

Water potential in ponderosa pine stands of different growing-stock levels

J. M. SCHMID,¹ S. A. MATA, R. K. WATKINS, AND M. R. KAUFMANN

USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, 240 W. Prospect,
Fort Collins, CO 80526-2098 U.S.A.

Received August 28, 1990

Accepted January 2, 1991

SCHMID, J. M., MATA, S. A., WATKINS, R. K., and KAUFMANN, M. R. 1991. Water potential in ponderosa pine stands of different growing-stock levels. *Can. J. For. Res.* **21**: 750-755.

Water potential was measured in five ponderosa pine (*Pinus ponderosa* Laws.) in each of four stands of different growing-stock levels at two locations in the Black Hills of South Dakota. Mean water potentials at dawn and midday varied significantly among growing-stock levels at one location, but differences were not consistent. Mean dawn and midday water potentials within growing-stock levels significantly decreased during the summer but showed minor increases during the overall decline. Stress levels were considered high enough to influence physiological functioning and, therefore, influence susceptibility to mountain pine beetle (*Dendroctonus ponderosae* Hopk.) attack. Mountain pine beetle infestations did not develop within the stressed stands, which suggests that resistance may be only one factor in the outbreak scenario.

SCHMID, J. M., MATA, S. A., WATKINS, R. K., et KAUFMANN, M. R. 1991. Water potential in ponderosa pine stands of different growing-stock levels. *Can. J. For. Res.* **21** : 750-755.

Nous avons mesuré le potentiel hydrique de cinq pins ponderosa (*Pinus ponderosa* Laws.) dans chacun des quatre peuplements présentant des niveaux de volume sur pied différents, sur deux sites dans les Black Hills, Dakota du Sud. Les potentiels moyens à l'aube et à midi des différents niveaux de volume sur pied étaient significativement différents à un des sites, mais ces différences n'étaient pas consistantes. Dans les niveaux de volume sur pied, les potentiels hydriques moyens à l'aube et à midi ont chuté significativement pendant l'été, malgré certaines hausses mineures. Nous considérons les niveaux de stress comme suffisant pour affecter les fonctions physiologiques, et donc la susceptibilité des arbres aux attaques du dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopk.). L'insecte n'a toutefois pas infesté les peuplements sous stress, ce qui suggère que la résistance de l'arbre n'est qu'un des facteurs dans un scénario de début d'épidémie.

[Traduit par la rédaction]

One current hypothesis explaining the onset of mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae)) outbreaks emphasizes the role of stress in reducing the resistance of host trees to MPB infestation. According to that hypothesis, MPB populations exist at endemic levels in susceptible-sized² stands because the current resistance of the stands prevents the populations from increasing (Berryman 1976). Each year, various stress agents weaken a few trees in the stands so that trees of low resistance are available for infestation and MPB populations are sustained (Berryman 1978). When the resistance of the stands is lowered by a stress agent such as drought, MPB populations increase and outbreaks begin.

The current hypothesis has evolved over the last 70 years, with major emphasis on drought as a predisposing stress factor. Early investigators had different thoughts on the role of drought (i.e., water stress) in MPB epidemiology. Blackman (1931) concluded that epidemics began during periods of rapid tree growth and ended during years of declining growth. Thus, epidemics began during periods of abundant moisture and declined when moisture became deficient (i.e., drought). In contrast, Beal (1943) concluded that most MPB outbreaks began during periods of reduced tree growth that resulted from deficient precipitation. Thus,

drought triggered MPB outbreaks. More recent investigators (Berryman 1978; Raffa 1988) have frequently cited drought as a critical stress factor that decreases the resistance of trees and thus increases the number of susceptible trees.

While the MPB-resistance hypothesis has gained in popularity, quantification of the stress necessary to change resistant trees to susceptible trees and to liberate MPB populations remains undetermined. As Amman (1978) points out, the various stress factors have not been studied in enough detail to establish their significance in MPB epidemiology and, thus, the levels necessary to cause the change in susceptibility. Further, our ability to measure conifer resistance and understand the nature of resistance-stress has not improved greatly (Berryman 1982).

In recent years, partial cutting of MPB susceptible-sized stands to lower stocking levels has reduced MPB-caused mortality (McGregor et al. 1987; Mitchell et al. 1983). This reduction in mortality has been attributed to increased tree vigor and resistance (Mitchell et al. 1983). Drought is often cited as a predisposing stress factor that lowers tree resistance and thereby creates conditions conducive to MPB outbreaks, although information to support this event is lacking. The present study is a first step in quantifying water stress in MPB susceptible-sized stands of different stocking levels and in examining the role of water stress in the susceptibility of trees to MPB infestation.

Methods

In another study designed to test the effect of stocking level on subsequent MPB-caused tree mortality, sets of different growing-

¹Author to whom all correspondence should be addressed.

²Susceptible sized is defined as host trees with a diameter at breast height ≥ 8 in. (1 in. = 2.54 cm).

stock levels³ (GSLs) were installed in stands considered susceptible to MPB attack. The original stands were cut to various levels, with emphasis on leaving uniformly spaced, large-diameter trees with good crowns and in apparent good health. The cut stands would thus be considered managed, while an uncut portion serving as the control would be considered unmanaged.

Two sets of these plots in the northern part of the Black Hills National Forest were used for water potential measurements: the Brownsville plots and the Black Hills Experimental Forest (hereafter referred to as Experimental Forest) plots, located, respectively, approximately 9 and 15 mi (1 mi = 1.6 km) southeast of Lead, South Dakota. The plots consist of essentially pure ponderosa pine (*Pinus ponderosa* Laws.), with the occasional nonhost species having been removed during the partial cutting of the plots or existing as saplings in the control plot. Topographically, the plots lie on the central crystalline area (see Boldt and VanDeusen 1974) at elevations of 5720 and 5860 ft (1 ft = 0.3 m), respectively.

The Brownsville plots consist of three 2.5-acre (1 acre = 0.4 ha) plots partially cut to GSLs of 60, 80, and 100 and one uncut 2.5-acre plot of GSL 146 serving as a control. The Experimental Forest plots consist of three 2.5-acre plots partially cut to GSLs of 40, 80, and 100 and one uncut 2.5-acre control plot of GSL 161. The Brownsville plots were cut in May 1986 and the Experimental Forest plots were cut by September 1988. Other information regarding average diameter, trees per acre, basal area, and age are listed in Table 1.

Water potential measurements were made on each of five trees in the 60, 80, and 100 GSLs and the control of the Brownsville plots and in the 40 and 80 GSLs and the control of the Experimental Forest plots during May, June, July and August 1989. In August, midday measurements were made on August 16 and 17 on the Brownsville plots and on August 15 and 23 on the Experimental Forest plots following showers and light rain on August 14 and 15. The five sample trees in each of the Brownsville plots were in the 12-in. (11.6–12.5 in.) diameter class and centrally located in the plots. Sample trees in the Experimental Forest plots were also centrally located, but they ranged in diameter from 7.7 to 14.8 in.

Twigs were clipped from the lower crowns of the sample trees, usually drawn from the south side, at approximately dawn (06:00) and midday (13:00) mountain daylight time. One twig was clipped from each tree from between 25 and 35 ft (8–11 m) above ground. After cutting, each twig was labeled and placed in a plastic bag in an ice chest that was maintained near freezing. Temporary storage in an ice chest does not significantly change water potential (Kaufmann and Thor 1982) and thus allows transportation to a more suitable location for water potential measurement. Upon completion of the clipping, all twigs were transported to a laboratory where water potential was immediately determined using the Scholander pressure chamber. The Scholander pressure chamber measures the amount of pressure needed to force water out of the base of the needle fascicle. The indicated pressure is thus a measurement of the tension under which the water is held by the tree. The pressure-chamber technique underestimated water potential in the -1 to -2 MPa range in some conifers but closely agreed with the more accurate psychrometer method at higher water potentials (Kaufmann 1968). Individual twigs were removed from the ice chest in the order of clipping. Three needle fascicles were removed from each twig and measured individually; measurements were recorded in megapascals. Two additional fascicles were measured if the range of the three measurements was not within

TABLE 1. Stand characteristics of the Brownsville and Experimental Forest GSL plots

	Basal area per acre (ft ²)	Mean diam. (in.)	No. of trees per acre	Average tree age (years)
Brownsville				
GSL 60	60	12.4	71	103
GSL 80	80	11.5	110	114
GSL 100	100	12.8	112	123
Control (GSL 146)	146	12.7	165	105
Experimental Forest				
GSL 40	40	10.9	62	94
GSL 80	80	10.9	124	93
GSL 100	99	9.2	212	91
Control (GSL 161)	153	8.7	368	91

0.10 MPa. The three most consistent measurements for each twig were averaged, and the average value was used as the water potential for that tree.

Twigs were also clipped in the same manner from the sample trees on the Brownsville plots in 1987 and 1988. Water potential measurements on the 1987 and 1988 twigs were made in the field immediately after clipping.

Water potential values for each sampling period were tested for significant differences among GSLs using a one-way analysis of variance. Prior to the testing of the mean values, the variance was tested for homogeneity. If significant differences occurred among mean values for the GSLs when the variances were homogeneous, Tukey's test was used to determine which means were different. When the variances were heterogeneous, which was rare, multiple comparison procedures for means with heterogeneous variance were used (Dunnett 1980). One-way analysis of variance was also used to test for significant change in water potential within each GSL during the sample periods in each year. All tests of significance were tested with $\alpha = 0.05$.

Results and discussion

Water potential among GSLs

Mean water potentials at dawn and midday were occasionally significantly different among GSLs at both Brownsville and the Experimental Forest plots in 1989 (Table 2). Within the Brownsville plots, mean water potential during midday was less in the GSL 100 plot than in the control trees in July and August but was not different from the GSL 60 trees. Midday water potentials were about 0.8 MPa less than dawn water potentials. In the Experimental Forest plots, mean water potential was significantly greater in the GSL 80 plot than in the control trees during one day in August, but generally differences among GSLs were not significant at dawn and midday.

In 1987 at Brownsville, mean dawn water potentials were significantly different among GSLs in June; in May and July, water potentials were not different (Table 3). Midday water potentials did not differ significantly among GSLs. In 1988, mean dawn water potentials were significantly different among GSLs in May but not thereafter (Table 3). Mean midday water potentials were significantly different in May and June but not in July.

Water potential among the different GSL stands appears to be relatively equal or at least not significantly different

³Growing-stock level (GSL) is defined as the residual square feet of basal area when average stand diameter is ≥ 10 in. (Alexander and Edminster 1980). When average stand diameter is so small that basal area is not a convenient measure, number of trees per acre is used (Myers 1967). See Table 1 for the appropriate basal area of each GSL.

TABLE 2. Mean water potential ($\pm$ SD) (MPa) in trees of different GSLs for dawn and midday periods in four months in 1989

	May		June		July		August*	
	Dawn	Midday	Midday	Midday	Dawn	Midday	Midday a	Midday b
Brownsville								
GSL 60	-0.92 $\pm$ 0.07a	-1.78 $\pm$ 0.11a	-1.86 $\pm$ 0.31a	-1.93 $\pm$ 0.14ab	-1.11 $\pm$ 0.03a	-1.74 $\pm$ 0.02a	-2.06 $\pm$ 0.13ab	
GSL 80	-0.88 $\pm$ 0.09a	-1.71 $\pm$ 0.19a	-1.87 $\pm$ 0.13a	-2.12 $\pm$ 0.08b	-1.30 $\pm$ 0.09b	-1.85 $\pm$ 0.16a	-2.23 $\pm$ 0.14b	
GSL 100	-0.91 $\pm$ 0.07a	-1.69 $\pm$ 0.22a	-1.82 $\pm$ 0.13a	-1.84 $\pm$ 0.21a	-1.25 $\pm$ 0.09b	-1.63 $\pm$ 0.21a	-2.03 $\pm$ 0.04a	
Control	-1.01 $\pm$ 0.13a	-1.65 $\pm$ 0.06a	-1.76 $\pm$ 0.14a					
Experimental Forest								
GSL 40			-1.71 $\pm$ 0.10a	-1.14 $\pm$ 0.11a	-1.33 $\pm$ 0.27a	-1.78 $\pm$ 0.17ab	-2.16 $\pm$ 0.15a	
GSL 80			-1.78 $\pm$ 0.12a	-1.19 $\pm$ 0.15a	-1.30 $\pm$ 0.09a	-1.68 $\pm$ 0.04b	-2.12 $\pm$ 0.10a	
Control			-1.62 $\pm$ 0.32a	-1.09 $\pm$ 0.11a	-1.45 $\pm$ 0.16a	-1.87 $\pm$ 0.08a	-1.97 $\pm$ 0.08a	

NOTE: Within each area and time period, means followed by the same letter are not significantly different at $\alpha = 0.05$.

*In August, midday measurements were made on August 16 (Midday a) and 17 (Midday b) on the Brownsville plots and August 15 (Midday a) and 23 (Midday b) on the Experimental Forest plots following showers and light rain on August 14 and 15.

from a statistical standpoint. When significant differences exist, they are probably temporary and not consistently related to stand density. This pattern of water potential among the different GSL stands contrasts sharply with previous work in smaller diameter but more heavily stocked stands of lodgepole pine (*Pinus contorta* Dougl. ex Loud), wherein Donner and Running (1986) found water potential significantly higher in thinned stands than in unthinned stands.

Most water-stress hypotheses assume that by thinning a stand, competition between adjacent trees is eliminated and more soil water becomes available for the residual trees. They expand their root systems (Kramer and Kozlowski 1979) and utilize this available water, thereby reducing summer water stress. Increased growth may not occur the 1st year after thinning because of thinning shock, but water stress should be reduced after 2 or 3 years. This does not seem to be the case in our GSL plots, especially in the Brownsville plots, which were thinned in 1986. Either the trees have still not yet utilized the available water or they are water limited in summer so that only above-average precipitation can alleviate the water stress and increase water potential.

One possible explanation is that the partial cutting of stands ≥ 150 GSL exposes the lower and middle crowns of the residual trees to more direct and intense sunlight, increasing the transpiration rate per tree and increasing evapotranspiration from the forest floor (see Kramer and Kozlowski 1979). This may offset the gain in available water obtained from partial cutting.

Seasonal water potential within GSLs

Mean water potential within each GSL generally decreased in both areas during the summer of 1989 (Table 2). In the Brownsville plots, water potential significantly differed between May and August in both dawn and midday readings. However, water potential did not continually decrease from May to August but exhibited both a decrease and increase during this period.

Mean dawn and midday water potentials within GSLs did not vary significantly from May to July in 1987 (Table 3). In 1988, mean dawn water potentials varied significantly among the three sampling periods. The trend was generally an increase in dawn water potential from May to June followed by a decrease from June to July. Mean midday water potential decreased significantly only in the GSL 100 trees; the other GSLs were not different.

The pattern of seasonal water potential is similar to that observed for lodgepole pine by Running (1984). The pattern reflects the increased evapotranspiration caused by seasonally higher temperatures and more direct solar radiation from May to July. Minor increases in water potential in June probably result from precipitation.

Water stress and MPB epidemiology

The current MPB - host resistance hypothesis assumes that a few trees are stressed each year by stress factors, such as lightning, ice or snowstorms, etc. Their relative frequency in the total host population is low, probably considerably less than 1%. Endemic MPB populations maintain themselves in such trees and increase to outbreak proportions only when the general level of host resistance is lowered such that the frequency of susceptible trees rises substantially (i.e., well above the 1% level).

TABLE 3. Mean water potential ($\pm$ SD) (MPa) in trees of four GSLs at Brownsville for dawn and midday period in May, June, and July of 1987 and 1988

	May		June		July	
	Dawn	Midday	Dawn	Midday	Dawn	Midday
1987						
GSL 60	$-2.17 \pm 0.61a$	$-2.97 \pm 0.77a$	$-1.58 \pm 0.11a$	$-3.12 \pm 0.35a$	$-1.63 \pm 0.10a$	$-2.59 \pm 0.31a$
GSL 80		$-2.65 \pm 0.17a$	$-1.54 \pm 0.18a$	$-2.83 \pm 0.59a$	$-1.57 \pm 0.10a$	$-2.71 \pm 0.31a$
GSL 100		$-2.76 \pm 0.09a$	$-1.57 \pm 0.08a$	$-3.14 \pm 0.40a$	$-1.67 \pm 0.20a$	$-2.99 \pm 0.31a$
Control	$-1.79 \pm 0.16a$	$-2.50 \pm 0.30a$	$-1.19 \pm 0.08b$	$-2.47 \pm 0.65a$	$-1.76 \pm 0.08a$	$-2.58 \pm 0.35a$
1988						
GSL 60	$-0.087 \pm 0.25a$	$-1.86 \pm 0.26ab$	$-0.99 \pm 0.13a$	$-1.90 \pm 0.28a$	$-1.16 \pm 0.18a$	$-1.95 \pm 0.17a$
GSL 80	$-1.01 \pm 0.18ab$	$-1.83 \pm 0.36ab$	$-0.88 \pm 0.10a$	$-2.19 \pm 0.26ab$	$-1.18 \pm 0.11a$	$-1.91 \pm 0.14a$
GSL 100	$-1.40 \pm 0.36b$	$-1.50 \pm 0.35a$	$-1.05 \pm 0.14a$	$-2.43 \pm 0.22b$	$-1.24 \pm 0.22a$	$-2.02 \pm 0.12a$
Control	$-1.22 \pm 0.08ab$	$-2.10 \pm 0.15b$	$-1.01 \pm 0.15a$	$-1.86 \pm 0.22a$	$-1.33 \pm 0.20a$	$-1.99 \pm 0.09a$

NOTE: Within each time period within each year, means followed by the same letter are not significantly different at $\alpha = 0.05$.

Extrapolating from our data, significantly more than 1% of the ponderosa pine on the plots were moderately to severely water stressed.⁴ Climatological data from Lead, South Dakota, indicated below-average precipitation for 4 of the last 5 years and an average deficiency during all 5 years $\geq 10\%$ (≥ 2.8 in. per year). We believe nearly all (more than 90%) of the ponderosa pines were thus moderately to severely stressed not only on the study plots but throughout the Black Hills every summer of below-average precipitation. Only those trees growing near streams or on underground aquifers may not have been stressed. Even in years of average or above-average precipitation, trees may be moderately or severely stressed, depending on the seasonal distribution of that precipitation. If the amount of precipitation during the previous fall and winter is below average, then trees enter the growing season moderately to highly stressed (Table 3, May 1987). As time progresses, stress levels may increase, remain about the same, or slightly decrease, depending on the amount of summer precipitation. Summer thundershowers, normally not a substantial contributor to total precipitation, may temporarily reduce water stress for 1 or 2 days (Table 2, August, Midday^a), but substantial reductions in stress result only from substantial precipitation.

Given these levels of stress during the attack period of the MPB (late July – August) for the past several years, a MPB outbreak would be expected. Endemic MPB populations existed in and around both sets of plots (J.M. Schmid, personal records). In addition, scattered groups of infested trees were evident in the northern Black Hills from the Experimental Forest to the Lead–Deadwood area in 1987–1988 (J. M. Schmid, personal observations). An outbreak was developing in the northern Black Hills in 1986–1987, but it disappeared in 1987–1988. In the southern Black Hills, two outbreaks progressed in opposite directions; one died out, and the other has increased substantially.

Based on the status of these infestations, host resistance or susceptibility appears to be only part of the outbreak scenario. We have, of course, not determined precisely the

relationship between water stress and resistance nor the level of water stress needed to change a resistant tree to a susceptible tree, so the argument could be made that the water stress has been insufficient to create trees susceptible to MPB attack. Considering the facts that the pressure-chamber method may underestimate water potential and that a single sample from the south side of the lower crown may not represent the water potential (stress) for the entire tree (see Reid and Gates 1972), this may be the case. Until the accuracy of the pressure-chamber method and the variation within ponderosa pine crowns are determined, our estimates can be questioned. However, water stress in large trees is best reflected in the needles (Lorio and Hodges 1968); stress increases slightly from lower to upper crown (Reid and Gates 1972), and the portable pressure-chamber method is currently the best for gathering instantaneous measurements in the forest. Thus, we assume that the water potential values represent a reasonable estimate of water stress.

Assuming that the stress levels are reasonable, the remaining question is how they relate to resistance. We assume that resistance is generally inversely related to water stress (that is, high resistance equals low stress, and low resistance equals high stress) while recognizing that low stress may increase resistance. However, resistance has either not been defined in physiological terms or is defined in terms of physiological indices, not stress levels, so relating the two concepts becomes clouded. Berryman (1978) defines resistance “as the ability of a lodgepole pine to defend itself against MPB attack.” Resistance has also been defined in terms of periodic growth rate (Mahoney 1977), sapwood growth / sapwood basal area (Waring and Pitman 1980), and grams of sapwood per square meter of foliage (Mitchell et al. 1983). These are indices of the physiological functioning of the tree but may not necessarily reflect the capacity of the tree to resist MPB attack during the attack period. It seems possible that trees may exhibit a “resistant level” because of early summer growth but be susceptible at time of MPB attack because of severe water stress. As Christiansen et al. (1987) note, the defensive capacity of the tree “is contingent on the tree’s capability to mobilize defensive chemicals in the distinct reaction zones surrounding the points of attack” at the time of attack (our emphasis). Our observed levels of water stress seem sufficient to affect most growth pro-

⁴Following Hsiao (1973), moderate stress is defined as -1.02 to -1.5 MPa and severe stress as ≤ -1.5 MPa.

cesses (See Hsiao et al. 1976), so it seems highly possible that the stress levels are high enough to limit the tree's defensive response. Thus, the lack of a substantial, ongoing outbreak suggests that resistance is but one factor in the outbreak scenario; other factors such as phloem quality are also important. As Amman and Cole (1983) and Raffa (1988) point out, susceptible trees are not always the most ideal from a population survival standpoint because the phloem is unable to support the brood. Bark samples in the outbreak in the southern Black hills indicated thin, dried phloem and poor brood survival. These infestations may be declining because of poor phloem quality even though the trees were susceptible, or low in resistance.

In the Introduction, we contrasted the hypotheses of Blackman (1931) and Beal (1943). Both hypotheses may be pertinent to MPB epidemiology; Beal's to the onset of outbreaks and Blackman's to outbreak longevity. If an outbreak develops during a drought (Beal's hypothesis), the outbreak may continue only if there is average to above-average precipitation (Blackman's hypothesis) to maintain phloem quality, i.e., phloem thickness and moisture. Otherwise, if the below-average precipitation condition continues, the phloem dries too rapidly after infestation, and brood survival is poor. A MPB population may be initially sustained in trees with declining growth because phloem thickness may be retained for several years (see Cabrera 1978). However, during our study, either the phloem quality was not adequate enough to sustain the MPB populations or other factors are operating to reduce MPB populations.

Host resistance and partial cutting

The success of partial cutting in reducing MPB-caused mortality is frequently attributed to the change in host resistance created by the reduction in stand density (Mitchell et al. 1983). The relatively equal but moderate to severe stress levels among GSLs observed in this study suggest that host resistance would be relatively equal among our GSLs. If host resistance is relatively equal, then differential MPB-caused mortality among various GSLs must be influenced by other factors, such as microclimate, as suggested by Bartos and Amman (1989). Host resistance by itself may not be totally responsible for the differential mortality.

- ALEXANDER, R.R., and EDMISTER, C.B. 1980. Management of spruce-fir in even-aged stands in the central Rocky Mountains. U.S. For. Serv. Rocky Mt. For. Range Exp. Stn. Res. Pap. RM-217.
- AMMAN, G.D. 1978. Biology, ecology and causes of outbreaks of the mountain pine beetle in lodgepole pine forests. In *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*. Symposium Proceedings, 25-27 Apr. 1978, Washington State University, Pullman. Edited by A.A. Berryman, G.D. Amman, and R.W. Stark. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow. pp. 39-53.
- AMMAN, G.D., and COLE, W.E. 1983. Mountain pine beetle dynamics in lodgepole pine forests. Part II: Population dynamics. USDA For. Serv. Gen. Tech. Rep. INT-145.
- BARTOS, D.L., and AMMAN, G.D. 1989. Microclimate: an alternative to tree vigor as a basis for mountain pine beetle infestations. USDA For. Serv. Res. Paper INT-400.
- BEAL, J.A. 1943. Relation between tree growth and outbreaks of the Black Hills beetle. *J. For.* **41**: 359-366.
- BERRYMAN, A.A. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. *Environ. Entomol.* **5**: 1225-1233.
- . 1978. A synoptic model of the lodgepole pine/mountain pine beetle interaction and its potential application in forest management. In *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*. Symposium Proceedings, 25-27 Apr. 1978, Washington State University, Pullman. Edited by A.A. Berryman, G.D. Amman, and R.W. Stark. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow. pp. 98-105.
- . 1982. Population dynamics of bark beetles. In *Bark beetles in North American conifers*. Edited by J.B. Mitton and K.B. Sturgeon. University of Texas Press, Austin. pp. 264-314.
- BLACKMAN, M.W. 1931. The Black Hills beetle (*Dendroctonus ponderosae* Hopk.). N.Y. State Coll. For. Syracuse Univ. Bull. 36.
- BOLDT, C.E., and VANDEUSEN, J.L. 1974. Silviculture of ponderosa pine in the Black Hills: the status of our knowledge. U.S. For. Serv. Rocky Mt. For. Range Exp. Stn. Res. Pap. RM-124.
- CABRERA, H. 1978. Phloem structure and development in lodgepole pine. In *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*. Symposium Proceedings, 25-27 Apr. 1978, Washington State University, Pullman. Edited by A.A. Berryman, G.D. Amman, and R.W. Stark. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow. pp. 54-63.
- CHRISTIANSEN, E., WARING, R.H., and BERRYMAN, A.A. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. *For. Ecol. Manage.* **22**: 89-106.
- DONNER, B.L., and RUNNING, S.W. 1986. Water stress response after thinning *Pinus contorta* stands in Montana. *For. Sci.* **32**: 614-625.
- DUNNETT, C.W. 1980. Pairwise multiple comparisons in the unequal variance case. *J. Am. Stat. Assoc.* **75**: 796-800.
- HSIAO, T.C. 1973. Plant responses to water stress. *Annu. Rev. Plant Physiol.* **24**: 519-570.
- HSIAO, T.C., ACEVEDO, E., FERERES, E., and HENDERSON, D.W. 1976. Stress metabolism. Water stress, growth and osmotic adjustment. *Philos. Trans. R. Soc. Lond. Biol. Sci.* **273**: 479-500.
- KAUFMANN, M.R. 1968. Evaluation of the pressure chamber technique for estimating plant water potential of forest trees. *For. Sci.* **14**: 369-374.
- KAUFMANN, M.R., and THOR, G.L. 1982. Measurement of water stress in subalpine trees: effects of temporary tissue storage methods and needle age. *Can. J. For. Res.* **12**: 969-972.
- KRAMER, P.J., and KOZLOWSKI, T.T. 1979. *Physiology of woody plants*. Academic Press, New York.
- LORIO, P.L., JR., and HODGES, J.D. 1968. Oleoresin exudation pressure and relative water content of inner bark as indicators of moisture stress in loblolly pines. *For. Sci.* **14**: 392-398.
- MANHONEY, R.L. 1977. Classifying lodgepole pine stands as resistant or susceptible to mountain pine beetle. M.S. thesis, University of Idaho, Moscow.
- MCGREGOR, M.D., AMMAN, G.D., SCHMITZ, R.F., and OAKES, R.D. 1987. Partial cutting lodgepole pine stands to reduce losses to the mountain pine beetle. *Can. J. For. Res.* **17**: 1234-1239.
- MITCHELL, R.G., WARING, R.H., and PITMAN, G.B. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *For. Sci.* **29**: 204-211.
- MYERS, C.A. 1967. Growing stock levels in even-aged ponderosa pine. U.S. For. Serv. Rocky Mt. For. Range Exp. Stn. Res. Pap. RM-33.
- RAFFA, K.F. 1988. The mountain pine beetle in western North America. In *Dynamics of forest insect populations*. Edited by A.A. Berryman. Plenum Press, New York. pp. 505-530.
- REID, R.W., and GATES, H.S. 1972. Relations between some

- physiological functions in lodgepole pine and resistance to the mountain pine beetle. Can. For. Serv. North. For. Res. Cent. Inf. Rep. NOR-X-15.
- RUNNING, S.W. 1984. Documentation and preliminary validation of H2OTRANS and DAYTRANS, two models for predicting transpiration and water stress in western coniferous forests. U.S. For. Serv. Rocky Mt. For. Range Exp. Stn. Res. Pap. RM-252.
- WARING, R.H., and PITMAN, G.B. 1980. A simple model of host resistance to bark beetles. Oreg. State Univ. For. Res. Lab. Res. Note 65.