

MOUNTAIN PINE BEETLE INFESTATION:
CYCLING AND SUCCESSION IN LODGEPOLE PINE FOREST

W. H. Romme
Department of Biology
Fort Lewis College
Durango, CO

J. B. Yavitt
and
D. H. Knight
Department of Botany
University of Wyoming
Laramie

J. Fedders
Department of Biological Sciences
Eastern Kentucky University
Richmond

Objectives

A research project was initiated in 1980 to study the effects of outbreaks of the mountain pine beetle (*Dendroctonus ponderosae*) on lodgepole pine forest (*Pinus contorta* spp. *latifolia*) in Yellowstone National Park and surrounding areas. This native bark beetle recently has killed millions of trees over thousands of square kilometers in the central and northern Rocky Mountains. Major outbreaks first occurred in Grand Teton National Park in the 1950's and in Yellowstone National Park in the 1960's. The outbreak in Yellowstone Park is still spreading.

The immediate effects of bark beetle outbreaks on stand structure are well documented (Roe and Amman 1970, Amman and Cole 1980), and much research has been directed toward understanding the beetles' population dynamics and the causes of outbreaks (Coulson 1969, Berryman 1976, 1982, Amman and Cole 1983). However, much less work has been done to clarify long-term effects of outbreaks on ecosystem processes and phenomena such as primary productivity, nutrient cycling, and succession. Mattson and Addy (1975) and McNaughton and Coughenour (1981) suggested that phytophagous insects like the bark beetle may regulate primary productivity through their effects on resource distribution and availability. Therefore, our research focuses on the effects of beetle outbreaks on (1) rates of growth in surviving trees and total stand productivity, (2) dead woody fuels and fire risk, (3) stand succession, and (4) nutrient cycling.

Methods

To measure effects on surviving tree growth, we selected a chronosequence of

10 stands affected by a major beetle outbreak from 1-20 years ago. In each stand we collected increment cores from surviving canopy, subcanopy, and understory trees, and measured mean annual ring width during the 5 years immediately preceding the beetle outbreak and during various periods after the outbreak. We also collected cores from two control stands unaffected by the beetles but otherwise similar to the affected stands, and measured mean annual ring width during comparable time periods.

To determine effects on total stand productivity, we sampled tree density before and after the beetle outbreak in four of our stands using belt transects in which we tallied living trees and trees killed by the beetles. We then calculated mean annual bole volume increment during 5-year intervals before and after the outbreak using radial growth and tree height data. We multiplied mean annual increment per tree by the number of trees per hectare to estimate total annual bole volume increment per hectare before and after the beetle outbreak.

We studied dead woody fuels using two methods. The first was a comparative stand approach in which we inventoried fuels using the planar intersect method (Brown 1974) in a chronosequence of 11 stands affected by beetle outbreaks from 0-20 years ago. All 11 stands had been similar prior to the outbreaks. Our second method was a simulation approach for which we collected data on tree size, density, and pre-outbreak fuel in three stands not yet affected by the beetles. We simulated a beetle outbreak in these three stands by selectively "killing" trees of certain size classes at various times in accordance with descriptions of the course of a major outbreak in this area (Parker 1973). The fuels contained in these dead trees were estimated using regressions developed by Brown (1978). By adding these new fuels to already existing fuel levels on the forest floor, and including the effects of normal background rates of litterfall and decomposition (Fahey 1983), we simulated changes in dead woody fuel mass for 20 years following a beetle outbreak.

To measure effects on nutrient cycling, we established 36 tube-tension lysimeters (Parizek and Lane 1970) in 1980 in two stands near West Yellowstone. Leachate was collected during the snowmelt periods of 1981, 1982, and 1983, and we will continue to collect it yearly. Elemental concentrations will be measured in our laboratory in Laramie, and will be used with our stand level hydrologic model for lodgepole pine forests (already developed with NSF funds) to estimate the magnitude of nutrient loss associated with a beetle outbreak.

Results

We have completed our analyses of the effects of beetle outbreaks on surviving tree growth and stand productivity, and have nearly completed writing this portion of our final report. In all 10 stands sampled, most surviving trees grew significantly faster after the outbreak than before. Total stand productivity decreased during the first 5 years after the outbreak, due to the death of many large trees, but after 10-15 years it had returned to its pre-outbreak level as a result of accelerated growth in the survivors. Annual wood production actually

increased after the outbreak in one stand. (See Figure 1 in our progress report for 1982 for more details).

In our comparative stand approach to fuels, we found that total dead woody fuels (kg/ha) increased significantly with increasing number of years since the beetle outbreak. However, most of this fuel mass consisted of large tree boles which do not ignite readily. Analyses of individual fuel components revealed no significant relationships between fuel quantities and time since the outbreak, nor significant differences between stands affected by beetles and stands not affected.

Results of our fuels simulation in one stand are given in Table 1. (Changes in the other two stands were similar but of smaller magnitude.) Total fuels increased dramatically over 20 years, but nearly all of the increase was due to the accumulation of large, sound fuels in the boles of toppled trees. As in our comparative stand approach, the smaller, more flammable fuels changed very little, except for a small peak in needle litter soon after the beetle-killed trees dropped their leaves. Decomposition of these added leaves brought the total needle litter back down to pre-outbreak levels within 20 years. We are still analyzing the possible implications of these trends for fire risk and the long-term influence of beetle outbreaks on natural fire cycles in lodgepole pine forests.

Conclusions

Mountain pine beetle outbreaks dramatically alter stand structure and accelerate natural forest succession by selectively killing a large fraction of dominant canopy trees, thus releasing understory trees from suppression. Total stand productivity decreases for ca. 5 years after an outbreak, but usually returns to pre-outbreak levels or higher within 10-15 years. Total dead woody fuel mass increases greatly during the first 20 years after an outbreak, but nearly all of this increase is in the form of large tree boles which do not ignite readily and usually do not burn completely in natural fires. Thus, despite the highly visible effects on large fuels, beetle outbreaks may have a very small influence on fire frequency in this region. Massive outbreaks of the type that we studied do not appear to regulate primary productivity in lodgepole pine forests, although smaller endemic populations may function in this manner.

Literature Cited

- Amman, G. D., and W. E. Cole. 1980. Mountain pine beetle dynamics in lodgepole pine forests. Part I: Course of an infestation. USDA For. Serv. Gen. Tech. Rep. INT-89.
- Amman, G. D., and W. E. Cole. 1983. Mountain beetle dynamics in lodgepole pine forests. Part II: Population dynamics. USDA For. Serv. Gen. Tech. Rep. INT-145.
- Berryman, A. A. 1976 Theoretical explanation of mountain pine beetle dynamics

Table 1. Simulated changes in dead woody fuels following a beetle outbreak in a 100-year old lodgepole pine forest in Yellowstone National Park. Fuel mass on the forest floor is reported in kg/ha for all components.

	YEARS AFTER ONSET OF OUTBREAK						
	0	2	4	6	10	15	20
% Original Canopy Basal Area Killed by Beetles (Cumulative)	0	5.3	35.8	40.0	40.0	40.0	40.0
Needle Litter	21,800	21,900	22,500	23,400	22,500	22,000	21,800
Twigs 0.63 cm dia.	440	450	590	810	870	750	660
Twigs 0.64 - 2.5 cm	1750	1750	1870	2010	2150	2200	2180
Branches 2.6 - 7.6 cm	900	900	990	1090	1240	1370	1430
Sound boles 7.6 cm	2040	2040	4200	6810	10,900	15,600	20,000
Decomposing boles	3950	3950	3950	3950	3950	3950	3950
Total fuels	30,800	30,900	34,100	38,100	41,600	45,800	50,000

- in lodgepole pine forests. *Env. Ent.* 5:1225-1233.
- Berryman, A. A. 1982. Mountain pine beetle outbreaks in Rocky Mountain lodgepole pine forests. *J. of For.* 80:410-413,419.
- Brown, J. K. 1974. Handbook for inventorying downed woody material. USDA For. Serv. Gen. Tech. Rep. INT-16.
- Brown, J. K. 1978. Weight and density of crowns of Rocky Mountain conifers. USDA For. Serv. Res. Pap. INT-197.
- Coulson, R. N. 1979. Population dynamics of bark beetles. *Ann. Rev. Entomology* 24:417-447.
- Fahey, T. J. 1983. Nutrient dynamics of above-ground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. *Ecol. Monog.* 53:51-72.
- Mattson, W. J., and N. D. Addy. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190:515-522.
- McNaughton, S. J., and M. B. Coughenour. 1981. The cybernetic nature of ecosystems. *Amer. Nat.* 117:985-990.
- Perizek, R. R., and B. E. Lane. 1970. Soil water sampling using pan and deep pressure-vacuum lysimeters. *J. Hydrol.* 11:1-21.
- Parker, D. L. 1973. Trend of a mountain pine beetle outbreak. *J. For.* 71:698-700.
- Roe, A. L., and G. D. Amman. 1970. The mountain pine beetle in lodgepole pine forests. USDA For. Serv. Res. Pap. INT-71.