Is Self-Thinning in Ponderosa Pine Ruled by *Dendroctonus* Bark Beetles?

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Abstract.—Stand density of even-aged stands of ponderosa pine in California seems to be ruled by *Dendroctonus* bark beetles, rather than the suppression-induced mortality common for other tree species. Size-density trajectories were plotted for 155 permanent plots in both plantations and natural stands. Bark beetle kills created a limiting Stand Density Index of 365 which differed little between stands on poor sites east and good sites west of the crest of the Sierra Nevada and Cascade Range. Although good sites would be expected to carry a greater stand density than would poor sites, more explosive bark beetle populations and density-related stem breakage cancel this site advantage.

INTRODUCTION

Northern California has experienced below normal precipitation for 6 of the last 8 years. This moisture deficit coupled with the rapid build up of stand density common in even-aged ponderosa pine (*Pinus ponderosa* Dougl.ex Laws. var. *ponderosa*), especially plantations, has placed many stands at risk from attack by bark beetles. Eaton (1941) was probably the first to recognize the importance of thinning in "bug proofing" stands. Unfortunately, fire destroyed his research plots in the Warner Mountains of northeastern California before results were achieved. Sartwell (1971) continued this work 15 years later and together with Stevens (Sartwell and Stevens 1975) and Dolph (Sartwell and Dolph 1976) established a threshold value of 34 m^2 per ha (150 ft^2 per acre) of basal area above which stands east of the Cascades in Oregon and Washington became susceptible to bark beetle attack. This value has since become well accepted in practice there, as well as, in California.

In California, and especially on the productive sites on the westslope of the Sierra Nevada and Cascade Range, bark beetle-stand density relationships are less well-known. In 1953, Clements was the first to recognize the relationship between stand density and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) mortality. Most entomological investigations, however, have been concerned with the western pine beetle (*D. brevicomis* LeConte) in large, mature trees, because of their high economic and aesthetic value. The influence of stand density on bark beetle mortality of young, even-aged stands of ponderosa pine on the westside is less well-known. Information that does exist is anecdotal because no formal studies have been undertaken.

Sartwell's work suggests that bark beetles are ubiquitous regulators of stand density in young, even-aged stands of ponderosa pine. If this is true, does the Self-Thinning Rule apply? And can a bark-beetle-limited Stand Density Index (SDI) (Reineke 1933) be defined? Also, a question remains as to whether Sartwell's threshold value of 34 m^2 per ha (150 ft^2 per acre) of basal area applies to California and especially to the productive westside sites. The size-density relationship for even-aged ponderosa pine is described and this relationship is compared east and west of the Sierra Nevada and southern Cascade Range crest. Long-term stand development and subsequent

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bark beetle mortality in two levels-of-growing-stock studies are presented as examples.

BARK BEETLES AND THE SELF-THINNING RULE

The Self-Thinning Rule, also known as the –3/2 Power Rule, was proposed some 30 years ago as a universal size-density relationship that applies equally well to fish in a pond and trees in a stand (Yoda et al. 1963). Sixty years ago, Reineke (1933) introduced the rule for forest stands, naming it Stand Density Index. It is calculated as

$$SDI = N^{(\log N + 1.77 * \log D - 1.77)}$$

in which

log = logarithm to the base 10
N = number of trees per acre
D = average stand diameter at breast height in inches.

Reineke proposed a slope for the maximum density line of –1.605. A slope of –1.77, however, has been found to be a better fit for ponderosa pine data sets both in California (Oliver and Powers 1978) and in central Oregon and Washington (DeMars and Barrett 1987). This slope fits this data set, as well. Stand Density Index is displayed with size on the "X" axis and density on the "Y" axis, hence the slope of –1.77. The Self-Thinning Rule is traditionally, displayed with the axes reversed, as in Figure 1.

SDI has a distinct advantage over basal area as a measure of stand density because it is not significantly affected by age and site quality. If a constant SDI indicates the same site occupancy across a range of stand diameters, and site occupancy is a true measure of bark beetle susceptibility; then, a single SDI value would indicate a threshold of susceptibility without reference to mean diameter, site quality, or age. No direct conversion from SDI to basal area per ha is possible, however, because many combinations of mean stand diameter and number of trees will produce identical SDIs but different basal areas.

Size-density trajectories were plotted for 155 long-term permanent plots in both plantations and natural stands throughout northern California (fig. 1A). Twenty-three percent of the plots suffered bark beetle mortality. A size-density relationship is demonstrated with a bark-beetle-limiting SDI 365. This value is considerably below the maximum SDI of 500 used in Region 5 or 429 used in Region 6 for the Forest Vegetation Simulators (Stage 1973) in their respective areas (Personal communication with Gary E. Dixon, USDA Forest Service, Timber Management Service Center, Ft. Collins, CO, April 25, 1995). The SDI values used by the Forest Vegetation Simulators are maximum values, intrinsic to the species, and caused by competition-induced mortality. Occasionally and for short periods, some stands may reach such high levels before bark beetles attack.

It could be argued that a SDI of 365 is the result of increased bark beetle activity during the recent drought. Though this is reasonable, it is refuted by the fact that SDI 365 is identical to the SDI value derived by DeMars and Barrett (1987) from a least squares fit of the natural stand data Meyer (1938) used to construct his normal yield tables.

My contention that bark beetles and ponderosa pine stand development are inexorably linked seems to be supported by the Meyer's basal area-age relationship. Basal area of most other species rises continuously, albeit progressively more slowly, throughout the range of ages presented. In contrast, Meyer's figure 4 shows basal area building up rapidly and then plateauing sharply at age 60 which is about the age when maximum stand density is reached. This is the age at which Sartwell (1971) claims mountain pine beetle outbreaks begin. Actual stand data would, of course, trace a sawtooth pattern after age 60 as episodes of beetle kills reduce the basal area and growth of surviving trees subsequently builds back the basal area.

Stands that approach SDI 365 usually suffer large losses from bark beetle epidemics—losses that equal or exceed periodic growth. However, less dense stands often experience low levels of mortality from endemic populations. Figure 2 suggests that beetle kills from endemic populations can begin when stands reach SDI 230. This stand density could be characterized as the beginning of a "zone of imminent bark beetle mortality." It should be noted, also, that bark beetle epidemics often continue to reduce stand density to levels far

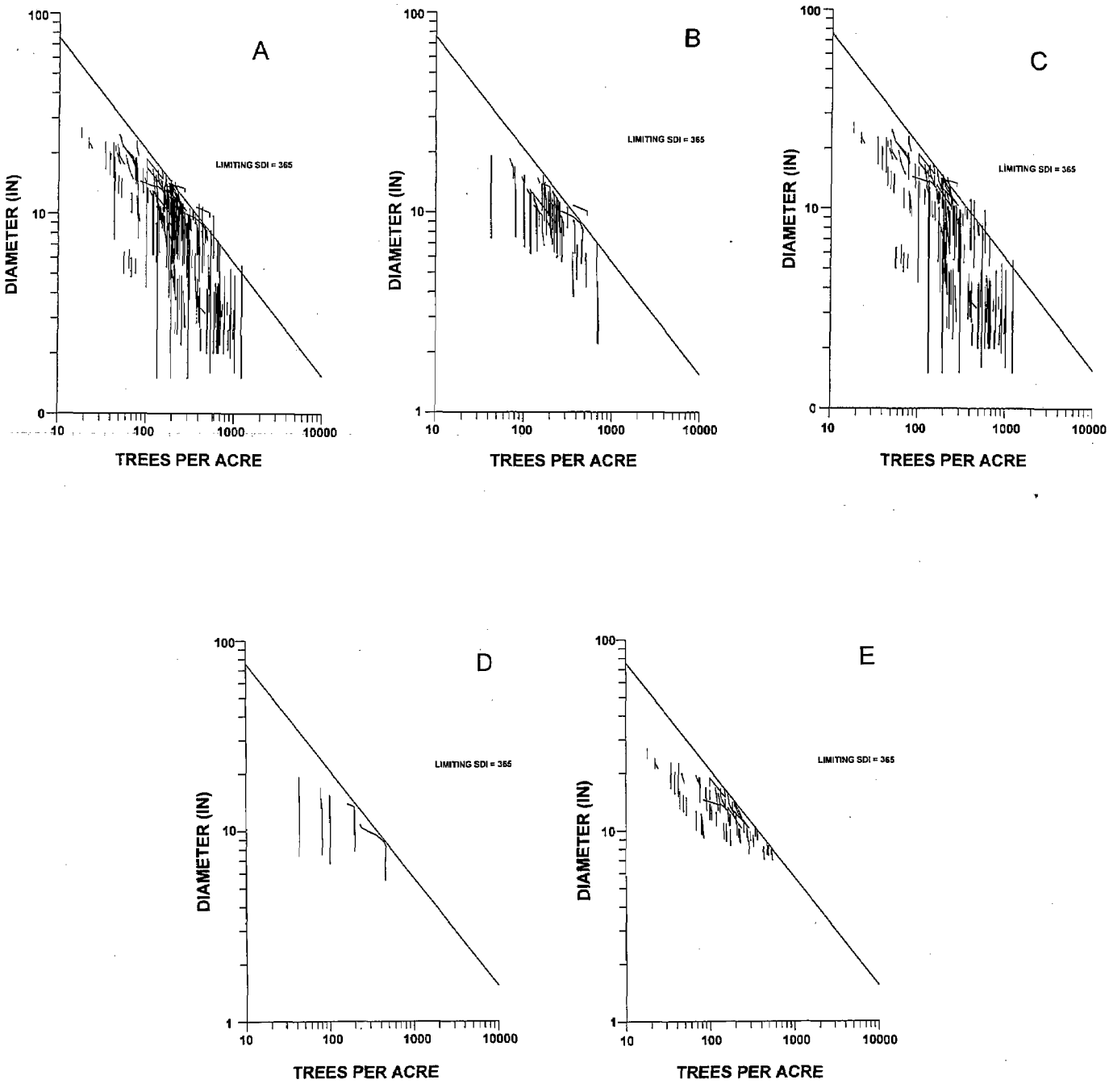

Figure 1.—Size-density trajectories plotted on log-log scales for (A) 155 permanent plots throughout northern California, (B) east and (C) west of the Sierra Nevada and Cascade Range, and levels-of-growing-stock studies at (D) Sugar Hill on the eastside and (E) Elliot Ranch on the westside.

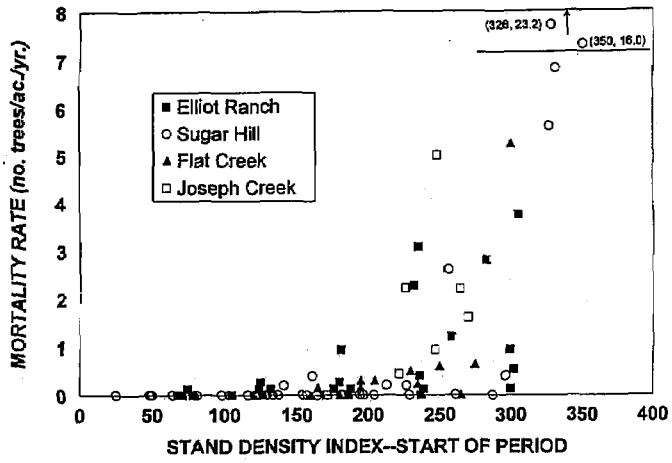

Figure 2.—The relationship of stand density to rate of mortality form *Dendroctonus* bark beetles did not differ between even-aged ponderosa pine stands east and west of the Sierra Nevada and Cascade Range. Flat Creek data from Cochran and Barrett (1993).

below the density that triggered the epidemic and well into this zone of imminent mortality.

The size-density trajectories shown in figure 1 often break off sharply when trees die, rather than forming a gently curving asymptote. In bark beetle epidemics, many trees are killed in a season, large as well as small. Because beetle kills do not cause an increase in average diameter of the residual trees, as when death is concentrated in the subordinate crown classes, the size-density trajectory tends to form a 90° angle.

Because plots are located both east and west of the Sierra Nevada and Cascade Range crest, differences in limiting SDI can be examined between these regions (fig. 1B and C). It appears that limiting SDI for eastside stands maybe a little lower than that for westside stands, but more data are needed to be certain real differences exist.

EXAMPLES FROM LEVELS-OF-GROWING-STOCK STUDIES

Bark beetle-stand density interactions in two levels-of-growing-stock studies, one east and the other west of the Sierra Nevada and southern Cascade Range crest, suggest reasons why differences in limiting SDI between east and west sides may be minor.

Sugar Hill

Four growing stock levels are under test in the extensive plantations at Sugar Hill in the Warner Mountains east of the southern Cascade Range crest (Oliver 1979a). (Incidently, Sugar Hill is near where Eaton (1941) attempted his pioneering study 50 years ago.) The site index of 29 m (95 ft) at 100 years (Barrett 1978) is better than average for the area. Trees were planted to a 2.4- by 2.4 m (8- by 8-ft) spacing in spring 1932. Early survival and growth were good for those days. By 1959, when the study began, the plantation was 28 years old, 15.2 cm (6 in.) in diameter at breast height (dbh) and 5.5 m (18 ft) tall. The four unreplicated plots were thinned to a wide range of SDIs—25, 50, and 128 and the unthinned control of 157. Plots have not been rethinned in the intervening 36 years.

At Sugar Hill stand density in the unthinned plot built steadily to SDI 327 at which time the mountain pine beetle began killing large numbers of trees (fig. 1D). The killing began at age 48 and has continued to the present, killing half the trees and reducing SDI to 264. Killing began 10 years later in the plot thinned to SDI 128, when that plot reached SDI 331. Beetles in this plot have killed 23 percent of the trees, reducing SDI to 291. Similar patterns were found in a nearby natural stand at Joseph Creek and in a plantation at Flat Creek in central Oregon (Cochran and Barrett 1993) (fig. 2).

Elliot Ranch

Five growing stock levels are under test in the Elliot Ranch Plantation on the west slope of the Sierra Nevada (Oliver 1979b). This plantation has a site index of 35 m (115 ft) at 50 years (Powers and Oliver 1978). Trees were planted to a 1.8- by 2.4-m (6- by 8-ft) spacing in spring 1950. By age 20, when the study began, SDI averaged 307 and occasionally exceeded 350. The average tree was 17.8 cm (7.0 in.) dbh and 10 m (33 ft) tall. Each of three plots were thinned to SDIs of 71, 122, 174, 227, and 286. Plots have been rethinned three times in the intervening 25 years.

The western pine beetle and occasionally the red turpentine beetle (*D. valens* LeConte) are at work in the Elliot Ranch Plantation. Again, stocking level

had a profound influence on mortality, but surprisingly, the threshold of bark beetle susceptibility seems no higher than at Sugar Hill. Plots with SDIs above 230 suffered low or endemic levels of bark beetle mortality—97 SDI units lower than at Sugar Hill. Epidemic levels, however, were reached when stand densities reached an SDI of 300—similar to the pattern found at Sugar Hill (fig. 2).

What could account for this startling result? Startling because the site index at Elliot Ranch is twice that of Sugar Hill, and the general belief is that good sites will support a greater stand density than will poor sites. Bark beetle species differences and/or climate may be involved. Three generations of the western pine beetle are often produced during the warm summers on the westside of the Sierra Nevada. In contrast, only one generation is usually produced by the mountain pine beetle during the cooler, shorter summers in the Warner Mountains.

The most important factor, however, may be the repeated presence of volatile resins which attract bark beetles. Western pine beetle populations have been high, historically, in the Elliot Ranch area. Also, the plots have been rethinned three times, each time releasing these resins. Indeed, a few trees were killed by beetles after each thinning—a common phenomenon.

Stem breakage from winter storms is a major source of volatile resins and is a major cause of mortality at Elliot Ranch. Stem breakage and bark beetle mortality would seem to be linked. Most stems broke in the lower crown, leaving a few whorls of living branches—sufficient only to sustain life for a few years. These weakened stems were an ideal substrate for bark beetles and probably sustained a high population which attacked undamaged trees. And, of course, the exposed wood in the break released volatile resins. Like beetle kills, snow breakage was confined almost exclusively to the higher stand densities—SDIs of more than 194. Snow breakage was particularly severe in the winter of 1981–82. Plots with the highest stand density, SDI 303, suffered the most damage. Twenty-eight percent of the trees lost portions of their boles. The proportion of damaged trees fell to 19 percent for plots with SDI 244 and to 7 percent for SDI 194. More lightly stocked plots received virtually no damage. The Sugar Hill plots suffered no stem breakage from winter storms. Indeed, such damage is virtually unknown in northeastern California.

CONCLUSIONS

Several conclusions seem evident from these observations.

a) Sartwell's threshold of 34 m^2 per ha (150 ft^2 per acre) of basal area above which density stands are susceptible to attack by bark beetles appears to be a reasonable average value for California. The eastside plots at Sugar Hill reached a SDI of 329, without disturbance, but then suffered catastrophic losses. The basal area per ha equivalent to SDI 329 is 39 m^2 of basal area per ha for 820 trees per ha, 24.6 cm in average diameter (332 trees per acre, 9.7 in. in average diameter). The westside plots at Elliot Ranch, in contrast, was continually disturbed, either by cutting or storm damage, reaching a SDI of 245 before bark beetles began killing trees. The basal area per ha equivalent to SDI 245 at Elliot Ranch is 31 m^2 of basal area per ha for 415 trees per ha, 31.3 cm in average diameter (168 trees per acre, 12.3 in. in average diameter). Losses at Elliot Ranch reached epidemic levels, however, at a stand density similar to that found at Sugar Hill—SDI 309. The basal area per ha equivalent to SDI 309 is 40 m^2 of basal area per ha for 632 trees per ha, 29.0 cm in average diameter (256 trees per acre, 11.4 in. in average diameter).
b) Self-thinning in even-aged ponderosa pine stands does seem to be ruled by *Dendroctonus* bark beetles. The Self-Thinning Rule usually thought to describe suppression-induced mortality applies equally well to bark-beetle-induced mortality. This outcome is not so surprising when one considers that the root cause of both mortality factors is competition for a fixed amount of site resources. The limiting SDI for ponderosa pine stands in northern California as defined by *Dendroctonus* bark beetles is 365. SDI 230 defines a threshold for a zone of imminent bark beetle mortality within which endemic

populations kill a few trees but net growth is still positive.

c) Bark-beetle-limiting SDI differs little between eastside and westside stands of ponderosa pine. Even though SDI is reported to be insensitive to site quality, the similarity in limiting SDI between the distinctly different eastside and westside growing conditions is surprising. Two mortality agents are more active on the westside and seem to cancel productivity differences. Western pine beetle populations are more explosive on the westside because more generations are produced in a single season. And stem breakage from winter storms, a regular density-related feature of westside stands, is virtually absent in eastside stands.

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