Predicting susceptibility of white fir dfring a drought-associated outbreak of the fir engraver, *Scolytus ventralis*, in California

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Received May 4, 1993

Accepted August 5, 1993

FERRELL, G.T., OTROSINA, W.J., and DEMARS, C.J., JR. 1994. Predicting susceptibility of white fir during a drought-associated outbreak of the fir engraver, *Scolytus ventralis*, in California. Can. J. For. Res. 24: 302–305.

Phenotypic traits were compared with a vigor (growth efficiency) index for accuracy in predicting susceptibility of white fir, *Abies concolor* (Gord. & Glend.) Lindl., during a drought-associated outbreak of the fir engraver, *Scolytus ventralis* LeC., in the central Sierra Nevada at Lake Tahoe, California. Predictor variables were estimated for 633 firs in six forest stands in 1987. After 2 years, virtually all of the trees had been attacked by the beetle, and 230 (36.3%) had been killed or were dying. In all of the predictor variables, firs that were killed differed significantly from those that survived. Compared with survivors, firs that died averaged shorter, more ragged crowns and lower growth efficiencies. Also, firs that died were more frequently dominant or codominant in the stand canopy and, when characterized in 1987, more often evidenced signs of being under current or recent (in 1985 or 1986) attack by the beetles. But, on either an individual tree or a stand basis, predictive accuracy was inadequate. On an individual tree basis, discriminant functions using either the phenotypic traits or vigor index as predictors produced overall percentages of correct classification little or no higher than would be obtained by predicting all trees would survive. On a stand basis, regression models using stand means for either the phenotypic traits or vigor index and white fir basal area as predictors statistically accounted for at least 95% of observed variation in basal area of white fir killed. But another model. using only white fir basal area, performed as well. The "best" model, containing white fir basal area and total stand basal area, accounted for over 98% of observed variation;

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Des caractéristiques phénotypiques furent comparées à un indice de vigueur (efficacité de croissance) dans le but de prédire la susceptibilité du sapin du Colorado, *Abies concolor* (Gord. & Glend.) Lindl,, au scolyte sculpteur du sapin, *Scolytus ventralis* LeC., durant une épidémie associée à une sécheresse dans le secteur du lac Tahoe situé en Californie dans la région centrale de la Sierra Nevada. Un ensemble de variables indépendantes fut mesuré en 1987 sur 633 sapins répartis dans six peuplements forestiers. Aprb 2 années, tous les arbres furent attaqués par le scolyte et 230 (36.3 %) d'entre eux ttaient morts ou mourants. Dans le cas de chacune des variables indépendantes, les sapins morts ttaient significativement différents des sapins ayant survécus. Les sapins ayant succombts Ctaient caractérisés par des cimes plus courtes et moins fournies de mime que par une efficacité de croissance inférieure à celle des arbres ayant survtcu. De plus, les sapins ayant succombé se retrouvaient plus souvent dans la strate des dominants et des codominants et montraient souvent en 1987 des dégâts d'attaques récentes par l'insecte en 1985 ou 1986. Toutefois, que ce soit sur une base d'arbre pris individuellement ou de peuplement. la precision des prédictions était inadbquate. Sur une base d'arbre pris individuellement, lcs fonctions discriminantes utilisant les caractéristiques phénotypiques ou l'indice de vigueur n'ont pas permis d'obtenir un pourcentage de bonne classification suptrieur à ce qui aurait été obtenu en prédisant que tous les arbres survivraient. Sur une base de peuplement, les modèles de régression utilisant les moyennes des caractéristiques phénotypiques ou les moyennes d'indice de vigueur et la surface terrière en sapin du Colorado comme variables indépendantes expliquaient au moins 95% de la variation de surface terrière d'arbre mort. Néanmoins, un autre modèle utilisant seulement la surface terrière de sapin du Colorado fut aussi performant que les précédents. Le « meilleur » modèle uiilisant la surface terrière de sapin Colorado et la surface territre totale du peuplement a permis d'expliquer plus de 98 % de la variation observée.

[Traduit par la rédaction]

Introduction

White fir, *Abies concofor* (Gord. & Glend.) Lindl., and other true firs (*Abies* spp.) in western North America are attacked and frequently killed by the fir engraver, *Scolytus ventralis* LeC. Biology; behavior, and ecological relationships of this bark beetle have been summarized recently by Berryman and Ferrell (1988). The beetle mines and reproduces in the cambial zone of the trunk. Most firs are resistant: only those weakened by disease, injury, intertree competition, or water stress are susceptible. Normally, fir engraver populations and the fir mortality they cause occur only at low levels, but sporadic outbreaks, associated with droughts or sometimes with epidemics of fir-defoliating insects, have caused greatly increased mortality of firs in nearly every decade of this century (Berryman and Ferrell 1988).

Hazard-rating systems, predicting which trees are susceptible to the fir engraver, have been developed for white fir in northern California (Ferrell 1980, 1989). These systems use phenotypic traits (crown and bole characteristics) to predict the probability of tree death within 5–10 years. Based on observations that long-standing stress caused by factors such as disease or intertree competition are usually reflected in poor crown or bole condition, these systems were developed for predicting fir mortality when fir engraver popula-

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Printed in Canada / Imprimé au Canada

tions are at their normally low levels. Whether such systems would be useful during outbreaks caused by rapid onset of stress during droughts was uncertain.

Waring et al. (1980) developed a vigor index estimating growth efficiency of trees as the quantity of wood produced per unit of leaf area. In a field experiment, this index was shown to respond to relatively rapid. changes in tree stress and was a valid indicator of tree susceptibility or resistance to bark beetles (Waring and Pitman 1985).

This paper reports a test of a large sample of white firs in which phenotypic traits were compared with a growth efficiency index to determine their usefulness in predicting tree susceptibility during a drought-caused fir engraver outbreak.

Methods

Transparencies of color aerial photos taken in April 1987 at a scale of 1:8000 of the Lake Tahoe Basin in the central Sierra Nevada of California were interpreted to detect stands containing white firs with recently faded crowns from fir engraver infestation in summer 1986. The stands selected as candidates for study were densely stocked with white fir as a major component and were not scheduled to be logged within the next 2 years. (Previous results (Berryman and Ferrell 1988) suggested that a continuation of the drought would likely lead to further increases in fir engraver-caused mortality in the region.) The stands also had to contain at least some trees recently killed by the fir engraver, a criterion not difficult to meet in most such stands because of subnormal precipitation in this region over the preceding 2 years. Six study stands were selected at random from a list of 23 eligible stands. These stands, all located at ca 2000 m elevation in the southern and western portions of the Lake Tahoe Basin, were considered to be a representative sample of currently infested stands in the area.

In May 1987, a sampling cluster was established within each of the study stands. Cluster locations were indicated on the photos and on the ground. Each cluster consisted of an L-shaped constellation of five points located at 40-m intervals: one at center, two along the North-South axis, and two along the East-West axis. Cluster location within the stand was selected by random coordinates to the central prism point from an arbitrarily selected starting point on the stand perimeter. Candidate clusters with any prism point lying within 30 m of the stand boundary were rejected. At each point a IO-factor prism was used to select white firs as test trees. Only firs with stem diameter at breast height (DBH. measured at ca 1.5 m above ground) greater than 10 cm were accepted as study trees because the fir engraver seldom attacks trees with smaller diameters. For the purposes of the test, bias introduced by prism selection of study trees was not considered to be serious because the fir engraver initially attacks living hosts over 10 cm DBH at random (Berryman and Ferrell 1988). Random attack implies that firs are initially attacked with probabilities proportional to their stem surface areas. Thus, as stem surface area is also a function of stem diameter, prism selection was expected to be relatively unbiased with respect to initial fir engraver attack of host trees.

Candidate predictor variables estimated for each tree are lefined in Table 1. The phenotypic variables were estimated visually and, except for pitch streamers, were those used in previous risk-rating systems for white fir (Ferrell 1980, 1989). Widths of the 1986 annual ring and the sapwood were measured ± 1 mm) on an increment core obtained by boring the stem on an arbitrarily selected radius at 1.5 m above ground. Sapwood was distinguished from the opaque heartwood by its translucency. These measurements were used to calculate the Waring Vigor Index based on the close correlation between cross-sectional area of sapwood and leaf area of trees (Grier and Waring 1974).

Status of test trees (live, dead, or dying) was surveyed in October 1989. *Crowns* and boles were examined for evidence of fir engraver attack and infestation. Dead and dying infested firs, resulting from fir engraver attack during the summer flight seasons of 1987–1989, were detected by dead or dying tree crowns and presence of boring dust in bark crevices. Fir engraver was confirmed as the agent of mortality by exposing the gallery patterns on the surface of the sapwood at ca 2 m above ground. Fir engraver attack of surviving firs was detected by pitch streamers issuing from gallery entrance tunnels.

The data *were* analyzed using MINITAB (Ryan et al. 1985). Status of the predictor variables in killed and surviving test trees was compared by r-test (continuous variables) or χ^2 contingency test (class variables) at p *(a)* = 0.05. Ability of the predictor variables to predict subsequent death or survival of individual trees was assessed by linear discriminant functions (pooled covariance matrix, equal prior probabilities). "Best" functions were those producing the highest overall percentages of correct classification. Ability of stand means for the predictor variables, for total (all tree species) basal area, and for basal area of white fir to statistically explain observed variation in the basal area of white fir test trees killed in the stands was assessed by comparing R^2 of all one- and two-variable linear regression models containing these as predictor variables. "Best" models were those with the highest R^2.

TABLE 1. Definition of phenotypic and growth efficiency variables assessed for predicting white fir susceptibility to fir engraver beetles

Variable	Definition
Live crown percentage	Percentage of tree height in live crown
Ragged percentage	Percentage of crown dead, dying, or missing
Crown class	Crown position in stand canopy, coded as (1) isolated, (2) predominant, (3) dominant, (4) codominant, (5) intermediate, (6) suppressed
Pitch streamers	Pitch streamers on bole from fir engraver attack, coded as (0) none, (1) l-10, (2) >10
Vigor index	Radial growth efficiency as ratio between cross-sectional areas of the most recent annual-ring and sapwood (Waring et al. 1980)

Results and discussion

By October 1989, 230 (36.3%) of 633 firs sampled had been killed or were dying from fir engraver attack. Virtually all test trees had been attacked by fir engravers, as evidenced by one or more pitch streamers on the bole surface, but we were unable reliably to distinguish those formed during the test from those formed earlier. Analyses of previous fir engraver outbreaks (Berryman and Ferrell 1988) suggest that the high levels of beetle attack and fir mortality were largely attributable to continued drought in 1988-1989.

Trees killed during the test differed significantly from surviving trees in each of the predictor variables (Table 2). Compared with surviving trees, killed trees tended to have shorter and more ragged crowns, were more frequently of the dominant or codominant crown class, and had a greater incidence of pitch streamers indicating fir engraver attack prior to the test. Also, in the year before the test (1986), growth efficiency (Waring Vigor Index) of killed trees averaged about 28% less than that of surviving trees.

TABLE 2. Status of phenotypic and vigor index variables in killed and surviving white firs during a fir engraver outbreak at Lake Tahoe, 1987-1989

Variable'	Killed trees	Surviving trees	Significance[b] (p)
N	230	403	
Live crown percentage (mean ± SE)	43±1	53±1	10.01
Ragged percentage (mean ± SE)	36±1	32±1	so.05
Crown class (percentage dominant or codominant)	71	57	so.01
Pitch streamers (percentage with one or more)	26	11	so.01
Vigor index (mean ± SE)	0.023±0.001	0.032±0.002	10.01

'See Table 1 for **definitions.**
[b]**Difference** significant according to r-test (continuous variables) or χ^2 (class variables).

TABLE 3. Accuracy of the "best" linear discriminant functions using phenotypic or vigor index' variables to predict death or survival of white firs during a fir engraver outbreak at Lake Tahoe, 1987-1989

Variable"	Percent accurate prediction		
	Killed trees	Surviving trees	Overall
N	230	403	633
Live crown percentage, pitch streamers	74.7	58.1	64.1
Vigor index	77.8	36.0	51.2

[a]**See** Table I for detinitions.

TABLE 4. Stand means for phenotypic traits, vigor index, stand basal area, and mortality of white firs assessed for susceptibility during a fir engraver outbreak at Lake Tahoe, 1987-1989

Stand	Crown (%)	Ragged (%)	Vigor index	Class (%)	Pitch (%)	Total BA[a] (m^2/ha)	Fir BA (m^2/ha)	Fir BAk (m^2/ha)
1	37	32	0.03	56	17	101	82	56
2	62	38	0.02	64	16	79	39	11
3	55	36	0.02	72	13	68	47	13
4	48	31	0.04	76	15	60	43	2
5	54	30	0.05	42	18	79	35	4
6	52	34	0.02	65	18	71	52	20

NOTE: See Table 1 for descriptions of columns 2-6. BA. basal area; **BAk**, basal **area** killed.
[a]**Total** stand basal area for **all** tree species.

Predictive accuracy of the "best" linear discriminant function using the phenotypic variables to predict mortality of individual test trees is compared with that obtained using the vigor index in Table 3. Overall percentage of correct classification was 64.1% for the phenotypic traits and 5 1.2% for the vigor index which either did not much exceed or was less than that obtained by simply predicting all the trees would survive (63.7%). Predictive accuracy for trees that were killed (>74%) appeared adequate, and this is considered important because trees likely to be killed are usually the focus of treatments designed to prevent their infestation by the beetles. But predictive accuracy for survivors seemed inadequate (<59%), as these must comprise the residual stand after treatment. No further attempts were made at prediction on an individual tree basis.

Stand means for the predictor variables, total (all tree species) basal area, white fir basal area, and basal area of white fir killed by the beetles, are given in Table 4. In terms of basal area, percentages of white fir in the stands ranged from 44 to 81%, of which from 5 to 68% were killed by the beetles in 1987-1989.

Among linear regressions using some combination of one or two of the stand means in Table 4 to predict basal area of white fir killed on a stand basis, three models each statistically explained at least 95% of observed variation in white fir basal area killed. Two models contained phenotypic traits (live crown percentage, ragged percentage), one contained the vigor index, and all three contained white fir basal area. But another model containing only white fir basal area performed as well, indicating that neither the phenotypic traits nor the vigor index added appreciably to predictive ability. The "best" model had both white fir basal area and total stand (all tree species) basal area as predictors (R^2 = 0.989). In all models in which they appeared, white fir basal area and total stand basal area had regression coefficients with positive signs, indicating that the higher basal area stands with a large component of white fir tended to suffer greater white fir mortality.

Results were similar to those obtained in the analysis of white fir mortality caused by fir engraver in these stands in 1986-1987 (DeMars et al. 1988).

Under conditions of our test, the phenotypic traits or the vigor index did not appear adequately to predict white fir susceptibility to the fir engraver on either an individual tree, or a stand, basis. Our test occurred during a drought-caused fir engraver outbreak when most white firs were probably to some degree susceptible because of widespread drought stress and epidemic populations of attacking beetles, both of which are known to cause increased susceptibility of fir engraver host trees (Berryman and Ferrell 1988). Under these conditions, neither phenotypic traits nor growth efficiency (Waring Vigor Index) may be very useful for predicting white fir susceptibility to the fir engraver beetle, but stand basal area and composition appear to be good predictors.

Acknowledgments

We thank Patti Weldon for field assistance, Laurie Swiadon for data management, and USDA Forest Service personnel of the Lake Tahoe Basin Management Unit for help in locating plots.

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