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Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodge pole pine stands in northern Utah

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Abstract

We examined the response of understory vegetation beneath monotypic, even-aged stands of lodgepole pine to increasing tree mortality following an epidemic of mountain pine beetles. We hypothesized that understory biomass would increase continually as the tree canopy was reduced and competition with trees for light and soil moisture decreased, but that plant species diversity and heterogeneity would peak at intermediate levels of beetle-caused tree mortality. Mean understory biomass clipped from 50 1-m2 circular plots/stand was an order of magnitude greater
(40 g m-2) in beetle-killed stands, with typical levels of overstory tree mortality (50-75%), than in unaffected stands (4 g m-2); and it increased exponentially with disturbance severity. Frequency of fruit occurrence was positively related to increasing tree mortality, but was highly variable. Understory plant species richness and, to lesser degrees indices of diversity that incorporate evenness, peaked in stands with moderate mortality. Measures of vegetation patchiness (the coefficient of variation in mean plot biomass and an index of habitat interspersion) also peaked in stands with intermediate levels of disturbance. The response of understory plant species diversity to increasing disturbance severity is consistent with the pattern predicted by the intermediate disturbance hypothesis. However, other explanations of this pattern are discussed. Although understory plant community richness was higher in beetle-killed stands than in unaffected stands, new species were not abundant and therefore did not contribute substantially to greater evenness in understory plant diversity.

Introduction

The role of natural disturbances in determining community states and transitions in various ecosystems throughout the world has received increasing attention from ecologists and land managers (Sprugel 1991). Disturbances influence the abundance, composition, and distribution of vegetation through modification of the physical environment and the spatial and temporal distribution of resources (Tilman 1982; Bazzaz 1983; White & Pickett 1985; Chaneton & Facelli 1991). Specifically, disturbance reduces live plant biomass (Reader et al. 1991), releases resources (light, space, soil moisture, nutrients) to surviving plants (Canham & Marks 1985), and permits new species to colonize the site (Grime 1973; Collins 1987).

The effects that natural disturbances have on communities depend on the disturbance type and regime (White & Pickett 1985). Moderate disturbances, in either frequency or severity, are hypothesized to enhance species diversity (Connell 1978) and maintain plant richness (Grime

1979; Huston 1979). Much of the attention that the 'intermediate disturbance hypothesis' has received focuses on the frequency rather than the intensity of the disturbance regime. Reader et al. (1991) provided a notable exception in the vegetation literature when they demonstrated that understory plant species composition changed following tree harvesting in a deciduous forest, but that plant diversity was not significantly higher on sites with intermediate levels of harvest compared to sites with low or complete tree removal.

The mountain pine beetle (Dendroctonus ponderosae) is the primary insect agent affecting the lodgepole pine (Pinus contorta) forest ecosystem, and, in association with fire, largely determines the successional dynamics in these forests (Cole & Amman 1980). Schowalter et al. (1981) concluded the same about the influence of southern pine beetles (Dendroctonus frontalis) on pine-hardwood forests in the southern United States. A mountain pine beetle epidemic differs from other types of disturbance because: (1) larger and older trees are selectively killed by the disturbance agent; (2) the understory and soil layers are not directly affected by the disturbance agent; (3) the return of nonvolatile nutrients to the soil and the response of vegetation production are slower than that which would occur following a stand-replacing fire; (4) it hastens successional progress towards a climax when lodgepole pine is seral; (5) repeated epidemics shift the stand structure from even-aged to uneven-aged; (6) disturbance severity can range widely with environmental conditions (elevation, climate, topography), but overs tory tree mortality is typically moderate, removing approximately 50% of the canopy cover and basal area in a few years; and (7) widely distributed gaps in the forest canopy may be created when six to seven neighboring trees succumb during the epidemic (Cole & Amman 1969; Roe & Amman 1970; Brown 1975; Cole & Amman 1980; Romme et al. 1986; W. H. Romme, personal communication).

The abundance and composition of understory vegetation in coniferous forests are significantly altered following epidemic attacks by bark beetles. Leuschner & Maine (1980) estimated a 340 to 1700 kg ha-I increase in herbage production beneath loblolly pine (Pinus taeda) stands following defoliation by the southern pine beetle. McCambridge et al. (1982) documented increases of555 and 962 kg ha -I in understory forbs, grasses, and sedges beneath two ponderosa pine (Pinus ponderosa) stands 3 years after a mountain pine beetle epidemic in Colorado. Kovacic et al. (1985) demonstrated that herbaceous biomass was 50100 times as great (increases of 1000-2000 kg ha -I) in ponderosa pine stands 5 years after mountain pine beetle infestation than in uninfested stands. Yeager & Riordan (1953) reported a 45% increase in herbaceous cover in stands of spruce-fir (Picea engelmannii-Abies lasiocarpa) following an epidemic of spruce beetles (Dendroctonus engelmannii), and more interestingly, twice as many understory plant species in beetle-killed stands than in similar uninfested stands (based on elevation, slope, aspect, soil type, and fire history). The biomass response following this type of disturbance is predictable because an exponential inverse relationship between understory biomass and overstory canopy cover is well documented for many forest

ecosystems (Ehrenreich & Crosby 1960; Halls & Schuster 1965; Blair 1967; Blair & Enghardt 1976; Ford & Newbould 1977; Satoo & Madgwick 1982). However, the response of plant diversity in the understory to increasing levels of tree canopy removal is not as well understood (Reader et al. 1991).

Mountain pine beetle epidemics of moderate mortality are likely to increase heterogeneity in the distribution of understory plant biomass. Herbaceous vegetation rapidly colonizes the forest floor beneath the canopy openings created when a group of large trees is killed by bark beetles (Kovacic et al. 1985). Sunny forest floor patches beneath canopy openings of >0.0145 ha often contain more abundant vegetation than shaded patches (Maine 1979). Amman (1977) reported that patches beneath lodgepole pine canopy openings created by the mountain pine beetle are eventually reseeded by the dominant overs tory species. Whether these patches are dominated by trees or herbaceous plants, the distribution of understory vegetation in the stand becomes more heterogeneous when production increases beneath these openings and remains low in shaded microsites. Understory production is likely to increase uniformly throughout the forest floor when epidemics result in nearly complete overstory tree mortality. This reduces heterogeneity in the distribution of understory vegetation.

We conducted this research to examine the understory vegetation response to a mountain pine beetle epidemic. Specifically, we sought to quantify the effects of decreasing overs tory tree canopy on the production, distribution and diversity of understory vegetation. Research opportunities in post-epidemic stands are uncommon because these stands are typically salvage-logged when economically feasible. Consequently, this is a type of disturbance that is poorly understood. The effects of bark beetle epidemics on the magnitude and duration of understory biomass production have received some attention (McCambridge et al. 1982; Kovacic et al. 1985), but the response of plant species diversity and distribution following an epidemic are generally unknown. Our study focused on the intensity of a single disturbance rather than the frequency of disturbance. The diversity response is the same for frequency and intensity of disturbance, but the mechanisms are slightly different (Connell 1978). Competition from survivors prevents new species from colonizing sites following a low intensity disturbance. Competitive exclusion of established species is the mechanism leading to low diversity when disturbances are infrequent. Severe disturbances operate similarly for both intensity and frequency by excluding all but the most tolerant species. Our research does not attempt to prove or disprove the tenets of the intermediate disturbance hypothesis, but our results can be viewed in that context to determine if the response of plant species diversity to increasing disturbance intensity is consistent with the pattern predicted by the hypothesis.

Methods
Study area and disturbance agent

We chose forty I-ha stands of mature lodgepole pine on the northern slope (elevation: 2770-2940 m) of the Uinta mountains in the Wasatch National Forest, Utah. An epidemic of mountain pine beetles occurred in this area from 1980 to 1987. We established three 30 m x 30 m plots in each stand to collect forest inventory data in order to select stands that had similar structure prior to the epidemic. In each 30 m x 30 m plot, we measured the diameter at breast height (dbh) of every tree taller than 2 m in height, assessed mortality (alive or dead) of each tree, aged 10 overstory trees with an increment borer, and determined the heights of 30 dominant trees with a clinometer and metric tape. The stand's basal area and mean percent tree mortality were computed from these data. In addition, the slope, aspect, and elevation of each stand was determined from U.S. Forest Service maps to ensure that the research stands were as similar as possible. These even-aged stands ranged from 87 to 117 years in age, and originated following stand-replacing fires near the turn of the century. Cumulative tree mortality during the epidemic typically ranged from 50 to 75% of overstory trees (U.S. Forest Service unpublished inventory data), but stand mortality ranged from 14 to 95% in the stands that we studied. Tree densities and basal area in these stands range from 1100 to 1500 trees ha-1 and 28 to 44 m2 ha-1, respectively. Most stands were located on gently rolling terrain with no appreciable slope, but several were located on 20 to 40% slopes.

The understory vegetation was sampled in 10 of these 40 stands in 1988 and again in 1989. Tree mortality in five of the stands ranged from 56 to 70%. Five stands were outside of the epidemic area and served as controls for initial biomass comparisons. These control stands experienced slight tree mortality from dwarf mistletoe and Armillaria root rot in the recent past. We sampled 10 additional stands ranging from 26 to 94% mortality in 1990, and 20 more ranging from 14 to 95% mortality in 1991, for a total of 40 stands. Patton's (1975) edge index was computed from data collected in 1991 only.

Understory vegetation
We randomly chose fifty I-m2 plots in each stand, clipping the aboveground vegetation below 2 m in height in each plot in late August. The samples were separated by species, oven-dried at 50°C for 1 week, and weighed to the nearest 0.5 g. The presence of fruit was recorded in each plot by species.

The patchiness of plant distribution was assessed, in part, by measurement of intra-stand edge between sunny patches beneath canopy gaps and shady patches beneath the forest canopy. Patches of sun and shade (150 m2 or larger) on the forest floor were mapped in each stand using the compass-traverse method (Mosby 1980) at or near midday. Forest floor patches from the maps were digitized using a digitizing tablet and ERDAS (ERDAS 1990) software to obtain patch perimeters and area. The intrastand edge of these sunny versus shaded patches was computed using Patton's (1975) edge index. This diversity index was plotted against percent tree mortality to determine if this indicator of vegetation patchiness was a function of

epidemic severity.

Data analysis
The plot mean, standard error, and coefficient of variation of understory plant biomass were computed for each stand. We used the coefficient of variation of plot biomass as another indicator of the distribution of understory vegetation and regressed it against percent tree mortality. We also summed biomass values in each stand by four vegetation classes: trees (<2 m), shrubs, forbs, and grasses/sedges.

Initially, we tested for significant differences in mean plot biomass between typical beetle-killed stands and similar, but unaffected, stands using a split-plot analysis of variance (ANOVA), with mortality status and sampling year as variables. On the basis of these results, we grouped all of the stands into classes of similar mortality (0 -25%,26-50%,51-75%,76-100%) by sampling year and examined the data for significant year effects using several one-way ANOVAs. We also tested for differences in the functional responses of mean plant biomass to tree mortality in different years by linearizing the responses with a log transformation of mean plot biomass for each year and testing the homogeneity of their slopes with an analysis of covariance. Results from these comparisons allowed us to pool the data from the 40 stands that were sampled from 1989 to 1991 for further analyses because the slopes of the log-transformed responses of vegetation to increasing tree mortality were not significantly different in those years.

The response of vegetation abundance to increasing epidemic severity was examined by regressing mean plot biomass by percent tree mortality with an exponential function. This approach does not determine causality between beetle-caused canopy removal and understory biomass, and it is limited by the inherent environmental variability in these different sites. However, it may be the only feasible approach to investigating the biomass response without introducing other extraneous variables, including annual variation in plant production, variation due to time since disturbance, and lag time in biomass response following successive removals of canopy cover. Finally, the frequency of fruit in the 50 plots sampled in each stand was computed and its response to increasing beetlecaused tree mortality was examined.

Species richness is simply the number of species detected in each stand. Diversity indices were computed using biomass (g) as a measure of the relative importance of an individual species in the understory community. We computed three diversity indices that vary in their sensitivity to richness versus evenness (Hill 1973): the Shannon-Wiener index (Shannon & Weaver 1963), Margalet's index (Margalef 1958), and the inverse of Simpson's index (Simpson 1949; Hill 1973). We calculated these values for stands with progressively higher beetle-caused tree mortality.

Results

Understory biomass

We identified 101 vascular plant species in the understories of the 40 forest stands; and 10 of these species produced fruit to varying degrees (Appendix). All are perrenials except for Collinsia parviflora. Four species of mushrooms, Aleuria aurantia, Armillaria mellea, Boletus crysenteron, and Russula emetica, were encountered, but they were infrequent and were not included in further analyses.

Mean plot biomass ranged from 3.4 to 7.0 g m-2 in stands with 0-25% tree mortality, 8.8 to 27.4 g m-2 in stands with 26-50% tree mortality, 28.7 to 52.1 g m-2 in stands with 51-75% tree mortality, and 60.1 to 108.8 g m-2 in stands with 76-100% tree mortality (Table 1). Mean plot biomass was significantly higher (p =0.003) in beetle-killed lodgepole pine stands than in unaffected stands (Table 2). Production of understory vegetation was also higher (p<0.001) in these stands in 1989 than in 1988, possibly due to extremely dry conditions in 1988. Further analysis (one-way ANOVA) revealed that the year effect was due to the biomass increase in the five beetle-killed stands rather than in all 10 stands (Table 2). We failed to detect significant (p =0.274) year effects in an examination of the slopes of the linearized mean biomass response functions to percent tree mortality (Fig. 1). Pooling all 40 stands (data from 1989 used for the 10 stands sampled twice) demonstrated that mean plot biomass increased exponentially as beetle-caused tree mortality became more severe (Fig. 2).

The frequency of fruit for all fruiting species combined was positively correlated (p<0.001, r=0.733) with beetle-caused tree mortality (Fig. 2), but the variability in the presence of fruit was high in moderately to severely infested stands.

Understory plant distribution

The coefficient of variation in mean understory biomass peaked at moderate levels of beetle-caused tree mortality (Fig. 2). This parameter, as well as the standard error (Fig. 2), indicates that variability in plot biomass peaks in stands with moderate mortality, and that the biomass of low and high mortality stands is more uniform. Intrastand habitat edge between sunny, vegetated patches beneath canopy gaps and shady, nearly-barren patches beneath forest canopies was highest in stands with intermediate levels of tree mortality (Fig. 2).

Understory plant diversity

Understory plant species richness and other indices of species diversity were highest at intermediate levels of beetle-caused tree mortality (Fig. 3). Richness demonstrated the strongest quadratic response to increasing tree mortality. Indices that are more sensitive to evenness demonstrated a poorer fit. Grasses/sedges dominate the understory community in stands with moderate and severe tree mortality. Forbs and shrubs had greater biomass in beetle-killed stands with 60% or more tree mortality than in stands with lower mortality (Fig. 4). Understory tree biomass appeared to increase in moderately killed (61-80% mortality)

stands.

Table 1. Means and standard deviations of understory vegetation in beetle-killed lodgepole pine stands with different tree mortalities sampled in different years.

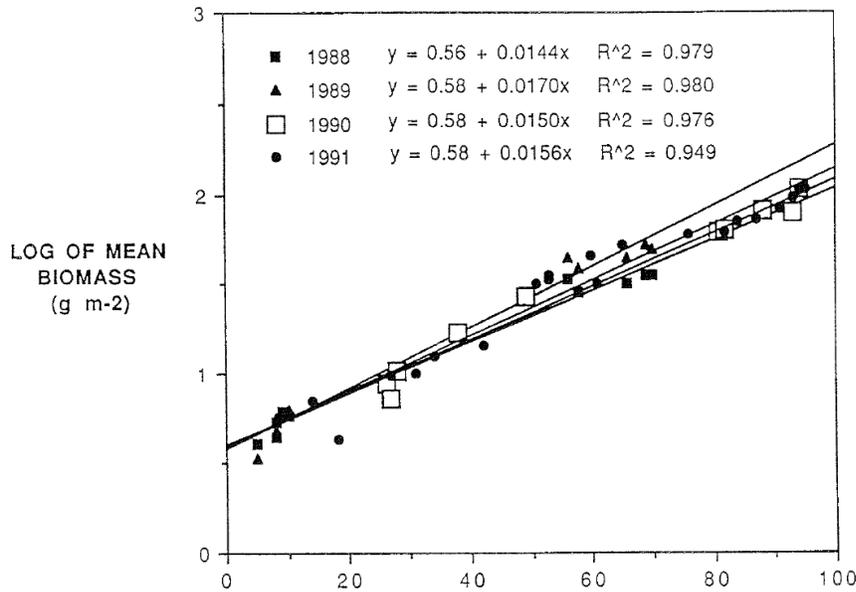| Stand	Year	Percent Tree Mortality	Mean Biomass (g m^2)	S.D.
01	1988	56	33.9	16.17
02	1988	58	28.7	15.17
03	1988	66	32.2	14.44
04	1988	69	35.7	28.46
05	1988	70	35.6	25.73
06	1988	8	4.4	1.70
07	1988	8	5.3	2.21
08	1988	5	4.1	1.47
09	1988	9	6.1	1.52
10	1988	10	5.8	1.58
01	1989	56	44.8	22.33
02	1989	58	39.3	18.21
03	1989	66	45.0	17.32
04	1989	69	53.2	32.57
05	1989	70	49.9	32.54
06	1989	8	4.8	1.40
07	1989	8	5.7	0.81
08	1989	5	3.4	0.53
09	1989	9	5.8	1.16
10	1989	10	6.4	1.15
11	1990	93	80.2	21.75
12	1990	81	62.0	21.65
13	1990	26	8.8	1.16
14	1990	38	17.1	7.40
15	1990	49	27.4	22.64
16	1990	27	7.3	1.06
17	1990	28	10.4	1.74
18	1990	88	81.9	18.01
19	1990	94	106.8	20.92
20	1990	82	63.9	29.70
21	1991	14	7.0	0.95
22	1991	18	4.3	0.73
23	1991	27	9.9	1.07
24	1991	31	10.0	1.93
25	1991	53	36.1	26.51
27	1991	65	52.1	33.30
28	1991	82	62.8	21.56
29	1991	93	96.7	25.67
30	1991	91	83.3	27.25
31	1991	61	32.2	27.93
32	1991	42	14.6	5.99
34	1991	76	60.1	27.88
35	1991	95	108.8	23.43
36	1991	53	33.7	30.48
37	1991	34	12.5	2.54
38	1991	94	107.1	14.08
39	1991	51	32.5	32.97
40	1991	84	71.7	29.92

Fig. 1. Relationship of log-transformed mean biomass production of understory vegetation and percent tree mortality in 40 beetle-killed lodgepole pine stands (10 stands sampled twice) for four consecutive years in the Uinta mountains north slope, Utah.

Discussion

Understory biomass

The observed responses of understory vegetation to increasing beetle-caused tree mortality is similar to those observed as the tree canopy is reduced by tree harvesting (Halls & Schuster 1965). Release from competition with trees for light, water, and nutrients probably allows many plants in the forest understory to grow and reproduce at higher rates. The curvilinear, exponential response of understory biomass to increasing tree mortality suggests that the effects of competition with trees are additive. Our results indicate that epidemics of bark beetles in coniferous forests increase the availability of forage and browse to livestock and wildlife. In the absence of intense grazing pressure by wild and domestic herbivores, these stands offer nesting and foraging cover to small mammals and birds.

Table 2. Test statistics for one-way analysis of variance comparisons of mean plot biomass of understory vegetation in beetle-killed lodgepole pine stands of similar tree mortality levels sampled in different years.

Comparison	F	p
1988 vs. 1989:		
0.25% mortality ($n = 10$)	0.02	0.905
51–75% mortality ($n = 10$)	23.75	0.000
1988 vs. 1989 vs. 1991		
51–75% mortality ($n = 15$)	5.90	0.016
1989 vs. 1991		
51–75% mortality ($n = 10$)	2.02	0.193
1990 vs. 1991		
26–50% mortality ($n = 8$)	0.12	0.739
76–100% mortality ($n = 12$)	0.01	0.926
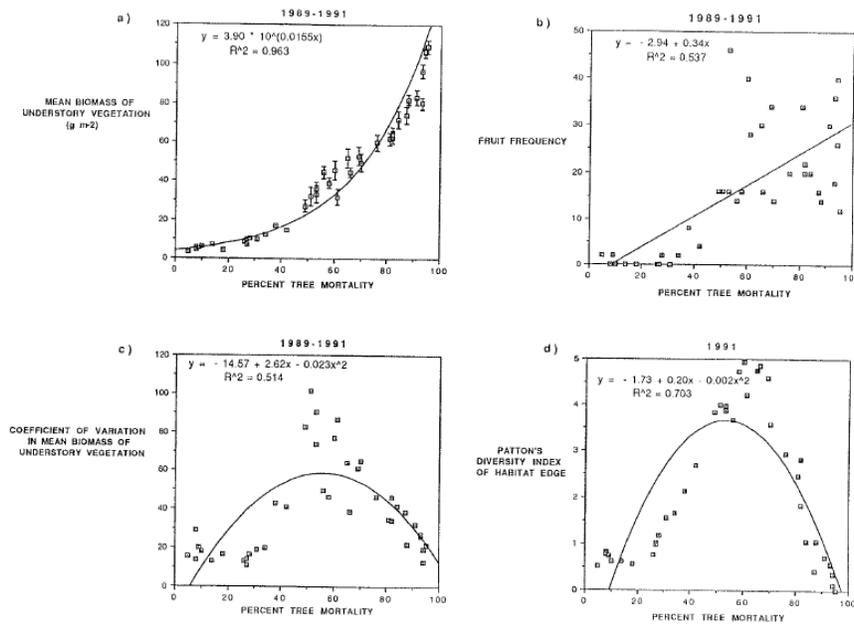
Fig. 2. Relationship of (a) mean biomass of understory vegetation, (b) frequency of fruit presence, (c) coefficient of variation of mean biomass, and (d) intrastand edge index between sunny and shady forest floor patches to percent tree mortality in 40 beetle-killed lodgepole pine stands in the Uinta mountains north slope, Utah.
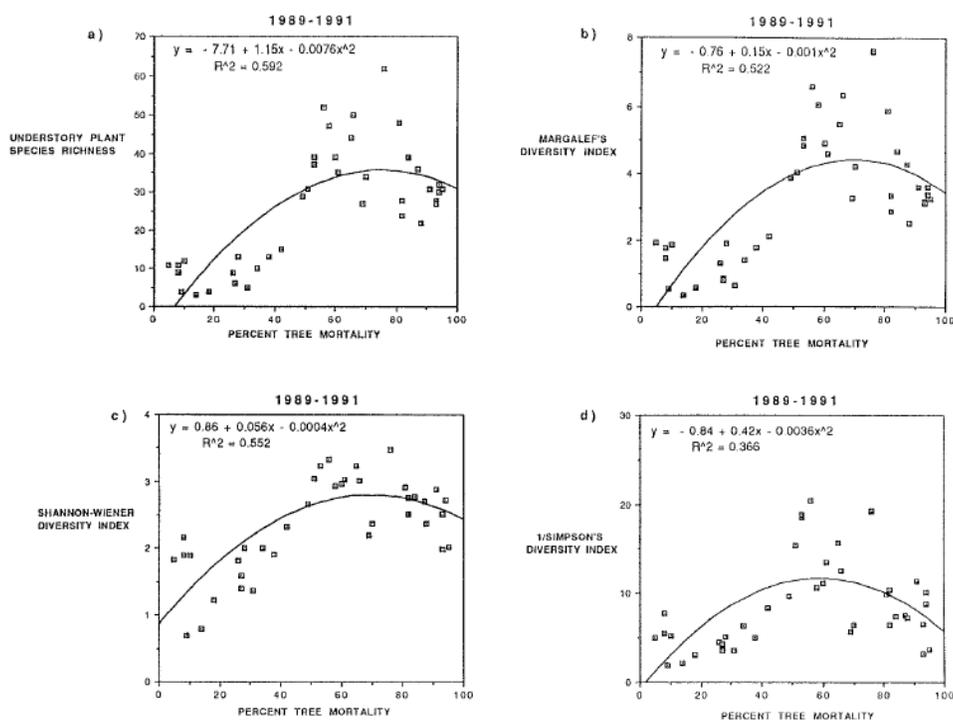
Fig. 3. Relationship of understory plant species biomass diversity, measured by four diversity indices, (a) species richness, (b) Margalef's simple diversity index, (c) the Shannon-Wiener diversity index, and (d) the inverse of Simpson's diversity index to percent tree mortality in 40 beetle-killed lodgepole pine stands in the Uinta mountains north slope, Utah, 1989-1991 (pooled).

The frequency of fruit presence is positively correlated to beetle-caused tree mortality. Most fruiting species are shrubs (Appendix) and the presence of fruit is partially a function of shrub abundance. Shrub biomass was highest in stands with greater mortality, but it is apparent from the variability in fruit frequency that other factors are contributing to the presence of fruit in these stands. One plausible factor is irradiance level, given the type of disturbance. Brighter light increases sexual reproductive effort (Pitelka *et al*. 1980; Bernier *et al*. 1981; Zimmer 1985; Dahlem & Boerner 1987) and reduces fruit absorption (Dahlem & Boerner 1987) in forest herbs. Pitelka et al. (1980) determined that sexual reproductive effort in Aster acuminatus increased linearly as light intensity increased, once a minimum light level was reached. The pattern of increasing fruit frequency in stands with higher tree mortality appears to be partly attributable to increased light levels following reduction of canopy cover in these stands.

Understory plant distribution
The detection of a peak in understory biomass variation in stands with moderate levels of beetle-caused tree mortality indicates that the distribution of understory vegetation is more heterogeneous in typical beetlekilled stands than in unaffected or severely disturbed stands. Additionally, the response of intrastand habitat edge to percent tree mortality reflects the

patchier distribution of understory vegetation in beetle-killed stands of intermediate mortality. Increases in vegetation abundance below a canopy gap are well documented (Moore & Vankat 1986; Mladenoff 1990). When this process is viewed at the landscape scale where many forest gaps are created by an intermediate disturbance, we observe an increase in the heterogeneity of vegetation distributed across the forest floor.

Understory plant diversity
Our results are consistent with the predictions of the intermediate disturbance hypothesis (Connell 1978). An examination of the responses of the different diversity indices suggests that plant species richness, but not the evenness of understory species, is substantially higher in stands with moderate tree mortality than in stands with low or high mortality. Richness and evenness are the components of indices that measure changes in diversity and indicate how community composition has been altered following environmental change. A few species of grass, especially Elymus elymoides, dominated the understory community in stands that had experienced severe epidemics. Trees appeared to increase in abundance in stands with intermediate mortality. However, this increase is a result of a previous epidemic (1959-1962) in stands where aspen contributed greatly to the understory and midstory vegetation layers. Mean tree biomass in this mortality class is comparable (3.80 g m-2) to that in the class above and below when these two stands are excluded from the analysis.

Alternative explanations of the plant species diversity response to disturbance that we observed include, but are not limited to, the environmental heterogeneity model (Bratton 1976; Ricklefs 1977), the intermediate productivity model (Tilman 1982), and the species-abundance curve model (Christensen & Peet 1982). Tilman & Pacala (1993) discuss the ecological merits of many of the competing hypotheses explaining the humpback diversity curve. Proponents of the environmental heterogeneity model could interpret our results to be caused by greater structural diversity in forest canopy cover in stands with moderate mortality. The heterogeneity in light and thermal regimes in these stands provides more niches (incorporating MacArthur's 1965 niche differentiation hypothesis) to plant species than a homogeneous environment.
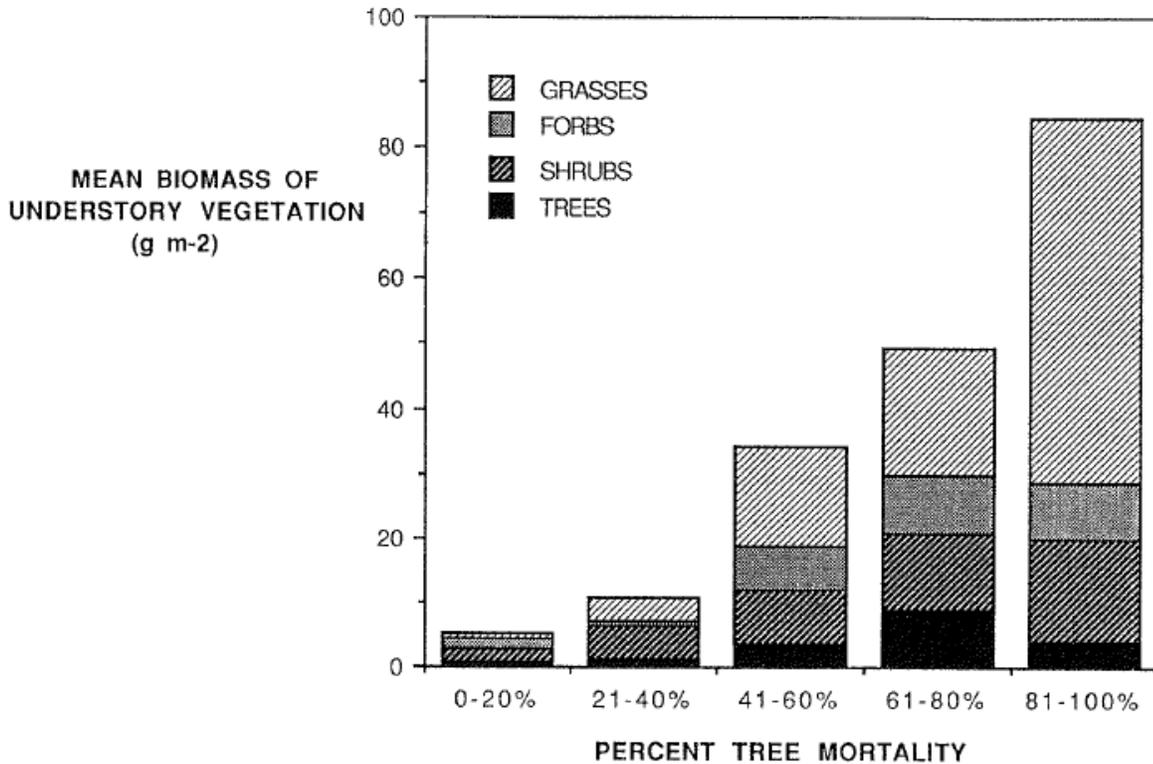
Fig. 4. Relationship of understory vegetation class biomass to levels of percent tree mortality in 40 beetle-killed lodgepole pine stands in the Uinta mountains north slope, Utah, 1989-1991 (pooled).

This model views competition as a force that maintains high diversity by restricting species to narrowly defined niches. In contrast, competition is perceived to exclude species in the absence of disturbance or predation by proponents of reduction-mediated models, of which the intermediate disturbance hypothesis is one variant. Tilman (1982) asserted that many features of plant communities change simultaneously along productivity gradients, including diversity. He hypothesized that plant species diversity is highest at intermediate levels of productivity which could occur without disturbance or nonequilibrium between species abundance. The species-abundance curve model maintains that an increase in plant abundance is sufficient to explain an increase in species richness. This model fits our results except in stands with severe tree mortality. Huston's (1979) general hypothesis of species diversity focuses on the nonequilibrium interactions of competing populations as the important mechanism leading to species diversity regardless of the cause of the nonequilibrium condition. Reader et al. (1991) listed several reasons to explain the failure of plant diversity to respond to disturbance intensity as predicted by the intermediate disturbance hypothesis. Further research on colonization and extinction rates in disturbed sites with varying levels of disturbance frequency or severity needs to be conducted to determine the role of competition and disturbance in shaping plant communities.

A stand with a high degree of interspersion of forest gaps, shaded areas, and boundary zones of intermediate conditions provides suitable conditions to a wider range of species with different physiological tolerances. Collins et al. (1985) discussed three types of understory plant responses to different light intensities, temperatures, soil moisture levels, and nutrient availabilities in forest gaps created by natural disturbances: sun herbs, light-flexible herbs, and shade plants. The modified environment within the gap (provided it is large enough) is more favorable to species of the first type and can be too harsh for the last (Collins et al. 1985).

The severity of a mountain pine beetle epidemic may have successional consequences for lodgepole pine stands. Cole & Amman (1980) measured a greater growth rate of subalpine fir beneath lodgepole pine stands with higher beetle-caused tree mortality, indicating a hastening of succession toward the climax forest. We observed that severely disturbed stands often (except on steep slopes) resemble wet meadows with dense stands of grasses and sedges. The few trees in the understories of these stands are sufficiently large to be considered residuals that were present prior to the disturbance. Grasses appear to suppress lodgepole pine regeneration in these stands. However, grass is less abundant in gaps of stands with moderate mortality, and there are numerous small seedlings of lodgepole pine and/or aspen present in these gaps (with no influence of fire). The presence and relative dominance of aspen in the understory communities of many disturbed stands with intermediate mortality are intriguing because of the consequences for the future development and management of disturbed stands. A reoccurrence of epidemic mountain pine beetle activity in stands where lodgepole pine is persistent could give aspen a competitive advantage in the midstory layer, allowing it to dominate lodgepole pine in the overstory for a number of years. An introduced or natural fire might favor the regeneration of lodgepole pine where cones are serotinous (Brown 1975), but many environmental factors would affect the outcome. Silvicultural techniques directed at favoring one outcome or the other (thinning pine or introducing fire) could be used when environmental conditions are appropriate for achieving management objectives in these disturbed areas.

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Appendix 1. Plant species collected in random plot biomass samples in beetle-killed stands in the Uinta mountains north slope, Utah, 1988-1992.

GRAMINOIDS

Agrostis humilis	Carex nova	Luzula spicata
Agrostis scabra	Carex rossii	Phleum alpinum
Agrostis variabilis	Danthonia intermedia	Phleum pratense
Bromus anomalus	Deschampsia caespitosa	Poa fendleriana
Bromus ciliatus	Elymus elymoides	Poa nervosa
Calamagrostis canadensis	Elymus glauca	Poa secunda
Carex geyeri	Elymus trachycaulus	Stipa nelsoni
Carex norvegica	Festuca saximontana	Trisetum spicatum

FORBS

Achillea millefolium*	Epilobium oregonense	Mertensia fusiformis
Agoserus glauca	Equisetum arvense	Osmorhiza depauperata
Allium brevistylum	Erigeron eximius	Oxytropis deflexa
Angelica pinnata	Erigeron peregrinus	Pedicularis bracteosa
Antennaria dimorpha	Erigeron simplex	Pedicularis racemosa
Antennaria microphylla	Erigeron speciosus	Penstemon procerus
Aquilegia coerulea	Erigeron ursinus	Penstemon whippleanus
Arabis drummondii	Fragaria vesca**	Phacelia sericea
Arenaria congesta	Galium boreale	Phlox multiflora
Arnica cordifolia	Gaultheria humifusa	Polygonum bistortoides
Aster chilensis	Gentiana affinis	Polygonum douglasii
Aster foliaceus	Geranium richardsonii	Potentilla gracilis
Aster glaucodes	Geranium viscosissimum	Pyrola virens
Astragalus miser	Habenaria hyperborea	Senecio multilobatus
Caltha leptosepala	Hieracium albiflorum	Taraxacum officinale
Castilleja rhexifolia	Hieracium gracile	Thalictrum fendleri
Cirsium arvense	Lewisia pygmaea	Thlaspi montanum
Cirsium eatonii	Lupinus argenteus*	Trifolium longipes
Collinsia parviflora	Lychnis drummondii	Viola nuttallii
Epilobium angustifolium		

SHRUBS

Arctostaphylos uva-ursi**	Pentaphylloides floribunda	Salix glauca
Berberis repens**	Ribes montigenum	Shepherdia canadensis***
Juniperus communis**	Ribes viscosissimum	Vaccinium caespitosum*
Lonicera involucrata	Rosa nutkana	Vaccinium scoparium**
Pachistima myrsinites	Rubus idaeus***	

TREES

Abies lasiocarpa	Pinus contorta	Pseudotsuga menziesii
Picea engelmannii	Populus tremuloides	

* rarely in fruit
* occassionally in fruit
** usually in fruit.