Eco-Physiology Approach to Projecting Tree Stress and Vigor in FVS

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Abstract—Tree stress and vigor affect, and are affected by, damage agents such as insects and pathogens. Stand density and tree growth rates serve as indicators of stress and vigor, but drought events and other disturbances are also important components of stress and vigor status. Site factors must also be considered when relating stand density to stress. In this paper, the FVS-BGC hybrid model has been used to analyze tree and stand vigor at different time scales, under a number of hypothetical management, climate, and site scenarios for lodgepole pine stands in the Central Rocky Mountains. Results suggest a quantifiable relationship between stand density, soil moisture, and tree vigor that can be projected using the FVS-BGC model. Example simulations using FVS-BGC relates stand density, site, and precipitation with a stem growth/leaf area vigor index. The timing of simulated moisture stress within a year appears to be correlated with the mountain pine beetle flight period. Results related to stand basal area appear to agree with management guideline to lower mountain pine beetle hazards. This approach may be useful in enhancing FVS insect and pathogen extensions and has the potential to better explain the limiting factors to growth for different sites and stand structures.

Consideration of insect and pathogen effects on stand projections is a component of the Forest Vegetation Simulator (FVS) system (Wykoff and others 1982). Tree stress and vigor affect, and are affected by, damage agents such as insects and pathogens, so direct estimates of these biological conditions could improve FVS projections. We use the term “stress” to refer to conditions that inhibit normal tree functioning, and “vigor” to generally refer to the efficiency with which a tree or stand is utilizing its resources.

Stress factors, such as limited soil moisture, affect basic physiological processes such as photosynthesis and allocation. Although these processes can be difficult to track individually, the net effects of these processes can be described in terms of growth efficiency, or vigor. In this study, we analyze the relationships between two stress factors—soil water availability and competition—and tree vigor. We represent vigor in terms of an index proposed by Waring and others (1980). Soil moisture availability is directly simulated; competition is expressed in terms of stand density (as basal area per acre).

Pine bark beetles are important forest mortality agents that appear to be sensitive to vigor conditions. It has long been held that tree “vigor” is an important factor in pine-bark beetle interactions (Eaton 1941; Johnson 1951). Moisture conditions are often limiting in pine forests and are thus a factor in determining tree and stand vigor (Berryman 1976). Stand moisture conditions are the result of site conditions including soil texture and depth, and of inter-plant competition, damage from other agents, and climate including variation in precipitation. Forest entomologists have developed semiempirical stand hazard rating systems for tree-vigor sensitive insects such as pine bark beetles. The systems primarily use measures of basal area, trees per area, or both, to represent the vigor status. Other factors, such as tree diameter or phloem thickness, have been included to represent suitable beetle habitat once the tree is successfully attacked. The problem with these systems is that they poorly account for variation in site and climate conditions, and not at all for annual variation in weather (Amman and Anhold 1989). More data-intensive rating systems include phloem thickness and changes in relative growth rates, based on ring measurements. This captures some of the variation in weather factors, but even these cannot be easily used to project future conditions because empirical growth projection systems, such as FVS, use average, multiyear time steps that ignore within- and between-year variability.

Tree growth is generally assumed to be directly correlated to photosynthetic production. However, not all of the fixed carbon is used for growing stems, roots, and leaves. In some trees, one important use is to produce oleoresin compounds (pitch), which are used by the tree to seal wounds and defend against insect attacks. The toxic, sticky resin produced by the tree can flow out through holes produced by bark beetles, and kill the beetles. It can also play a role in limiting the spread of beetle-introduced fungi through the phloem.

In pine trees, resin is produced under two conditions. It may be *preformed* in resin canals in the phloem, or it may be *induced* as a response to wounding. There is evidence that production of preformed resin may occur during times of moderate moisture stress (Lorio 1986, 1993; Lorio and Sommers 1986; Wilkens and others 1998), and that induced resin is more available during times when high levels of carbohydrates are moving through the phloem to the roots (Herms and Mattson 1992), in times of low moisture stress. In times of high moisture stress, little or no photosynthesis takes place, and the tree must rely on whatever preformed resin was produced earlier. The preformed resin reserves

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are limited and will be exhausted if the tree is attacked by a large number of beetles. The relationship of tree vigor and resin defenses has been used to relate tree vigor to mountain pine beetle attacks (Waring and Pitman 1985).

In recent years, a number of tree physiology growth models have been developed that simulate photosynthesis processes (Battaglia and Sands 1998). Some of these models provide outputs that correlate with tree vigor status and defensive resin production. Stand-BGC (Milner and Coble 1995) is a process-based model that has been designed to simulate the allocation of total stand photosynthate back to individual trees. FVS-BGC (Milner and others, these proceedings; McMahan and others 2002) is an adaptation of the Stand-BGC model designed to function as an extension of the Forest Vegetation Simulator (FVS) system (Wykoff and others 1982). FVS-BGC links the process-based modeling approach from Stand-BGC to the FVS empirical growth approach, and uses the management options in FVS to simulate stand manipulations.

The FVS-BGC extension provides a suite of carbon- and water-cycle output files at the tree and stand levels, at both daily and yearly time steps, as well as standard FVS stand tables derived from the process model. The inputs to FVS-BGC include the primary factors that determine tree and stand vigor (namely, site and climate), and the outputs correspond to observable indicators of stress and vigor status. We have used the FVS-BGC model to demonstrate its usefulness for analyses of stand and tree vigor as it relates to pine bark beetles.

Methods

FVS-BGC requires two sets of inputs: those required for a standard FVS simulation; and BGC specific inputs, which include climate files, soils data, and physiology parameters. The simulation was performed on a lodgepole pine stand, from the White River National Forest, in central Colorado. The initial stand, chosen to be typical of the area, had these characteristics:

Basal area:	174 ft^2/acre	[≈ 40 m^2 / ha]
Trees per acre:	534	[≈ 216 / ha]
Q.M.D.:	7.7 inches	[≈ 19.6 cm]
Mean top height:	71 ft	[≈ 21.6 m]

FVS thinning keywords were used to create five additional levels of stand density. Stands were created having basal areas of 80, 100, 120, 140, and 160 ft^2/acre. These stands were created (using FVS keyword THINDBH) by removing a constant proportion from every tree record in the tree list; consequently, the stand's diameter distribution structure was not altered.

A single year's daily climate input from Vail, CO, was used as input. The year chosen had a total annual precipitation close to the 20-year mean for that site (μ=22.0; σ = 4.5 inches); it also had similar monthly means, hence the intraannual distribution of moisture was similar to patterns under which the stand developed.

The MTCLIM model (Hungerford and others 1989) was used to adjust the weather data for the elevation of the stand. Seven separate weather input files were created representing a range of dry to wet conditions. These files were created by scaling each daily precipitation event by a constant so that the year's total precipitation would sum to 60, 75, 90, 100,110, 125, or 140 percent of the long-term average annual precipitation. (This range captures most of the observed variability, and represents approximately two standard deviations on either side of the mean annual precipitation.) The simulations were run for 3 years each. All simulations used the average precipitation file in the first year, followed by 2 years of one of the proportionally adjusted precipitation files. Soil data were obtained from a forest soil survey.

Results

Within-Year Stress

Figure 1 displays the relationship between daily precipitation and simulated soil water potential for one of the modeled combinations of stand density and precipitation during the summer months. Before July 1, soils in this area generally have high water availability (less negative water potentials) from snowmelt. The simulated drying process results from evapotranspiration exceeding precipitation.

Figure 2 displays the simulated soil water potential for three of the modeled precipitation levels during the summer months, for the 120 ft^2/acre stand. Mountain pine beetles (MPB; *Dendroctonus ponderosae*, Hopkins) in this area primarily emerge and attack sometime between early July and early September, with the attack period generally concentrated in the middle of the that time. Actual MPB flight times can vary year to year and can occur over small time intervals. Note that the amount of time this stand is under moisture stress varies significantly during the normal beetle attack period depending upon the amount of precipitation. The possible temporal correspondence of MPB flight to the period of moisture stress might influence the successfulness of MPB attacks.

Figure 3 displays the simulated soil water potential for three of the modeled stand density levels, all simulated using the average (100 percent) precipitation level throughout the simulation. This range of stand densities bracket the

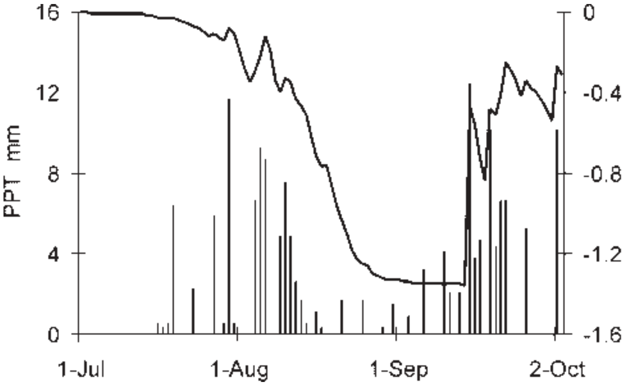

Figure 1—Daily precipitation (PPT, in millimeters [bars]) and simulated soil water potential (SWP, in megapascals [line]) for July through September for an "average" precipitation year.

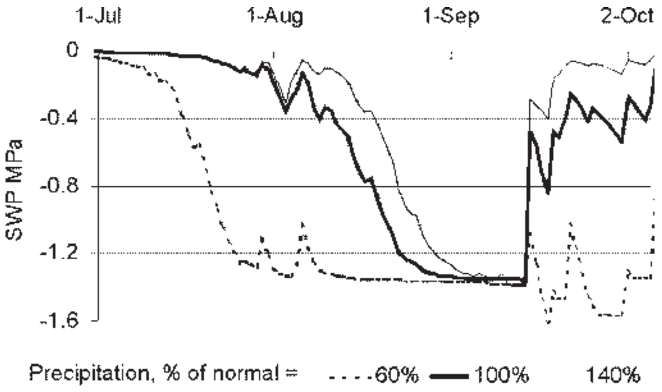

Figure 2—Soil water potentials in year 3 for the 120 ft²/acre basal area stand under three precipitation regimes. Increasing simulated precipitation delayed the onset date of moisture stress; decreasing simulated precipitation quickened the onset of moisture stress. The period over which the mountain pine beetles are known to fly in this area is shaded.

levels that are regarded as having low to high risk for beetle infestation. Again, note that the amount of time this stand is under moisture stress varies significantly for this range of stand densities.

Annual-Level Vigor

Waring and colleagues (Waring and others 1980; Larsson and others 1983; Mitchell and others 1983; Waring and Pitman 1985) performed a series of studies involving pines and mountain pine beetle susceptibility that were based on the assumption that photosynthate allocation is hierarchical. They proposed that allocation to defensive oleoresins was lower in the hierarchy than either leaf or stem growth. They produced a vigor index (Waring and others 1980) that they defined as:

$$\frac{grams/year\ of\ stemwood\ produced}{m^2\ leaf\ area\ (projected)}$$

The Waring vigor index (WVI) was based on the premise that the ratio of stem growth to leaf area was indicative of the amount of photosynthate available for oleoresin production.

As applied in field studies by Waring and others, this value used stemwood production estimated from diameter increment, and leaf area estimated from sapwood area. In FVS-BGC, stemwood growth and leaf area are available as simulation outputs, so we can estimate the WVI with the model.

A field study (Waring and Pitman 1985) related the estimated WVI of lodgepole pine trees on an Oregon site to mountain pine beetle attacks. The study showed a distinct threshold at about 100 grams of stemwood production per m^2 of leaf area. Trees below this level suffered many attacks; with a positive linear relationship between the WVI below this level and the number of attacks it took to kill the tree. Above this level, few trees were attacked, none successfully.

Figure 4 shows WVI values for individual trees from FVS-BGC simulations for two stand densities, at average precipitation levels, of our example lodgepole stand. In these simulation scenarios, trees in the less dense stand fix more net carbon per unit of leaf area than trees in denser stand. The 80 ft^2/acre represent the thinning density recommended for this area to lower mountain pine beetle hazard (Angwin and others 1996); 180 ft^2/acre for this stand structure would be considered to be at high risk. Note that most of the trees in the 80 ft^2/acre stand fall above the 100 WVI level, and all of the trees in the 180 ft^2/acre stand are below it.

The six levels of stand densities and the seven levels of precipitation were simulated for all 42 combinations, and the stand level WVIs calculated. Figure 5 shows the results of WVI values when plotted, and isopleths estimated, to

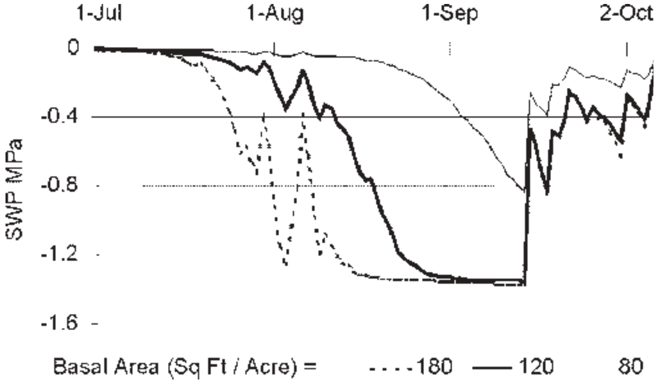

Figure 3—Soil water potentials in year 3 for stands of differing densities during an "average" precipitation year. Decreasing stand density delayed the onset of moisture stress; increasing stand density quickened the onset of moisture stress. Compare with figure 2.

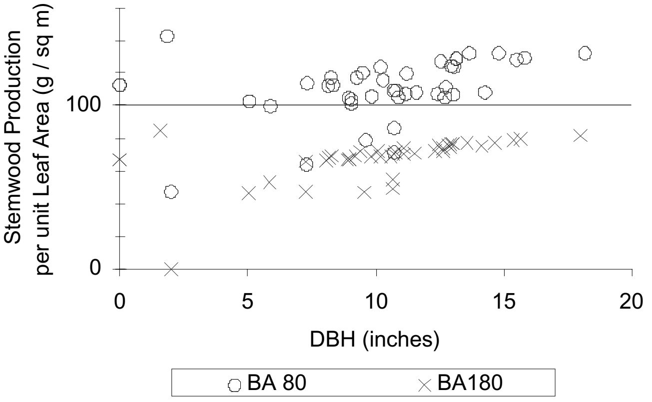

Figure 4—Simulated Waring vigor index values for individual trees from two stands with different stand basal areas (BA). These values are from year 3 of a simulation using the average precipitation for a consecutive 3 years. Note the "threshold" Waring vigor index at 100 g/m².

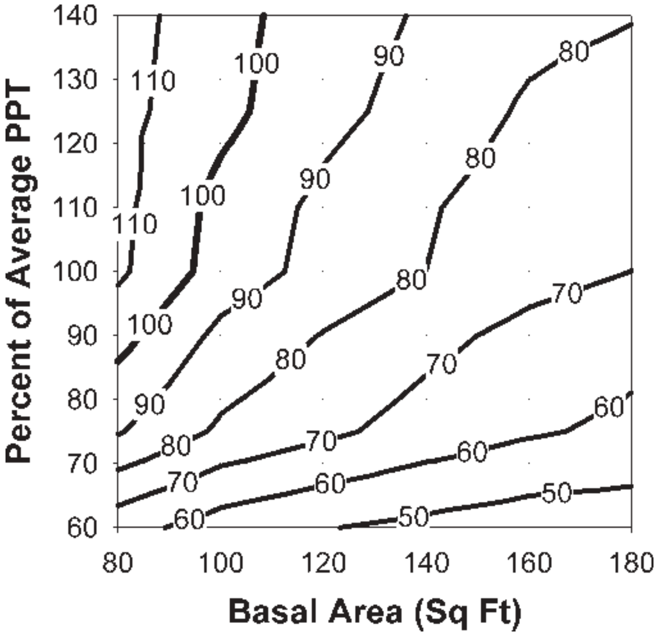

Figure 5—Waring vigor index isopleths by stand density and precipitation for a given site and stand structure. Isopleths connect lines of equal vigor and were generated using SigmaPlot®, from vigor index estimates from 42 simulations (six stand densities times seven precipitation regimes).

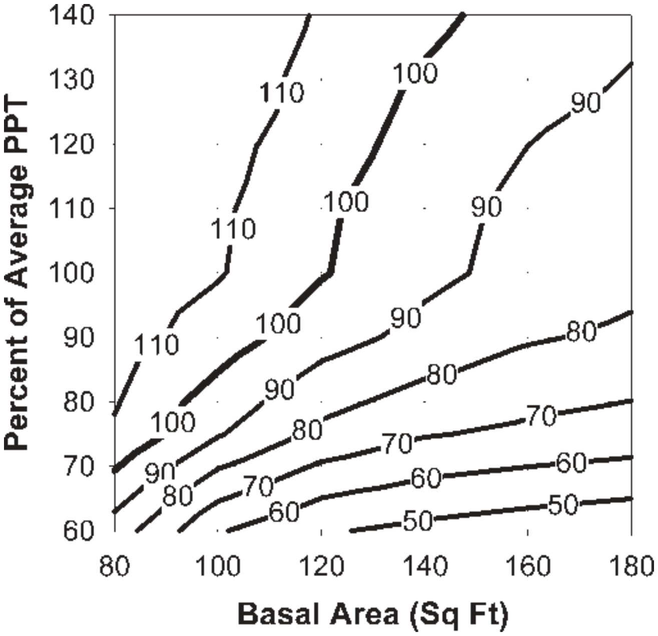

Figure 6—Vigor isopleths generated from 42 simulations that used the same stands and climate files used in the previous example, but simulated on a different site, one having deeper soil with higher total available water. Compared with figure 5, isopleths have shifted to the right and down, indicating generally higher Waring vigor indices for any given moisture/density combination.

show lines of equal vigor conditions. For this site and stand structure, the 100 g/m^2 WVI level corresponds, under average precipitation conditions, to about 92 ft^2/acre basal area. One should not consider the 100 g/m^2 WVI level as being a well-defined threshold because it is based on estimates of the independent variables and the study has not been replicated. These simulation results, however, suggest that the 100 g/m^2 value does correspond to local guidelines where stand conditions would be considered on the border of being at risk.

The soil conditions used for these simulations represent one of two major soil types found in the area from which the example stand was taken. A second soil type in the area, which is deeper and has a different texture, provides more available water to plants. As a way of simulating the effects of varying site qualities, we ran a second set of the same 42 combinations of stand densities and precipitation levels using the second soil type as FVS-BGC input. The results are displayed in figure 6. Note that for average precipitation conditions, the 100 g/m^2 WVI level corresponds to a stand density of approximately 125 ft^2/acre basal area in this better soil.

Conclusions

The physical and biological outputs from the FVS-BGC model can be compared to measurable values obtained from field studies. This creates the potential for validation studies that directly compare simulated results and measured values for the same stand conditions. The simulation results produced by these examples are consistent with the findings of other studies and with local management guidelines. If further testing confirms that the model has the ability to reliably represent stress and vigor conditions for forest stands, the model's outputs may be used to supplement base FVS information and enhance insect and pathogen models. The ability to separate the contributions of site components to both growth and vigor may allow the development of more biologically insightful hazard rating systems. Use of a BGC-based vigor rating system from within FVS also has the potential to improve current FVS insect impact extensions, especially the Mountain Pine Beetle model and the Westwide Pine Beetle model.

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