the organic food industry [86]. The organic food industry finds it roots in rural India, where Sir Albert Howard, arguably the father of "organic" agriculture, developed composting methods capable of killing the pathogens that abound in animal manures and human wastes so that these could be used safely as fertilizers in agriculture [30]. Even as synthetic fertilizers were increasingly being used around the world, the organic movement grew in the UK and Europe, eventually finding an American champion in Jerome Rodale, founder of the Rodale Press, and pesticide crusader Rachel Carson, author of *Silent Spring*, the book that has been credited with starting the environmental movement [87].

With the establishment of organic retailers, such as Whole Foods and Wild Oats, the organic food business grew rapidly and certification organizations proliferated. To bring some uniformity to what was being certified as "organic," Congress established the National Organic Standards Board (NOSB) under the USDA through the Organic Food Production Act and charged it with developing national standards [30]. These were eventually published in 2000 and are generally referred to as the Organic Rule. According to the NOSB, organic agriculture is a production system that makes minimal use of off-farm inputs and seeks to enhance "ecological harmony." The Organic Rule expressly forbids the use of GM crops, antibiotics, and synthetic nitrogen fertilizers in crop production and animal husbandry, as well as food additives and ionizing radiation in food processing.

Organic food is food produced in compliance with the Organic Rule; the USDA's Organic Seal is a marketing tool that makes no claims about food safety or nutritional quality. But a number of organic food industry marketers have systematically used false and misleading claims about the health benefits and relative safety of organic foods compared with what are now called "conventionally grown" foods [86]. Indeed, such organic marketers represent conventionally grown foods as swimming in pesticide residues, GM foods as dangerous, and the biotechnology companies that produce GM seeds as evil, while portraying organically grown foods as both safer and more healthful. Recent "labeling" campaigns have the objective of promoting the organic food industry by conveying the message to consumers that food containing GM ingredients is dangerous [86].

The future

In 1798, Thomas Malthus told us that humanity was doomed to famine and strife because population growth would always outstrip our ability to produce food [12]. The human population of the Earth then numbered about a billion. The ensuing two centuries have seen a more than sevenfold expansion of the human population as a result of rapid scientific and technical developments in agriculture and a decline in the number of chronically hungry from half of humanity to about a sixth. But as Nobel Laureate Norm Borlaug, Father of the Green Revolution, observed in his Nobel Prize lecture (http://www.nobelprize.org/nobel_prizes/peace/laureates/1970/borlaug-acceptance.html), "We may be at high tide now, but ebb tide could soon set in if we become complacent and relax our efforts." Said another way, agriculture must ever race to maintain today's status quo.

And yet agriculture is now threatened in a sense by its very success. The demographic shift of population from rural to urban areas has been particularly dramatic in the developed world, with less than 2 % of the population supplying the food for the rest today. But the very fact that we are largely urban dwellers and have access to food through a global food system that supplies our food retailers with abundant produce blinds us to the basics of agriculture and makes us vulnerable to the increasingly strident opponents of modern agriculture who use fear to promote their economic interests.

Will we have the wisdom to overcome our fear of new technologies and re-invest in the kind of agricultural research and development that can simultaneously increase agricultural productivity and decrease its environmental impact, so that we might preserve what remains of our extraordinary biological heritage? Can we continue to keep food prices down through agricultural innovation based on modern genetic methods and better farm management? Or will poverty-based social instability continue to spread and consume governments as population continues to climb while climate warming squeezes agriculture?

The answers to these questions will, for better or worse, shape our future civilizations.

Abbreviations

DNA: deoxyribonucleic acid; EU: European Union; FAO: the U. N. Food and Agriculture Organization; GE: genetically engineered; GM: genetically modified; GMO: genetically modified organism; NGO: non-governmental organization; NOSB: National Organic Standards Board; PRSV: papaya ringspot virus; R-DNA: recombinant DNA; SDN: site-directed nuclease; UK: United Kingdom; USDA: U.S. Department of Agriculture.

Compliance with ethical guidelines

Competing interests

The author declares that she has no competing interests.

Received: 26 March 2015 Accepted: 31 July 2015

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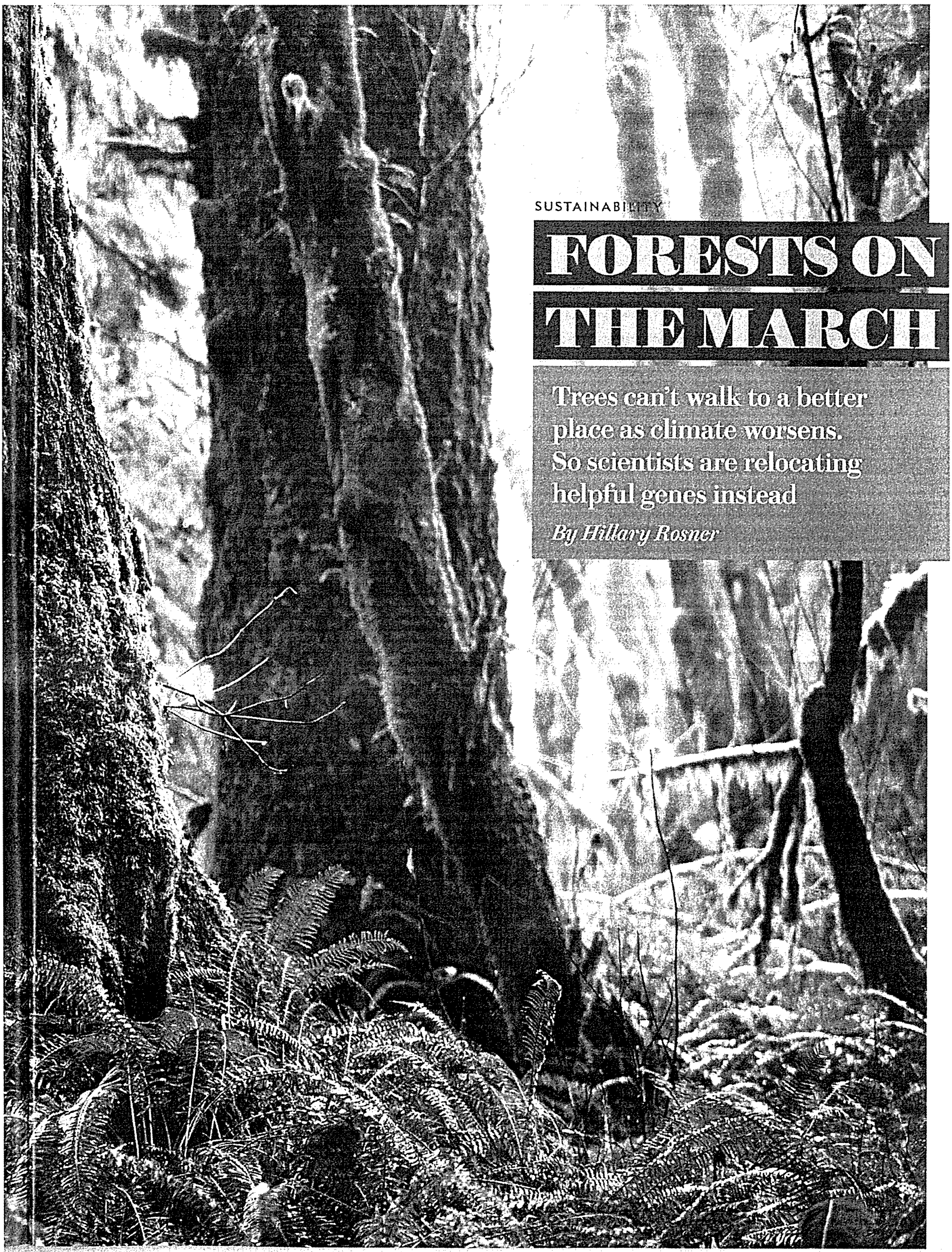


SUSTAINABILITY

FORESTS ON THE MARCH

Trees can't walk to a better place as climate worsens. So scientists are relocating helpful genes instead

By Hillary Rosner

Hillary Rosner is a freelance writer based in Colorado. She has written for *National Geographic*, the *New York Times* and *Wired*, among other publications.

IN A FIELD IN VANCOUVER, ACROSS THE ROAD FROM A ROW OF TIDY WHITE TOWNHOMES, roughly 500 bushy Sitka spruce trees climbed toward the sun. On a spring day in 2013 the trees, triangle-shaped with tightly packed, deep-green needles, were crammed shoulder to shoulder—or, in some cases, shoulder to waist. Although the spruces were all planted at the same time, seven years earlier, their height varied like primary school children assembled for a group photograph.

The smallest trees, around two feet tall, hailed from Kodiak Island, Alaska; the tallest, at nearly seven feet, originated in Oregon. Height was not the only visible difference. The spruces from Alaska produced buds a full three months earlier—an entire season—than those from Oregon. The Alaska trees also stayed green and healthy no matter how low the temperature dropped.

The spruces had been rooted in this field, at one end of the University of British Columbia's rambling campus, as an experiment to highlight how trees adapt to local environments. That trees match their habitats may sound obvious. But the details are important because of a looming threat: those habitats are changing as the planet warms—and trees can't exactly get up and walk to a new home. If a species cannot keep pace with a changing climate, it is doomed.

Because the trees themselves cannot relocate, scientists are exploring a novel solution: relocating the plants' DNA. That is why Sally N. Aitken planted the spruce garden. Aitken, director of the university's Center for Forest Conservation Genetics, believes saving the forests of British Columbia—and others around the world—may hinge on a practice called assisted gene flow. It could help species adapt to future conditions by moving organisms with particular traits from one part of their natural range to another. The tree from Oregon and the tree from Alaska just might have some genes that could help each other out. But without intervention, they would never meet.

Like an arboreal matchmaker, a forester could take seeds from spruces or lodgepole pines at a low elevation, say, and plant them farther upslope. As temperatures on the higher slopes warmed, the relocated trees would grow up and breed with their local counterparts, spreading their warm-adapted genes throughout the area and thus helping the forest adjust. Assisted gene flow could give species an evolutionary hand.

But you can't simply take a tree from Oregon, plant it 1,000 miles away in northern British Columbia and wait for the mercury to rise. The reasons that you can't come from the same local genetic adaptations that make the gene-flow idea attractive. Lodgepole pines, for instance, grow in different regions throughout much of the Canadian province. Their genes help some trees better tolerate heat or cold or drought or fend off local diseases or pests. If an Arctic cold front moves through Vancouver, hitting transplants from warmer regions, they will suffer. "We need to shift these things starting with baby steps," Aitken says. "The changes projected over the next few decades are really big, but we still have a lot of year-to-year and week-to-week and month-to-month variation that those trees have to survive."

Figuring out how to match today's seeds with tomorrow's climates is no easy task. But in British Columbia, where forestry accounts for a third of all exports and commercial forests make up nearly half of the total forest cover, it is vital. Provincial law requires that forests be replanted after logging, to bolster future timber supplies and healthy ecosystems. Roughly 250 million seedlings are planted annually. Just where those seeds should come from and how far they can or should be moved is a complicated—and pressing—question. Do it wrong, and you could be dooming the forests for decades to come.

The Sitka spruce experiment, which involved trees from 14 different locations ranging from central California up to Alaska, was Aitken's small proof of concept for a larger effort to avoid this type of fatal misstep. The research yielded 35 segments of DNA associated with cold tolerance and bud timing.

IN BRIEF

Forests adapt genetically to survive in local conditions, but climate is changing faster than trees can adjust.

To prevent forest death, scientists are moving trees with genes tied to water use and heat tolerance near other trees that need this DNA so they can breed.

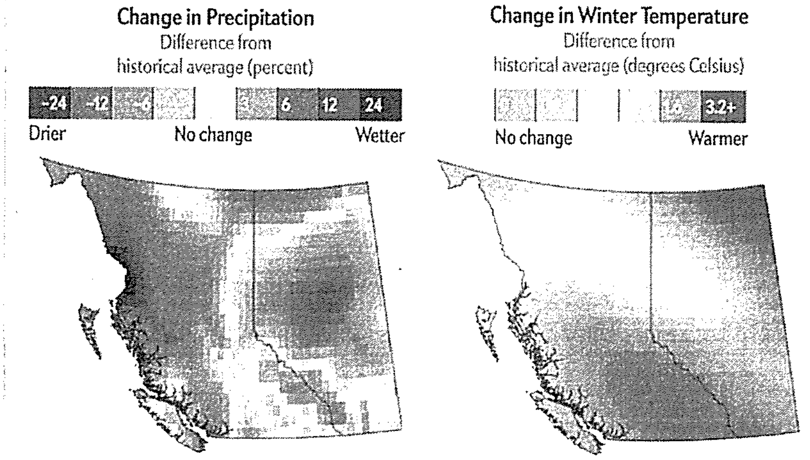
Assisted gene flow, as the strategy is called, is being tested on trees from different climate zones in British Columbia.

PRECEDING PAGES: TJ WATT

FOREST ECOLOGY

Weather Trends for Trees

Scientists compared the past with the present to figure out recent climate trends in British Columbia and Alberta and whether they depart from what trees experienced during the latter half of the 20th century. Researchers gathered direct observations from weather stations throughout the provinces between 1961 and 1990. The scientists compared this baseline with averages from a more recent period, 1997 through 2006. For the recent period, they noted whether the averages were wetter, drier or warmer or did not change from the earlier averages. They learned that the climate has become much wetter along the Pacific coast, which the researchers link to outbreaks of a previously rare pine needle blight. At the same time, it has become drier in the interior, which may account for spruce and aspen deaths there. Winters have been warmer all over the provinces, allowing the tree-killing mountain pine beetle to spread to more forests. (Methods for this analysis were published in the journal *Agricultural and Forest Meteorology* in 2009.)



Now Aitken and her team are sifting through more tree genomes to find genes responsible for proteins that are linked to other environmental traits. Their hope is that beneficial versions of these genes—called alleles—would spread through populations that need the traits, in rough synchrony with the climate changes that make those genes useful.

The larger project, called AdapTree, could help pave the way for future assisted gene-flow projects around the world, work that could in turn help other species that are key ecosystem architects. Corals in the sea, for instance, harbor food and provide shelter for all kinds of other species. Researchers in the U.S., Abu Dhabi, Qatar and Australia have suggested moving corals from the Persian Gulf to the Indo-Pacific to help spread genes for heat tolerance. And in the American Midwest, efforts to restore grasslands have shown that it is important that replanted seeds come from a broad range of habitats.

Aitken and Michael C. Whitlock, a population geneticist in the university's zoology department, coined the phrase "assisted gene flow" in a 2013 paper. Over the past decade scientists and conservationists have been arguing over a more grandiose idea, "assisted migration," which generally refers to moving species greater distances, outside their natural ranges. But assisted gene flow within a species' range is a more measured approach with genetic rigor at its heart. By the time AdapTree wraps up in several years, researchers will have assembled DNA sequence information for 12,000 lodgepole pine and spruce trees from more than 250 populations across British Columbia and Alberta.

CLIMATE ZONES

THOSE TREES are already feeling the effects of a changing climate. Back in the 1970s, British Columbia's government produced a climatic map of the province, organizing it into a series of biogeoclimate zones. That map has underpinned forest planning in western Canada for four decades, helping to govern which seeds can be planted where. Today, though, thanks to climate change, nearly a quarter of the map is obsolete. Some zones have moved, and others have dwindled dramatically. High-elevation zones and some interior plateaus have already lost around half their habitat—and could shrink by more than 80 percent by 2100. Seeds of trees that once would have thrived in a particular area might today be unable to even grow there. Zones may morph into ecosystems that are fundamentally different from what existed before, although exactly how much change is required before an ecosystem is "fundamentally different" is unclear and controversial.

Whether a particular population can adapt to change depends in part on how quickly the organism reproduces. Each new generation represents a chance to acquire useful new traits. So a pine beetle, which reproduces quickly, has a much better chance of adapting than a tree, which is long-lived and slow to reproduce. A single bug may witness no change at all during its life span. A tree, though, has a front-row seat to global warming.

A stand of forest is most at risk during its first 20 years of life. Once the trees are established, they become far more resilient, "able to stick around for a while," says Brad St. Clair, a research geneticist at the U.S. Forest Service in Corvallis, Ore. But in the era of global warming, local conditions can change considerably over those two crucial decades.

"If you're going to move things to higher elevations so they'd be adapted to future climates," St. Clair says, "then they have to be adapted to cold-hardiness now." In other words, if you move warm-adapted trees now into a zone that is projected to warm in the future, those trees could be in short-term trouble because the zone is still cold today.

"We've got a moving target," Aitken admits. "Do we want to best match trees with climate when they're seedlings? Or 10 years old? Or 30 years old?" One way to manage risk is to increase diversity—which might mean mixing local and nonlocal seeds.

Maps by Andreas Hamann

"You don't want to do the same thing on every hectare of ground. You can't plan around a single climate change scenario."

Assisted gene flow may be a good way to bulk up a forest's genetic diversity, sprinkling its gene pool with the ingredients that give trees a boost. As the environment shifts, some trees may suffer in the short term, but other trees will have genetic material that could help the forest weather tough times. "As those individuals that are more fit reproduce more," Aitken says, "we expect populations to start expanding again." The critical element, she says, is maintaining enough healthy trees to mate and survive while the process of adaptation unfolds.

Aitken, an avid backpacker and backcountry skier who owns a cabin in the woods of central British Columbia, hopes her work will help set new, smarter forest policy. She believes that if we do not begin practicing assisted gene flow, tree populations may begin to fail at the far northern or southern edges of species' ranges. "Trees might persist a long time, but they might stop reproducing," she says. "They'd be evolutionarily toast." They would become, she adds, a "land of the living dead." What's worse, they would hog space and sunlight that seedlings desperately need. Closer to the middle of a range, things would be a bit less dramatic. But trees might still grow more slowly or have trouble surviving. "Does that mean the populations there are just going to die?" Aitken asks. "Probably not. There's a lot of variation within populations. The species aren't going to go extinct, but I imagine you'd have pretty unhealthy-looking forests in the meantime." The poor health would harm other plants and animals because trees anchor entire ecosystems, providing food and shelter, regulating water flow and preventing soil erosion.

Around the world, Aitken says, "there has been very little attention paid to the movement of individuals within existing species ranges." The ecological risks are lower than transplanting truly foreign trees because such foreigners are not already part of the ecosystem, even though they may possess some desirable traits.


1
2

SEEDS OF CHANGE: The AdapTree experiment gathers seeds from different habitats (*1*). Pine seedlings grown in the project's greenhouse (*2*) show variation in shape (*3*). Some needles are tested with a probe (*black rod*) to see whether they can resist freezing temperatures (*4*).

COURTESY OF JACK WOODS *AdapTree project, University of British Columbia* (seeds); COURTESY OF CONNOR FITZPATRICK *AdapTree project, University of British Columbia* (greenhouse)

There are still risks to a gene-flow approach. It could, for instance, add local gene variants that would actually harm a larger population's chance for survival. "There is a risk that you could be introducing unwanted alleles," says Andrew Weeks, a geneticist at the University of Melbourne. But the problem would likely correct itself, he adds. "That's the beauty of natural selection, which will weed out these variants. By increasing the gene pool, you are giving the population the best chance for the future."

With British Columbia's forests worth $10 billion a year—as well as providing vital services such as preventing floods and soil erosion—doing nothing may pose an even greater risk. British Columbia has already seen what global warming can do to forests. Since the mid-1990s beetle invasions and wildfires, both linked to warming temperatures, have destroyed millions of acres of forest and consumed hundreds of homes. "We've had lots of wake-up calls here in terms of climate change," says Greg O'Neill, a research scientist at British Columbia's Ministry of Forests, Lands and Natural Resource Operations. The insects and fires, O'Neill says, left people in the province "quite cognizant of climate change—and not that it's some abstract thing in the future, but it's already happening."

The losses jolted the provincial government into action. In 2009 British Columbia began revising its rules on moving seed. That same year O'Neill began an assisted migration trial for the province's forests, hoping to determine whether, where and how foresters might plant completely different species after harvesting. At 48 sites throughout Canada and the western U.S.—from Whitehorse to Sacramento—researchers planted 15 species of commercially important trees, moving them from their home range and, in some cases, relocating them thousands of miles away.

The extreme migration, O'Neill says, is merely a research tool, a way to provide a better overall picture of how the trees will fare. It is not intended as a guide for long-distance moves.

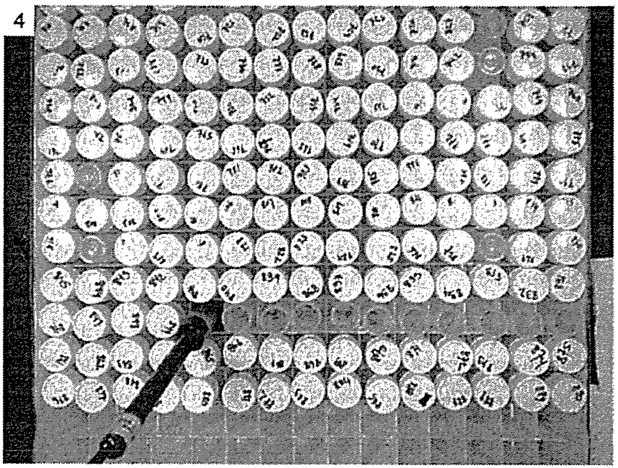
SCIENTIFIC AMERICAN ONLINE Watch biologist Sally N. Aitken explain moving genes in forests at ScientificAmerican.com/aug2015/moving-genes

Any actual changes in planting patterns will be incremental. "Something like 'Do not move your trees downhill' or 'Do not move your trees south,' " he says. There is a weather station at each site, and the study will show how the growth and survival of the seedlings relate to the local conditions. Then, O'Neill says, scientists will be able to predict how the trees will respond to climate change.

The genetic analysis of AdapTree offers a complementary way to predict how the trees will fare. Researchers on the sprawling project pored over DNA sequences from millions of locations in the genomes of interior spruce and lodgepole pine trees. They developed a quick screening method—similar to that used by the human genome screening business 23 And Me—that looks at roughly 50,000 short strings of genetic code, known as single nucleotide polymorphisms, or SNPs. With that done, they are "digging in," as Aitken puts it, trying to zero in on the specific polymorphisms that match a tree to its home base. Initial work on 600 young trees in the AdapTree project identified genetic markers that explain many of the differences in how trees from various regions grow and cope with cold, heat and varying amounts of water.

3

4



COURTESY OF JACK WOODS *AdapTree project, University of British Columbia (needles)*; COURTESY OF FIA SMETS *AdapTree project, University of British Columbia (vials)*

The raw genetic data from AdapTree are dizzying. Printed on both sides of sheets of 8 ½ by 11 paper, Aitken notes, the stack would rise about 150 kilometers. And that is only part of the information. Researchers are now looking at how the genes actually function—how their instructions are carried out—when the trees encounter stresses such as drought or high temperatures.

FORESTS OF THE FUTURE

A FEW DEGREES of latitude south, specialists in the U.S. Forest Service are beginning to weigh the pros and cons of assisted gene flow. "Where we're at is a lot of talk and discussion," St. Clair says. In the U.S., foresters historically did not focus on specific climate variations within zones where they collected and planted seeds. Moving seeds in a zone did not appear to involve enough temperature change to affect plant health.

Now foresters generally agree they need to get much better at moving seed. For as long as people have been planting trees, we have been relocating seed across rivers, villages, continents or oceans. "If you go back far enough, people used to move seed around all the time, and you'd often end up with failed plantations because people had no idea what they were doing," says Glenn Howe, a forest geneticist at Oregon State University. Partly as a result of those failures, over time the forestry community developed an aversion to risk. In the western U.S., seed zones, which guide how far seeds can be moved for planting, are narrow and conservative. "That's probably appropriate in a static climate," Howe says. "But with climate change, a very conservative approach could be a problem."

British Columbia is forging ahead, but challenges remain. Beyond the scientific problem lie management issues. The government's provincial tree seed center contains enough seed for more than six billion trees; you can't change that inventory overnight. Nor can you change human behavior: researchers will need to convince resource managers to trust in genomic data, something they cannot see for themselves in the field. It is crucial that all those nucleotide polymorphisms and sequence data "translate into a forester's lexicon," Aitken says.

Because ultimately all those strands of DNA make up living, breathing trees—the ones we depend on to construct our built environments as well as our natural ones. To thrive in a changing world, some of those trees may need to branch out into new territory. And to do that, they are going to need our help. SA

MORE TO EXPLORE

Placing Forestry in the Assisted Migration Debate. John H. Pedlar et al. in *BioScience,* Vol. 62, No. 9, pages 835–842; September 2012.

Assisted Gene Flow to Facilitate Local Adaptation to Climate Change. Sally N. Aitken and Michael C. Whitlock in *Annual Review of Ecology, Evolution, and Systematics,* Vol. 44, pages 367–388; November 2013.

Evaluation of Demographic History and Neutral Parameterization on the Performance of F_{ST} Outlier Tests. Katie E. Lotterhos and Michael C. Whitlock in *Molecular Ecology,* Vol. 23, No. 9, pages 2178–2192; May 2014.

AdapTree project: **http://adaptree.forestry.ubc.ca**

FROM OUR ARCHIVES

The American Chestnut's Genetic Rebirth. William Powell; March 2014.

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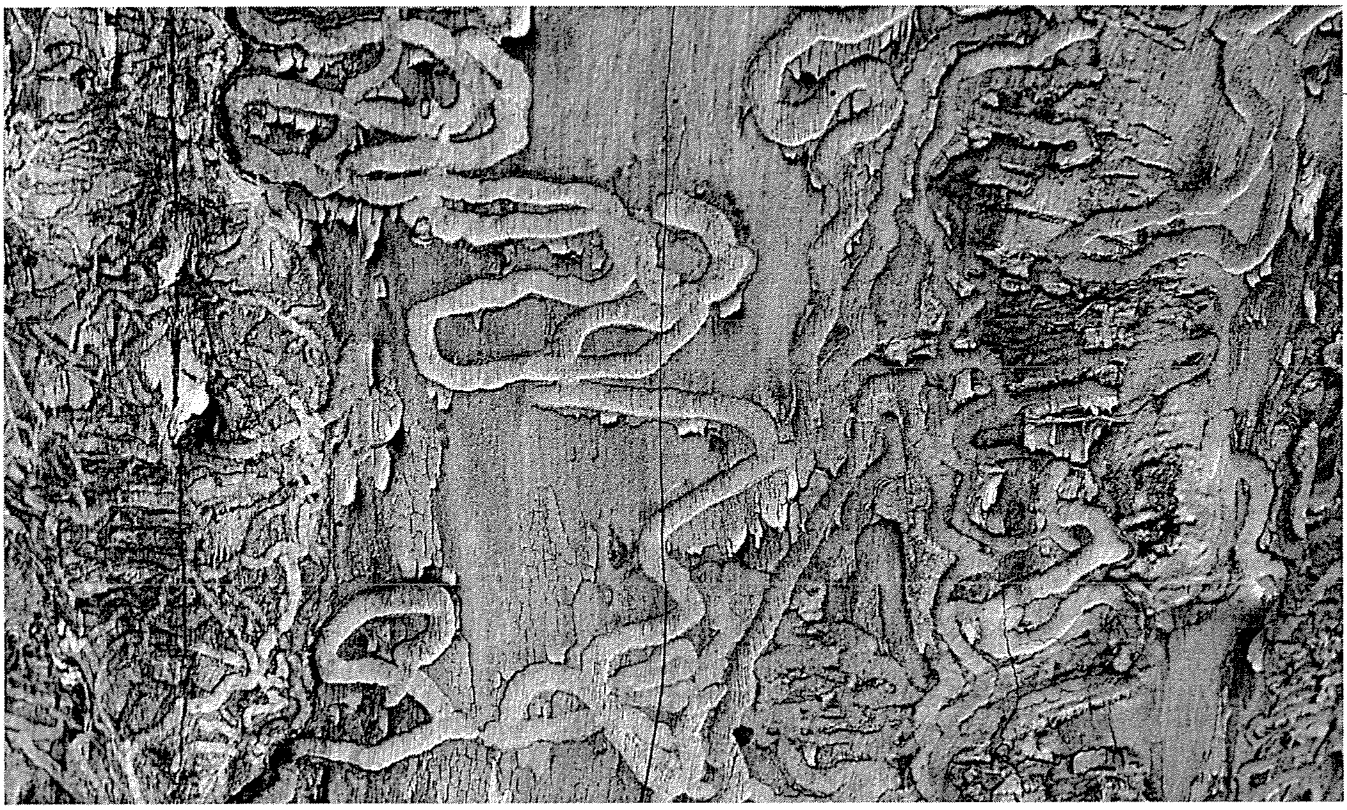

Traces of the emerald ash borer on the trunk of a dead ash tree in Michigan, USA. This non-native invasive insect from Asia threatens to kill most North American ash trees.

BIOTECHNOLOGY

Genetically engineered trees: Paralysis from good intentions

Forest crises demand regulation and certification reform

By **Steven H. Strauss**[1*], **Adam Costanza**[2], **Armand Séguin**[3]

POLICY

Intensive genetic modification is a longstanding practice in agriculture, and, for some species, in woody plant horticulture and forestry (*1*). Current regulatory systems for genetically engineered crops, in which recombinant DNA is used to asexually insert or modify DNA, were created decades ago with good intentions for caution and forethought. Likewise, forest certification systems were created to promote responsible forest management and sustainable practices. However, both systems are at odds with the need for rapid and innovative biotechnologies to help forests cope with growing pest epidemics and mounting abiotic stresses as a result of global travel and climate change. As the U.S. government recently initiated an update of the Coordinated Framework for the Regulation of Biotechnology (*2*), now is an opportune time to consider foundational changes.

Difficulties of conventional tree breeding make genetic engineering (GE) methods relatively more advantageous for forest trees than for annual crops (*3*). Obstacles include multiyear delays until onset of flowering, intolerance of inbreeding, and, as a consequence, introgression of genes from other species or populations is usually not possible in an acceptable time frame. GE methods improve on conventional breeding by enabling rapid modifications without shuffling the genotype during meiosis and without the maladaptation of early hybrids from wide crosses. GE could help in refining wood characteristics for specific products, responding to emerging pest problems (see the photo), adding high-value coproduct traits, improving growth, or accelerating adaptation to changing climates. It can also provide a means for strong containment of tree species when spread beyond plantations is problematic (*4*).

Although only a few forest tree species might be subject to GE in the foreseeable future, regulatory and market obstacles prevent most of these from even being subjects of translational laboratory research. There is also little commercial activity: Only two types of pest-resistant poplars are authorized for commercial use in small areas in China and two types of eucalypts, one approved in Brazil and another under lengthy review in the USA (*5*).

METHOD-FOCUSED AND MISGUIDED. Many high-level science reports state that the GE method is no more risky than conventional breeding, but regulations around the world essentially presume that GE is hazardous and requires strict containment during research and breeding (*6*). Regulatory systems in the EU and most other countries are focused almost exclusively on GE as a method. In the United States and Canada, regulations try to focus on trait novelty or use existing trait-associated authorities. In practice, however, the regulatory triggers have become predominantly method-based and have drifted far from the intent of their authorizing statutes. The U.S. Environmental Protection Agency (EPA) regulates pest-resistant genetically engineered plants as pesticide-producers even if they produce no novel or broadly toxic pesticides (and may regulate genetically engineered plants with genes that are simply growth regulators) (*7*). The U.S. Department of Agriculture uses plant pest sequences that, on their own, are of no conse-

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PHOTO: CORNELIA SCHAIBLE/GETTYIMAGES

quence to plant pest risk or that use a former plant pathogen as a vector (now disarmed), as triggers for regulation. No GE regulatory system adequately accounts for the costs of not using a genetically engineered technology or product.

Most genetically engineered trees are scrutinized as any other genetically engineered crop would be by the regulatory system, and subject to strict, zero-tolerance isolation requirements: Regardless of genomic familiarity, trees are placed very far from wild, feral, or planted populations of interfertile species; a large area nearby is monitored for possible spread (e.g., many km^2); and trial trees generally must be cut down before flowering. To develop trees that can actually be used, long-term trials are needed in a variety of environments and genotypes (*7*), where trees will be grown normally—beyond onset of flowering and to a size that will make absolute containment of experimental populations infeasible.

GE can modify complex abiotic stress-tolerance traits in crops—in some cases, where conventional breeding has shown limited success (*8*). This is likely to require multiple gene modifications and extensive phenotypic screening for high levels of resistance without unacceptable pleiotropy—for which the regulatory focus on single insertion events, mostly studied in artificial, contained environments, is a barrier. Many gene combinations and events will need to be studied and tested in conjunction with conventional breeding, so that adding genetically engineered modifications does not unacceptably slow breeding progress. Containment of every event and gene combination over many years during breeding, followed by years of regulatory review before approval of every event of interest, is restrictive, costly, and opens developers to legal liabilities (*7*).

FAST-TRACK AND REGISTER. A better regulatory approach would give agencies legal authority to fast-track or exempt field research with a genetically modified product intended to provide options for existing or emerging forest health problems, or that have high genomic familiarity. Agencies could rapidly (e.g., in 60 days) perform a categorical assessment when a species, or its ecological function, may be threatened by a spreading pest. This should be a presumptive, categorical exemption when intragenic, homologous, gene-edited, or otherwise functionally familiar genes are used, whose benefits and risks are similar to those of conventional breeding.

In the United States, EPA might take the regulatory lead, with the possible benefit of embedding decisions based on the National Environmental Policy Act in the overall risk assessment of the product rather than having a separate environmental impact statement. This would create stronger authority for future mitigation because of the ongoing registration and renewal process already in place for such products. In contrast to current EPA timing and demands for data, it would need to be more rapid and nimble, with most data generated along the way in an adaptive management framework and opportunities for legal challenges greatly narrowed, especially at the research stage. EPA should categorically exempt plant-incorporated protectants that do not produce broadly toxic pesticides, e.g., genetically engineered plants with genes that induce RNA interference or the various R-genes that trigger natural response pathways.

Environmental risk assessments of forest trees also need reconsideration, given the time required and the constraints to doing ecologically relevant field studies (i.e., complete containment). Such studies often become irrelevant as soon as they are produced owing to ongoing "no-analog" changes to ecosystem structure as a result of climate change (*9*) or introduced insects or diseases. Major changes in the rules and, possibly, new legislation are required.

> ***"No GE regulatory system adequately accounts for the costs of not using a genetically engineered technology or product."***

We are not suggesting separate regulations for genetically engineered trees. Fundamental regulatory reforms for all crops, discussed for years (*6*, *10*), are needed. In addition to the reforms discussed above, changes should focus on the novelty of functional traits compared with conventional breeding rather than on GE methods. A more realistic and responsive approach would include (i) best management practices rather than strict legal limits for dispersal from most types of research trials; (ii) globally recognized and workable tolerances for adventitious presence during research and commercial use (to avoid costly trade problems due to biologically trivial levels of adventitious presence); and (iii) exemptions for familiar markers and genetic modifications, which are usually more precise and less disruptive than conventional breeding.

A revised system might also require organisms modified using any GE method to be registered before use in the environment—to facilitate detection for trade or market certification and to ensure that they are not missed by regulatory agencies should they pose unanticipated hazards. Registration, however, should not preclude exemptions or accelerated review pathways based on trait and/or genomic familiarity or urgency.

MARKET REFORM. Regulatory processes are not the only obstacles to GE tree research and breeding. All major "sustainable certification" systems prevalent in forestry and forest products preclude use of genetically engineered trees in certified forests (*11*). Although the reason given is often a lack of data, legally authorized research is also not allowed on certified land (*12*). This signals to forest companies that investments in GE are risky and GE field research more difficult and costly. A cautious approach was perhaps warranted when GE tree research was nascent. But the Forest Stewardship Council first put in place genetically engineered tree preclusion in 1999; there have since been hundreds of scientific studies, many of them field tests, and none has shown categorical risks once feared (*13*). A product-not-process approach seems appropriate.

Despite confidence from the majority of scientists, there is public concern over genetically engineered crops and their safety. However, public attitudes vary widely among GE applications (*14*); views toward forest health and genomically familiar applications are likely to be received most favorably. Nonetheless, stakeholder dialogue use will be required for change.

It would be prudent and precautionary to ensure that GE tools are available to address urgent forest health and productivity problems. Regulatory agencies and certification systems should reconsider the foundations for their policies, refocusing on trait novelty and need, not method. ■

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MODELLING THE IMPACT OF THE EXOTIC FOREST PEST NECTRIA ON THE NEW ZEALAND FOREST SECTOR AND ITS MAJOR TRADING PARTNERS

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(Received for publication 19 April 2007; revision 16 October 2007)

ABSTRACT

The possible impact of *Nectria fuckeliana* Booth on the forests and forest industries of New Zealand, a significant exporter of industrial roundwood, was estimated for different scenarios of the spread of the fungal pest and trade measure responses in export markets. An economic model was used to assess the direct effect of the pest and the potential impact of trade bans and phytosanitary regulations to prevent pest arrival in New Zealand's major export markets — China, Japan, and South Korea. Depending on the assumed area affected by *N. fuckeliana*, the net present value of New Zealand's forest sector gross revenue was US$34 million to US$612 million lower, due to reduced harvest and log exports, even without foreign trade measures. A possible measure, requiring the debarking of New Zealand log exports, would reduce the present value of New Zealand growers' revenues by US$1,200 million, even if *N. fuckeliana* were confined to the already

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New Zealand Journal of Forestry Science 37(3): 383–411 (2007)

affected area. If China, Japan, and South Korea banned imports of New Zealand logs altogether, and the pest continued to spread at historical rates, the present value of New Zealand growers' revenues would decrease by US$8,200 million. Estimated losses to growers could be, to varying extents, offset by increased domestic production of processed wood products, under both trade measures. The debarking and import ban policies would increase gross revenues for producers in China and South Korea, but also increase the cost to consumers of wood products.

Keywords: exotic forest pests; international trade; phytosanitary regulations; forest sector model.

BACKGROUND

New Zealand's wood product exports were worth US$1,551 million at year end February 2006, accounting for 9.2% of all exports by value (Statistics New Zealand 2006). These exports are based on highly productive plantation forests of *Pinus radiata* D. Don and *Pseudotsuga menziesii* (Mirb.) Franco (Brown 1997), which face a significant threat from exotic forest pests, such as Nectria disease caused by the fungus *Nectria fuckeliana*.

More than 400 pest threats known to affect *P. radiata* are currently not present in New Zealand (Flux *et al.* 1993), but the growth of global trade is increasing the risk of unintentional introductions (Tkacz 2002). The severe threat that exotic pests pose to forest ecosystems has led to a variety of measures, such as phytosanitary regulations — fumigation and heat treatments, debarking, visual inspections, phytosanitary certificates — or import bans, to reduce the risk of importing pests (Powell 1997; New Zealand Forest Research Institute 1999; Roberts 1999; Roberts *et al.* 1999).

These trade measures can affect domestic and foreign wood product industries and consumers in numerous ways. There are clear benefits from reducing the risk of damage to forest resources and hence loss of production and exports (Rose 1983; USDA Forest Service 1991; Pimentel *et al.* 2000; Turner *et al.* 2004). However, trade regulations have a cost. Exporting countries may lose access to markets. Importing countries may have to forego cheaper foreign products and raw materials (Roberts *et al.* 1999; Mumford 2002).

The full economic impact of regulations to prevent the importation of exotic pests can be assessed by measuring price and quantity changes for producers and consumers along the wood product value chain from the forest to the end consumer, through various stages of manufacture. At each stage, consumer and producer surplus should be assessed, to the extent possible.

To capture these various effects Roberts *et al.* (1999) suggested an economic framework (1) which is easily understood, (2) is comprehensive enough to represent a range of trade measures, and (3) into which empirical data on trade regulations and exotic pest impacts can be incorporated for the estimation of trade, production, consumption, and welfare effects. To this list we would add, (4) the ability to represent the temporal effect of exotic pests on forest resources — because forest pests are biological organisms that grow, reproduce, multiply, actively and passively disperse, interact with ecosystems in unpredictable ways, and randomly evolve (Powell 1997) — and (5) the ability to represent complex interactions, through trade, among countries. This is necessary to determine how regulations in a particular country or its trading partners affect their forest sector. It depends on how world prices are affected by the regulation and whether the affected exporter is able to sell in other markets (Roberts *et al.* 1999).

Market equilibrium models have been a fruitful approach for predicting the effects of regulations to reduce the risk of importing exotic pests (Beghin & Bureau 2001). They have the characteristics necessary to fully assess the main impacts, and they have already been applied successfully to policy analysis.

Studies of the economic and trade effects of phytosanitary regulations in the agricultural sector (Roberts *et al.* 1999) commonly conclude that the short- and long-run effects of pests, and policies to reduce the risk of their import, are to lower aggregate wealth and to redistribute it within a country and beyond its borders. In the country imposing the policy consumers pay higher prices, while producers benefit. In the exporting country, producers experience production losses.

Krissoff *et al.* (1997) and Calvin & Krissoff (1998) examined technical regulations imposed on United States apple exports to Japan, South Korea, and Mexico. Sumner & Lee (1997) determined the cost of complying with Asian regulations on vegetable imports from the United States. Orden & Romano (2006) estimated the effect of production losses in the United States avocado industry resulting from the possibility of pest infestation from Mexican imports. They measured the benefits to United States producers of a ban on avocado imports from Mexico, as well as the cost to United States consumers. Roberts *et al.* (1999) assessed the economic effects of easing the United States ban on the importation of avocados from Mexico, distinguishing between regulatory protection, supply-shift, and demand-shift effects.

Paarlberg & Lee (1998) calculated the "optimum tariff" on imports of beef from regions with foot-and-mouth disease. The "optimum tariff" was set to maximise the difference between the consumers' gains from trade and the costs to the domestic industry from the spread of the disease. James & Anderson (1998) assessed the costs and benefits of quarantine restrictions in Australia while explicitly taking into account the probability of contamination.

Past analyses of the impact of exotic pests on the forest sector (Kuchler & Duffy 1984; Holmes 1991; USDA Forest Service 1991; Turner *et al.* 2004) have not considered phytosanitary regulations. Prestemon *et al.* (2006) seem to have made the only attempt to determine the full costs and benefits of regulations on United States imports of softwood logs from Russia, which potentially carry the Asian gypsy and nun moths. They used the Global Forest Products Model (Buongiorno *et al.* 2003) to simulate different interventions — phytosanitary, direct trade barriers, and detection and control — by the United States and to assess their cost and efficacy, and hence their effect on producers and consumers.

The objective of this study was to predict the potential economic impact of the fungus *Nectria fuckeliana*, which has been found in exotic timber plantations in the South Island of New Zealand (Wang & Thode 2004; Dick *et al.* 2006). Both the direct effect of the pest, in terms of forest loss, and the indirect effect due to trade measures imposed by importers of New Zealand logs were considered. By studying New Zealand we assessed the implications of forest pests and phytosanitary regulations from the perspective of a significant exporter of industrial roundwood, while Prestemon *et al.* (2006) focused on the United States as an importer. The implications in terms of aggregate timber production, prices, consumption, and net trade are, therefore, likely to be very different. Below, we discuss first the economic model, outline the alternative pest spread and policy scenarios, and then describe in detail the results and their implications.

METHODS AND MATERIALS

Economic Model

The impact of *N. fuckeliana* on wood product production, trade, and prices, and on forest resources in New Zealand, its markets, and competitors was predicted from 2002 to 2030 with the Global Forest Products Model (Buongiorno *et al.* 2003). The GFPM has previously been used to forecast forest sector development (Turner, Buongiorno, Maplesden, Zhu, Bates & Li 2006) and to study issues such as the effects of accelerated tariff liberalisation (Zhu *et al.* 2001) and of trade agreements on the New Zealand forest sector (Turner *et al.* 2001), the global impact of waste paper recycling in the United States (Zhu & Buongiorno 2002), effects of illegal logging on the United States forest sector (Seneca Creek 2004), and the impact of the Free Trade Area of the Americas on forest resources (Turner *et al.* 2005).

The GFPM is a dynamic market equilibrium model that integrates wood supply, processing industries, product demand, and trade. Wood producing, consuming, and manufacturing activities are modelled with supply and demand equations, and activity analysis. Countries are linked by trade. Inter-temporal linkages are exogenous, as for changes in techniques of production in pulp and paper, or endogenous, as for shifts in wood supply and changes in forest area and forest stock*.

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* The mathematical specification of the GFPM is given in Appendix A. Turner, Buongiorno, Zhu & Li (2006) have provided a complete description of model assumptions. Model assumptions specific to New Zealand are given in Appendix B. Model data are available from the authors upon request.

Forest resources and harvests are represented in the GFPM by equations describing the annual roundwood harvest, and the changes of forest stock and forest area (Turner, Buongiorno & Zhu 2006). The harvest volume is a function of prices, forest stock (endogenous), and gross domestic product per capita (exogenous).

Forest stock evolves according to a growth-drain equation (Brooks 1987):

$$I_{i,t+1} = (1 + g^{a}_{it} + g^{u}_{it})I_{it} - S_{it} \qquad [1]$$

where S_{it} is the total roundwood harvest in country i and year t, g^{a}_{it} is the rate of change in forest stock (I_{it}) due to forest area change (afforestation/deforestation), g^{u}_{it} is the rate of forest growth on a given area, without harvest and under normal conditions — in particular without exotic forest pests.

The annual relative change of forest area in all countries (except for New Zealand in this study, see below) is a function of income per capita (*Y/N*), as in the environmental Kuznets curve for forestry (Vincent *et al.* 1997):

$$g^{a}_{it} = \alpha_0 + \alpha_1 (Y_{it} / N_{it}) + \alpha_2 (Y_{it} / N_{it})^2 \qquad [2]$$

The annual relative change of forest stock due to growth is an inverse function of forest density – stock per unit area, *I/A* (Oliver & Larson 1996):

$$g^{u}_{it} = \gamma_0 (I_{it} / A_{it})^{-a} \qquad [3]$$

The effect of an invasive species was represented by reducing this rate of growth of forest stock by various amounts, g^{u*}_{it}, over time, to simulate different rates of pest spread. These changes in forest stock would then affect future harvests and growth via the wood supply equation and Equation [3].

New Zealand's industrial roundwood harvests are almost entirely from plantations; 0.1% of harvests in 2005 were from native forests (NZFOA 2006). Thus, only the planted forest estate was considered in this study. In 2003 New Zealand had 1.83 million ha of planted forest with a volume of 398 million m^3 (NZFOA 2005), growing at 18 to 24 m^3/ha per year (Brown 1997) — or $g^u = 8.3\%$ per year of the current growing stock. Estimates of new plantings are 30 100 ha in 2002 and 22 100 ha in 2003 (NZFOA 2005). For the projections we assumed a long-run average planting rate of 20 000 ha per year (NZMAF 2000) — equivalent to $g^a = 1.09\%$ per year addition to the plantation estate (Table B.3).

Impacts of Nectria

Nectria fuckeliana is found in New Zealand; it is found in Scandinavia, Northern Europe, and North America generally at latitudes greater than 50°N, although it has been recorded in Oregon and Northern California. In New Zealand the fungus commonly, but not exclusively, enters trees through the pruning stub and this leads to stain and decay within the stem (Dick *et al.* 2006), affecting the most valuable section of the tree, the pruned log (NZFOA 2005).

Nectria may have arrived in New Zealand in the late 1980s or early 1990s, according to anecdotal reports. The first formal collection was made in 1996, and by the end of 2005 targeted surveys had demonstrated that the fungus was present throughout the wood supply regions of Southland and Otago, and occurred in parts of Canterbury (Waimate, Timaru, and Mackenzie territorial authorities). Those regions contain 34 million m^3 — 8.6% — of New Zealand's total forest stock (NZMAF 2004). Further surveys were carried out in Canterbury in 2006 and 2007. By April 2007, the northernmost find was at Banks Peninsula, approximately 140 km from the nearest known location recorded in April 2004.

Regional incidence surveys carried out in Southland and Otago in 2006 showed 20% of the trees were affected to some extent. Wang & Thode (2004) suggested 4 to 39%. The volume loss per tree could be 5 to 10%, given that 8% of trees were assessed as having medium damage and 5% were assessed as having severe damage, but as Nectria affects the most valuable section of the stem*, we assumed a volume loss of 10%. Taken together, the assumptions imply a reduction in New Zealand's total forest stock of 0.172% (8.6% × 20% × 10%). The assumed pattern of stock reduction was 0.109% in 2003, reflecting the stock lost from 1990 to 2003, an additional stock reduction of 0.028% in 2004, 0.036% in 2005, and no further reduction from 2006 to 2030.

If Nectria's spread continued at historical rates — approximately 100 km every 2 years — the fungus could affect Southland, Otago, and Canterbury by 2008, and all of the South Island (excluding the West Coast) by 2014. This study also considered the possibility of Nectria establishing itself, by either natural or unnatural means, in the North Island. It was assumed that the disease would arrive in the North Island in 2007 and be completely established by 2011 (Fig. 1). This rate of spread was assumed to be more rapid than in Canterbury and Nelson, due to the more favourable climate in the central North Island and the abundance of suitable host material. The rate of stock reduction under this scenario is shown in Fig. 2.

Log Importer Policy Response

Of the 8.3 million m^3 of logs exported by New Zealand in 2002, 20% went to the People's Republic of China, 18% to Japan, and 48% to South Korea (FAO 2005). We assumed that these countries might respond to the spread of Nectria in New Zealand in three ways (G. Hosking, Hosking Forestry, pers. comm.): (1) do nothing, (2) allow imports of debarked roundwood only, or (3) ban all industrial roundwood imports from New Zealand. These represent the range of possible responses. Others include inspections, certification in New Zealand, or fumigation,

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* 60% of the tree value is in the pruned log of 27-year-old *P. radiata* grown on a direct sawlog regime (NZFOA 2005)

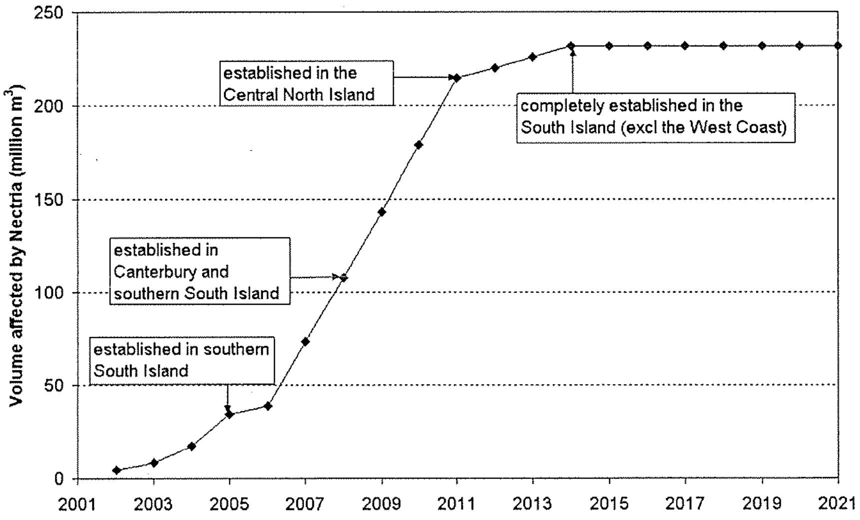

FIG. 1–Assumed volume of New Zealand's plantation forest affected by the spread of Nectria.

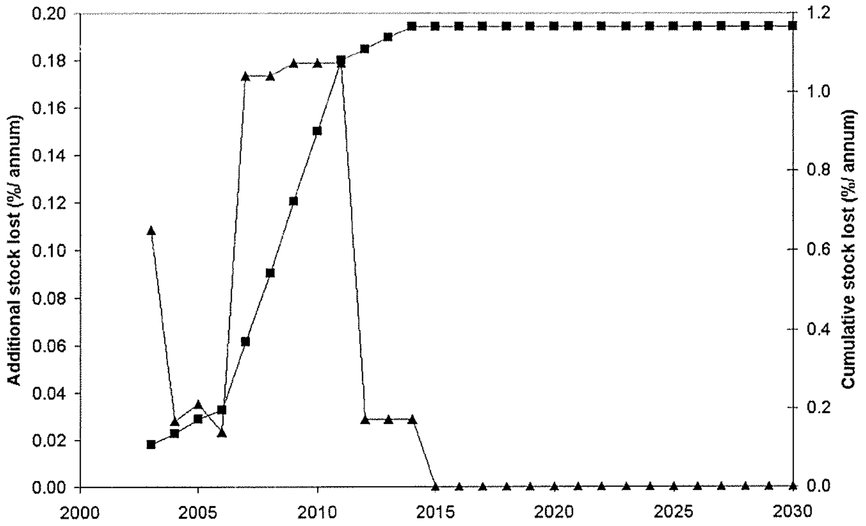

FIG. 2–Annual additional (▲) and cumulative (■) New Zealand forest stock lost due to Nectria spread to all of the South Island (excluding the West Coast) and the North Island.

which, like debarking, add to varying degrees to the cost of freight for New Zealand industrial roundwood.

Each response was analysed under two levels of Nectria invasion — staying confined to its current area, or spreading to all of the South Island (excluding the

West Coast) and the central North Island (Fig. 2). While it is likely that the fungus will spread throughout the North Island, we confined the response analysis to the central North Island on the conservative assumption that the disease would not cause significant damage in other regions due to climatic factors. Each of the six response-spread scenarios was compared with the status quo scenario in which there would be no Nectria in New Zealand and thus no need for a response by China, Japan, and South Korea.

Debarking was estimated to cost US\$4.42/m^3, based on costs of NZ\$4.27/m^3 to NZ\$6.39/m^3 in 1988 New Zealand dollars (W.Blundell & G.Murphy unpubl. data), adjusted to 2005 US dollars using the New Zealand consumer price index and a New Zealand to US dollar exchange rate of 0.55 in 2005. The cost includes log handling, which is 40 to 60% of the total cost. This cost of debarking was modelled as an increase in the level of the industrial roundwood freight cost (Equation A.11) for New Zealand log exports to China, Japan, and South Korea.

RESULTS AND DISCUSSION

No Response by China, Japan and South Korea

For no policy action by China, Japan, and South Korea, depending on the extent of Nectria spread, New Zealand forest stock was predicted to be 200 000 m^3 to 20 million m^3 lower in 2030 than without the pest (Table 1). From 2002 to 2030, the average annual harvest was 20 900 m^3 to 1.3 million m^3 per year lower, 0.1 to 4.5% (Table 2). This reduction in New Zealand harvests led to substantially lower industrial roundwood exports — a 1.4 million m^3 per year or 7.0% reduction were Nectria to spread beyond its current extent. There were modest changes in New Zealand's production and net trade (exports minus imports) of all other wood products — less than 4% — with larger reductions for sawnwood, wood-based panels, and wood pulp than for paper products (Table 2).

Total net imports of industrial roundwood by China, Japan, and South Korea were unchanged – less than 1% per year difference (Table 2) – because reduced imports from New Zealand were replaced by imports from Brazil (8% per year increase) and Chile (1% per year increase) (Table 3). New Zealand industrial roundwood exports to China, Japan, and South Korea were barely affected by Nectria at its current extent (Table 4) and, as a result, harvest and stock in China, Japan, and South Korea were unchanged (Tables 1 and 2). However, were Nectria to spread throughout the South Island and central North Island, industrial roundwood exports to Japan and the rest of the world would be lower by 252 000 m^3 per year and 1.4 million m^3 per year, respectively (Table 4). Log exports to China would remain unchanged, reflecting China's strong demand for wood driven by rapid economic growth and the relatively small increase in the price of New Zealand industrial roundwood (Fig. 3).

TABLE 1–Impact of Nectria on forest stock (million m^3 and %) in 2030.

	Do nothing		NZ debarks log exports		CJK* ban NZ logs	
	(million m^3)	(%)	(million m^3)	(%)	(million m^3)	(%)
Nectria confined to current area						
New Zealand	–0.2	–0.1	41.5	6.0	319.7	46.1
China	0.0	0.0	0.0	0.0	–55.4	–0.8
Japan	0.1	0.0	–0.8	0.0	–1.5	0.0
South Korea	0.0	0.0	–0.6	–0.2	–25.4	–9.4
Nectria at maximum spread						
New Zealand	–20.4	–2.9	16.4	2.4	253.4	12.5
China	0.0	0.0	0.0	0.0	–55.4	–0.8
Japan	–0.3	0.0	–1.3	0.0	–1.4	–0.0
South Korea	0.1	0.0	–0.8	–0.3	–25.4	–9.4

* CJK = China, Japan, and South Korea

Unexpectedly, New Zealand's log exports to South Korea were predicted to be slightly higher — 5000 m^3 to 219 000 m^3 per year, depending on the extent of Nectria spread (Table 4). This was due to the dynamics of the impact of the stock loss on New Zealand industrial roundwood prices, harvests, and log exports. The initial effect was to increase industrial roundwood prices (Fig. 3), reducing demand for New Zealand roundwood exports, and increasing harvests in South Korea. As

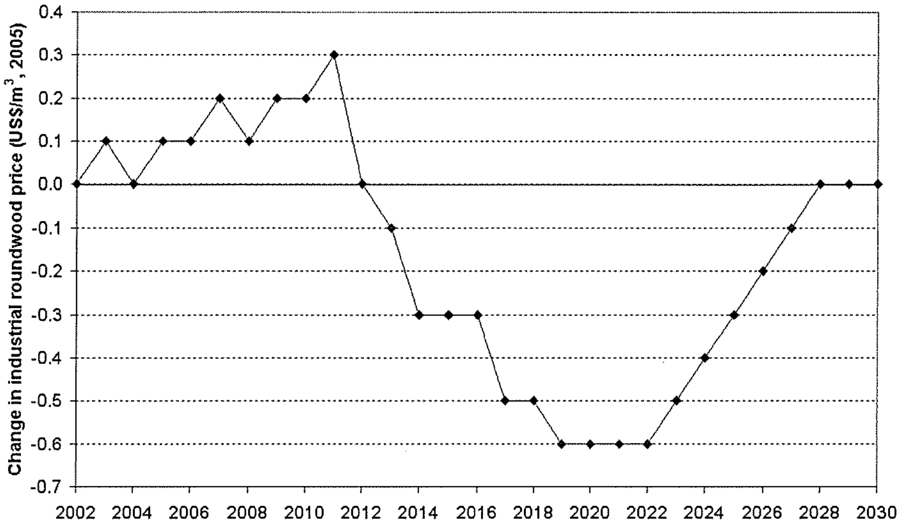

FIG. 3–Change in New Zealand industrial roundwood price (US$/m^3, 2005) due to spread of Nectria through the South Island and central North Island of New Zealand.

TABLE 2–Percentage change of average annual production and net trade volume due to Nectria in New Zealand with three policy responses, from 2002 to 2030.

Product	Country	Do nothing		NZ debarks log exports		CJK ban NZ logs	
		Production	Net trade	Production	Net trade	Production	Net trade
Nectria confined to current area							
Industrial roundwood	New Zealand	-0.1	-0.1	-3.9	-14.7	-31.3	-62.3
	China	0.0	0.0	0.0	0.0	2.3	-5.8
	Japan	0.0	0.0	0.1	-0.9	0.2	-0.9
	South Korea	0.0	0.1	1.4	-0.7	78.7	-21.8
Sawnwood	New Zealand	-0.1	-0.4	21.5	79.1	32.0	115.3
	China	0.0	0.0	0.0	0.0	-2.5	0.0
	Japan	0.0	0.0	-0.2	0.6	-0.4	0.9
	South Korea	0.0	0.0	-0.3	0.3	-11.4	0.6
Wood-based panels	New Zealand	-0.2	-0.3	6.9	15.1	14.3	30.4
	China	0.0	0.0	0.0	0.0	-1.6	0.0
	Japan	0.0	0.0	-0.4	0.4	-0.8	0.7
	South Korea	0.2	-0.1	-1.1	0.6	-15.6	2.0
Wood pulp	New Zealand	-0.1	-0.2	43.2	125.4	71.5	186.0
	China	0.0	0.0	0.0	0.0	-2.1	0.0
	Japan	0.0	0.0	-0.7	4.1	-0.4	1.7
	South Korea	0.0	0.0	-0.2	0.0	-14.0	-5.3
Paper & paper board	New Zealand	0.0	0.1	1.1	9.7	15.3	129.9
	China	0.0	0.0	0.0	0.0	-0.4	0.7
	Japan	0.0	0.0	0.0	1.1	-0.1	2.0
	South Korea	0.0	0.0	0.0	0.0	-5.8	-30.9

TABLE 2–cont.

Product	Country	Do nothing		NZ debarks log exports		CJK ban NZ logs	
		Production	Net trade	Production	Net trade	Production	Net trade
Nectria at maximum spread							
Industrial roundwood	New Zealand	-4.5	-7.0	-7.9	-17.8	-31.3	-62.3
	China	0.0	0.0	0.0	0.0	2.3	-5.8
	Japan	0.1	0.0	0.2	-0.6	0.2	-0.9
	South Korea	-0.3	0.7	1.9	-0.8	78.7	-21.8
Sawnwood	New Zealand	-0.2	-0.7	15.2	57.4	31.9	115.3
	China	0.0	0.0	0.0	0.0	-2.5	0.0
	Japan	0.0	0.0	-0.2	0.5	-0.4	0.9
	South Korea	0.1	-0.1	-0.4	0.4	-11.4	0.6
Wood-based panels	New Zealand	0.7	1.5	4.8	10.5	14.2	30.3
	China	0.0	0.0	0.0	0.0	-1.6	0.0
	Japan	-0.1	0.1	-0.5	0.4	-0.7	0.7
	South Korea	1.6	-0.9	-1.2	0.6	-15.6	2.0
Wood pulp	New Zealand	1.4	3.8	32.0	94.9	70.5	185.8
	China	0.0	0.0	0.0	0.0	-2.1	0.0
	Japan	0.1	-0.4	-0.3	1.7	-0.4	1.7
	South Korea	0.1	0.0	-0.2	0.0	-14.0	-5.3
Paper & paper board	New Zealand	0.1	1.0	1.0	8.3	14.1	119.3
	China	0.0	0.0	0.0	0.0	-0.5	0.7
	Japan	0.0	0.0	0.0	0.9	-0.1	2.1
	South Korea	0.0	0.0	0.0	0.0	-5.8	-30.9

TABLE 3–Percentage change of average annual industrial roundwood net-trade in major countries due to Nectria in New Zealand with three policy responses, from 2002 to 2030

Country/Region	Do nothing	NZ debarks log exports	CJK* ban NZ logs
Nectria confined to current area			
AFRICA	0.03	1.05	1.71
South Africa	0.02	1.89	3.53
N&C AMERICA	0.04	0.14	2.56
Canada	-0.14	-0.29	-7.97
United States	0.00	0.00	0.01
SOUTH AMERICA	-0.06	2.85	4.63
Brazil	-0.30	6.65	14.57
Chile	-0.03	2.16	2.90
ASIA	0.00	-0.42	-6.58
Malaysia	0.01	0.68	1.13
OCEANIA	-0.02	-7.17	-29.70
Australia	0.01	0.48	0.94
EUROPE	0.03	6.29	9.77
Finland	-0.06	-4.44	-6.13
Russian Federation	0.00	0.00	0.00
Sweden	-0.02	-0.83	-2.08
Nectria at maximum spread			
AFRICA	0.38	1.39	1.74
South Africa	0.59	3.02	3.34
N&C AMERICA	0.01	0.25	2.57
Canada	0.09	-0.89	-7.99
United States	0.00	0.01	0.00
SOUTH AMERICA	2.09	4.05	4.45
Brazil	7.98	10.88	13.49
Chile	1.02	2.92	2.82
ASIA	-0.02	-0.39	-6.57
Malaysia	0.36	0.91	1.11
OCEANIA	-3.28	-8.61	-29.71
Australia	0.25	0.79	0.93
EUROPE	3.30	7.58	9.85
Finland	-1.96	-4.91	-6.18
Russian Federation	0.00	0.00	0.00
Sweden	-2.02	-1.90	-2.15

* CJK = China, Japan, and South Korea

New Zealand harvests decreased, due to reduced demand, the stock loss due to Nectria was partially recovered (Fig. 4). This increased the potential supply of New Zealand industrial roundwood and lowered its price (Fig. 3). At the same

TABLE 4–Effect of Nectria on New Zealand average annual exports of industrial roundwood, by destination, from 2002 to 2030

	Do nothing		NZ debarks log exports		CJK* ban NZ logs	
	(10^3 m^3)	(%)	(10^3 m^3)	(%)	(10^3 m^3)	(%)
Nectria confined to current area						
China	0	0.0	0	0.0	–4710	–86.2
Japan	–5	–0.2	–1521	–49.3	–2476	–86.2
South Korea	5	0.1	–2907	–35.4	–6459	–86.2
Rest of the world	–10	–0.2	1212	18.1	1229	18.4
Nectria at maximum spread						
China	0	0.0	0	0.0	–4710	–86.2
Japan	–252	–9.7	–1496	–48.7	–2476	–86.2
South Korea	219	2.3	–2707	–33.2	–6459	–86.2
Rest of the world	–1361	–27.5	278	1.7	1229	18.4

* CJK = China, Japan, and South Korea

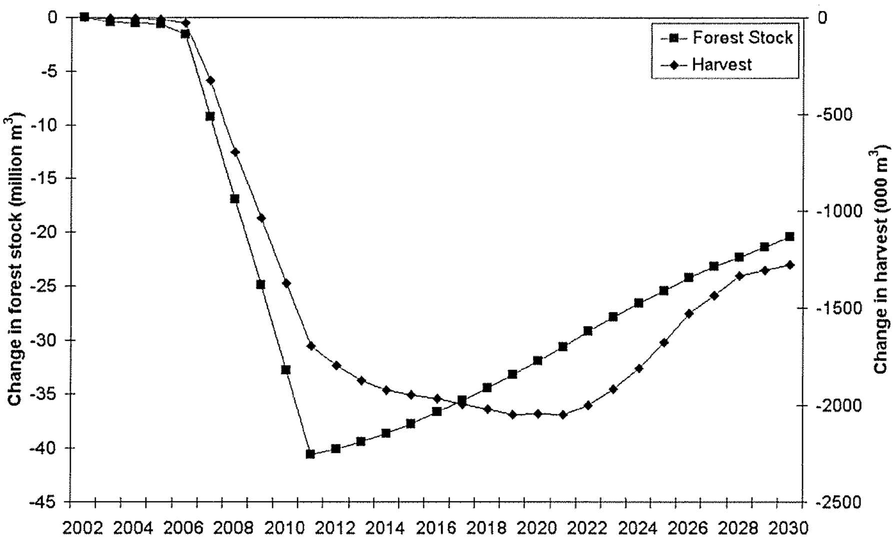

FIG. 4–Change in New Zealand plantation forest stock and industrial roundwood harvests due to spread of Nectria through the South Island and central North Island of New Zealand.

time South Korea's industrial roundwood price increased because of its more expensive domestic harvests. In response, South Korea increased its imports of New Zealand industrial roundwood in the 2020s.

Depending on the extent of Nectria spread, the net present value — at an 8% discount rate — of New Zealand producers' gross revenue[*] would decrease by US$34 million to US$612 million (Table 5). The gross revenue loss to industrial roundwood producers was US$9 million to US$746 million (Table 6). Most of the reduction in harvests went to a reduction in industrial roundwood exports. New Zealand consumption of industrial roundwood was unchanged.

Producer revenue in New Zealand's markets increased slightly due to some production moving to these countries. World producer revenue increased as other countries increased their production to replace New Zealand's exports to China, Japan, and South Korea.

TABLE 5–Gains and losses[†] in different countries due to Nectria and countervailing trade measures

	Do nothing		NZ debarks log exports		CJK[‡] ban NZ logs	
	Producers	Consumers	Producers	Consumers	Producers	Consumers
Nectria confined to current area						
New Zealand	-34	4	1,654	-110	-5,100	-985
China	-5	-2	-29	-7	17,321	12,101
Japan	0	1	-415	19	-228	67
South Korea	20	0	75	230	2,195	11,149
World	45	42	-1,197	121	19,118	22,683
Nectria at maximum spread						
New Zealand	-612	88	239	0	-4,644	-824
China	31	10	21	9	17,317	12,105
Japan	96	47	-113	73	-236	63
South Korea	166	-8	133	311	2,204	11,152
World	1,525	668	962	879	19,604	22,911

† Net present value of producers' revenue and consumers' expenditure, in US$ million 2005, with an 8% per year discount rate

‡ China, Japan, and South Korea

Debarking of Log Exports Required

The imposition of a debarking requirement by China, Japan, and South Korea further reduced New Zealand harvest and log exports. Lower industrial roundwood prices — 4.1% to 4.3% on average between 2002 and 2030, depending on the extent of Nectria spread (Table 7) – contributed to harvests which were 1.2 million m^3 to 2.4 million m^3 (4–8%) per year lower on average (Table 2).

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[*] Gross revenue is the value of production — quantity produced multiplied by price per unit— ignoring changes in the cost of raw material inputs to production.

TABLE 6–Gains and losses* of different sub sectors in New Zealand due to Nectria and countervailing trade measures

	Do nothing		NZ debarks log exports		CJK† ban NZ logs	
	Producers	Consumers	Producers	Consumers	Producers	Consumers
Nectria confined to current area						
Industrial roundwood	–9		–1,202		–8,222	
Sawnwood	–12	0	1,087	–49	797	–440
Wood based panels	–10	0	368	–31	482	–47
Wood pulp	–6		1,395		1,618	
Paper and paperboard	0	0	24	–11	408	–119
Nectria at maximum spread						
Industrial roundwood	–746		–1,687		–7,979	
Sawnwood	–25	–2	669	–42	873	–403
Wood based panels	27	–1	222	–27	523	–226
Wood pulp	38		938		1,647	
Paper and paperboard	2	0	18	–10	384	–108

* Net present value of producers' revenue and consumers' expenditure, in US$ million 2005, with an 8% per year discount rate.

† China, Japan, and South Korea

Japan's and China's industrial roundwood harvests were almost unchanged, but South Korea's yearly harvest was 14 800 m^3 to 20 400 m^3 (1.4–1.9%) higher (Table 2), in accord with a 1.2–1.6% average increase in the price of industrial roundwood. The reduction in New Zealand's harvest offset the loss of forest stock due to Nectria, so that by 2030 New Zealand's forest stock was 41.5 million m^3 (6%) higher (Table 1), with Nectria confined to its current extent. Were Nectria to spread throughout the South Island and central North Island the increase in New Zealand's forest stock would be less — 16.4 million m^3 higher (2%) by 2030.

The extent to which such a gain in forest stock would occur depends on how New Zealand land use changes due to the lower wood price. It is possible that existing plantation forests may be converted to agriculture due to lower returns from land in forestry.

New Zealand industrial roundwood exports to China were unchanged, reflecting China's strong demand for wood. However, New Zealand exports to Japan and South Korea were significantly lower — 1.5 million m^3 (49%) and 2.8 million m^3 (34%) on an average year, respectively (Table 4) — regardless of the extent of Nectria spread. These countries replaced imports from New Zealand, predominantly with imports from other countries, particularly Brazil (7–11% per year) and Chile (2–3% per year) (Table 3).

TABLE 7–Percentage change of average prices due to Nectria in New Zealand, with three policies, from 2002 to 2030

Product	Do nothing	NZ debarks log exports	CJK* ban NZ logs
Nectria confined to current area			
Industrial roundwood	0.0	–4.3	–30.2
Sawnwood	0.0	–1.3	–9.7
Veneer & plywood	0.0	–0.8	–5.5
Particleboard	0.0	–1.2	–8.8
Fibreboard	0.0	–0.7	–5.0
Mechanical pulp	0.0	–0.9	–6.9
Chemical pulp	0.0	–0.9	–7.5
Newsprint	0.0	–0.2	–0.6
Printing & writing paper	0.0	0.0	–0.3
Other paper and paperboard	0.0	–0.4	–3.1
Nectria at maximum spread			
Industrial roundwood	–0.3	–4.1	–27.6
Sawnwood	–0.1	–1.2	–8.8
Veneer & plywood	–0.1	–0.7	–5.0
Particleboard	–0.1	–1.2	–8.0
Fibreboard	0.0	–0.6	–4.6
Mechanical pulp	–0.1	–0.9	–6.2
Chemical pulp	–0.1	–0.9	–6.9
Newsprint	0.1	–0.1	–0.5
Printing & writing paper	0.0	0.0	–0.3
Other paper and paperboard	0.0	–0.4	–2.8

* CJK = China, Japan, and South Korea

The reduction in New Zealand roundwood exports to the major markets due to the debarking requirement was partly offset by increased exports to the rest of the world (Table 4), due to increased demand for New Zealand industrial roundwood in these markets because of its lower price (Table 7). With Nectria confined to its current extent, exports to the rest of the world were 1.2 million m^3 per year higher (Table 4). However, were Nectria to spread further, the greater reduction in industrial roundwood harvests would limit the growth in exports to the rest of the world to 278 000 m^3 per year (Table 4). Overall, New Zealand's industrial roundwood exports were 3.2 million m^3 to 3.9 million m^3 per year lower, depending on the extent of Nectria spread.

New Zealand production and net-export of processed wood products — particularly sawnwood, wood-based panels, and wood pulp — were higher (Table 2), due to the availability of cheaper industrial roundwood (Table 7). However, this increase would not be as large were Nectria to spread throughout the South Island and central North Island (Table 2), due to the greater reduction in industrial roundwood harvests and less price decline with the greater Nectria spread.

The prices of all New Zealand wood products were slightly lower with this scenario, generally less than 1% from 2002 to 2030, with slightly larger reductions in sawnwood and particleboard prices (Table 7). These lower prices were offset by increased production, so that the present value of gross revenue to New Zealand's manufacturing industries increased (Table 6) — US\$669 million to US\$1,087 million for sawnwood, US\$222 million to US\$368 million for wood-based panels, and US\$938 million to US\$1,395 million for wood pulp, depending on the spread of Nectria. Industrial roundwood producer gross revenue decreased by US\$1,202 million to US\$1,687 million. These changes led to a gross revenue increase for the entire sector of US\$239 million to US\$1,654 million (Table 5). The gain of producers was smaller if Nectria spread widely because the attendant reduction in stock reduced domestic supply by more than the reduction of log exports, so that domestic production and revenues were curtailed.

World producer revenue was lower, as New Zealand production and net exports of processed wood products led to lower prices and production in other countries, especially United States, Brazil, Finland, and Sweden. However, New Zealand's lower production were Nectria to spread further meant that world producer revenue was higher due to less competition from New Zealand exports.

Log Import Ban

A ban on imports of New Zealand logs by China, Japan, and South Korea would have a significant negative impact on the New Zealand forest sector, regardless of the extent of Nectria spread.

The loss of exports to China, Japan, and South Korea was partly compensated for by higher exports to the rest of the world, 1.2 million m^3 per year (Table 4). Nevertheless, there would be an overall decrease of 12.4 million m^3 per year (62%) from 2002 to 2030. The higher exports to other markets were partly due to the lower price of New Zealand industrial roundwood, 28–30% on an average year (Table 7).

As a result of the ban on roundwood imports from New Zealand, domestic harvests would increase in China, Japan, and South Korea (Table 2). Reflecting the importance of New Zealand logs to South Korea (44% of South Korea's log imports in 2002) its annual harvest was 79% higher on average. This resulted in 9% less forest stock in South Korea by 2030 (Table 1). The impact on China's and Japan's harvests was less significant, and the impact on their forest stock was negligible (Table 1), as these countries increase industrial roundwood imports from other countries, particularly Brazil (13–15% per year) and Chile (3% per year) (Table 3).

Lower industrial roundwood prices contributed to New Zealand harvests being 9.1 million m^3 (31%) lower per year (Table 2). This decrease completely compensated for the loss of forest stock due to Nectria, so that New Zealand's forest stock was 253 million m^3 to 320 million m^3 (13–46%) higher in 2030, depending on the extent of Nectria (Table 1).

New Zealand production and net exports of processed wood products — particularly sawnwood, wood-based panels, and wood pulp — were higher (Table 2), due to the cheaper industrial roundwood. The prices of all New Zealand wood products were lower, generally 5–10% between 2002 and 2030 (Table 7).

The ban on New Zealand log imports by China, Japan, and South Korea resulted in their slightly lower production of sawnwood, wood-based panels, and wood pulp (Table 2). South Korea's industries were the most affected, due their current reliance on New Zealand logs.

The large reduction in New Zealand harvests and prices decreased the forest growers' net present gross revenue by US$8,222 million, regardless of the spread of Nectria (Table 6). Increases in gross revenue for New Zealand's other wood product industries — due to increased production — failed to compensate for the loss to the growers, resulting in total gross revenue losses of US$5,100 million (Table 5).

The imposition of debarking or a ban on log imports from New Zealand generally increased gross revenues for producers in China and South Korea, but also increased consumer expenditures (Table 5). This fits with the general finding that "consumers pay for quarantine in higher prices and that domestic producers benefit" (Mumford 2002). In New Zealand instead, both producer's gross revenue and consumer's expenditures* were lower (Table 5), due to lower wood product prices.

The increase in consumer expenditures in China and South Korea due to the log import ban needs to be weighed against the potential loss to producers that would arise were Nectria to become established. To estimate this potential loss requires estimates of the likelihood of establishment and potential forest loss (Prestemon *et al.* 2006) in these countries.

CONCLUSION

The economic impact of Nectria on the New Zealand forest sector, a significant exporter of industrial roundwood, was studied for a scenario confining the pest to the current area, and another where it spread at historical rates to affect the South Island and central North Island of New Zealand.

If the main importers of New Zealand logs — China, Japan, and South Korea — did nothing and Nectria were confined to the current area, the net present value

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* Consumer expenditure is the value of consumption, quantity consumed multiplied by price per unit.

of New Zealand's forest sector gross revenues would be US$34 million lower over the period 2002 to 2030. Were Nectria to spread throughout the South Island and the central North Island of New Zealand, the gross revenue loss could reach US$612 million.

Nectria alone would leave New Zealand's production of processed wood products relatively unaffected, regardless of its spread. Most of the change would be in lower industrial roundwood exports because of lower harvests tied to the stock reduction due to Nectria.

Trade measures imposed by the main importers of New Zealand logs in response to the presence of *N. fuckeliana* in New Zealand would have an impact on the New Zealand forest sector well beyond the direct effect of the pest on the volume of growing stock. If debarking of logs or another costly phytosanitary measure was imposed by importers, or if they banned New Zealand logs altogether, New Zealand growers could lose US$1,202 million to US$8,222 million, depending on the extent of *N. fuckeliana* spread and on the response of importers. Nevertheless, these losses to growers would be partly, and in some cases more than totally, offset by increased domestic production of processed wood products due to the lower cost of industrial roundwood.

Overall, the predicted changes to forest sector gross revenue varied from a loss of US$4,644 million for the scenario where Nectria spread throughout the South Island and the central North Island and New Zealand logs were banned by China, Japan, and South Korea, to a gain of US$1,654 million when Nectria was confined to its current area and China, Japan, and South Korea demanded that logs be debarked.

For producers in New Zealand and consumers in importing countries the best trade measure, in terms of changes in producer revenues and consumer expenditures, is debarking. The imposition of a debarking requirement by New Zealand's export markets would have less impact on the New Zealand total sector, and on forest grower producer revenue, than a ban. Producers in the export markets would benefit more from a ban, in terms of both increased producer revenue and reduced likelihood of forest loss due to establishment of Nectria. Consumers in export markets, however, would be worse off with the imposition of any trade measure.

In interpreting these results it must be remembered that the analysis involves a number of assumptions about disease behaviour and impact that may not necessarily be fulfilled. Currently there is no evidence that Nectria has spread by unnatural means beyond the current infected area, nor that the disease will be vectored on logs. A study is under way at present to determine fungal survival on forest produce and debris. Also, the analysis does not allow for the impact of disease management strategies that are being developed under a research programme currently under way (Dick *et al.* 2006).

Nonetheless, this assessment provides information about the possible long run effects on producers and consumers, considering trade policy responses by New Zealand's principal trading partners. This information will be helpful in deciding how much to spend to manage pest spread. The estimated effects of Nectria — US$34 million to US$612 million depending on the extent of the spread, even without reaction from importers of New Zealand logs — suggests that research aimed at reducing Nectria spread and impact, such as tree selection, planting alternative species, or modified silvicultural treatments, could yield significant benefits.

The study findings also contribute to assessment of possible trade measure responses by New Zealand's export markets, by determining the costs and benefits to producers and consumers of wood products in New Zealand and in its export markets China, Japan, and South Korea. To identify the best policy response, however, would require additional technical information on the efficacy of alternative phytosanitary regulations, the likelihood of Nectria establishment, and magnitude of potential forest loss associated with establishment in the export markets.

ACKNOWLEDGMENTS

The research leading to this paper was supported in parts by FRST contract C04X0203, the New Zealand Forest Research Institute Ltd, the ISAT Linkages Fund, the USDA-CSREES NRI grant 2003-35400-13816, the PREISM program of the USDA-ERS, the USDA Forest Service Southern Research Station, and McIntire-Stennis Grant 4879. We thank Gordon Hosking for his help in developing, and providing data for, the Nectria spread and policy scenarios. The paper benefited from very useful comments from Hamish Marshall, the Nectria Focus Group, and six anonymous reviewers. Any remaining errors are our sole responsibility.

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Appendix A

GFPM MATHEMATICAL FORMULATION

Spatial Global Equilibrium

(All variables refer to one specific year)

Objective function

The objective function of the Global Forest Products Model follows Samuelson (1952), identifying production, consumption, and trade flows so that producer plus consumer surplus minus transfer costs is a maximum:

$$\text{(A.1)} \quad \max = Z \sum_i \sum_k \int_0^{D_{ik}} P_{ik}(D_{ik})\, dD_{ik} - \sum_i \sum_k \int_0^{S_{ik}} P_{ik}(S_{ik})\, dS_{ik}$$
$$- \sum_i \sum_k Y_{ik} m_{ik}(Y_{ik}) - \sum_i \sum_j \sum_k c_{ijk} T_{ijk}$$

where i,j = country, k = product, P = price in U.S. dollars of constant value, D = final product demand, S = raw material supply, Y = quantity manufactured, m = cost of manufacture, T = quantity transported, c = cost of transportation.

End product demand

$$\text{(A.2)} \quad D_{ik} = D^*_{ik} \left(\frac{P_{ik}}{P_{ik,-1}}\right)^{\delta_{ik}}$$

where D^* = current demand at last year's price P_{-1}, δ = price elasticity of demand (Table B.1). D^* depends on last year's demand, and country GDP growth (A.7).

Primary product supply

$$\text{(A.3)} \quad S_{ik} = S^*_{ik} \left(\frac{P_{ik}}{P_{ik,-1}}\right)^{\lambda_{ik}}$$

where S^* = current supply at last year's price, λ = price elasticity of supply (Table B.2). S^* depends on last year's supply, and on exogenous or endogenous supply shifters (A.8 and A.9).

For recycled paper, $S_{ik} \le S_{ik}^{U}$, where S^U = upper bound on supply, which depends on domestic paper consumption in the previous year (A.10).

Country total wood supply is $S_i = S_{ir} + S_{in} + \theta_i S_{if}$, where r = industrial roundwood, n = other industrial roundwood, f = fuelwood, θ = fraction of fuelwood that comes from the forest (Table B.3). $S_i \le I_i$ where I_i = forest stock.

Material balance

$$\text{(A.4)} \quad \sum_j T_{jik} + S_{ik} + Y_{ik} - D_{ik} - \sum_n a_{ikn} Y_{in} - \sum_j T_{ijk} = 0 \qquad \forall\, i, k$$

where a_{ikn} = input of product k per unit of product n (Table B.4). The shadow prices of the material balance constraints give the market clearing prices, P.

Trade inertia

(A.5) $T^{L}_{ijk} \leq T_{ijk} \leq T^{U}_{ijk}$

where the superscripts L and U refer to lower and upper bounds, respectively (see Equation A.12).

Manufacturing cost

Manufacturing is represented by input-output coefficients and a manufacturing cost (Table B.4). The latter is the cost of the inputs not recognised explicitly by the model (labour, energy, capital, etc.):

(A.6) $m = m^{*}_{ik} (\frac{Y_{ik}}{Y_{ik,-1}})^{S_{ik}}$

where m^* = current manufacturing cost at last year's output, s = elasticity of manufacturing cost with respect to output (Table B.4). m^* depends on last year's manufacturing cost.

Market Dynamics

(Unless otherwise indicated, variables and parameters refer to one country, one commodity, and one year)

Shifts of demand

(A.7) $D^* = D_{-1}(1 + \alpha_y g_y)$

where g_y = GDP annual growth rate, α = elasticity (Table B.1).

Shifts of supply

Industrial roundwood and fuelwood:

(A.8) $S^* = S_{-1}(1 + \beta_I g_I + \beta_{y'} g_{y'})$ for $k = r,n,f$

where g_I = rate of change of forest stock (Equation 1), $g_{y'}$ = GDP per capita annual growth rate, β = elasticity (Table B.2).

Waste paper and other fibre pulp (Table B.2):

(A.9) $S^* = S_{-1}(1 + \beta_y g_y)$

The upper bound on waste paper supply shifts according to:

(A.10) $S^U = \sum_{k} r_k D_{k,-1}$

where r_k is the maximum possible recovery rate for paper of grade k, which may change exogenously over time.

Changes in manufacturing coefficients

The input-output coefficients, the a_{ikn}'s in (A.4), may change exogenously over time, in particular to reflect increasing use of recycled paper in paper manufacturing (Table B.4).