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Pest interactions and canopy gaps in ponderosa pine stands in the Black Hills, South Dakota, USA

J.E. Lundquist

Rocky Mountain Forest and Range Experiment Station, 240 W. Prospect Road, Fort Collins, CO 80526. USA

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Abstract

Gap frequency and size, cause (predisposing factors, killing agents, and tree response), and coarse woody debris composition (snags and downed logs) were assessed in three stands differing in management history. Disturbance agents were usually coupled concurrently and sequentially. A qualitative model (relational diagram) developed to display these interactions and the activity distributed among different disturbance pathways suggests that management activity (1) diminishes pest-caused structural diversity in the forest ecosystem, (2) decreases functional diversity associated with interacting diseases, insects and other disturbance agents, and (3) alters the abundance and decomposition distribution of dead wood.

Keywords: Canopy gaps; Disturbance; Disturbance interactions; Pest complexes

1. Introduction

Disturbance processes are integrated and expressed in the forest ecosystem by altering rates and patterns of tree mortality and reproduction. These processes generate and maintain patterns within stands that impact biodiversity, wildlife habitat, scenic quality, recreation, timber volume, and other forest resources.

Stands of *Pinus ponderosa* Douglas ex P. Laws in the Black Hills of South Dakota have historically been managed as units of uniform structure and age (Boldt et al., 1983). Recent pest surveys (Lundquist, 1991a,b, 1993a) indicated, however, that most stands have discrete gaps in the canopy caused by the loss of one or more trees. The following disturbance agents were associated with these gaps: *Armillaria* root disease (caused by *Armillaria* spp.), mountain pine beetle (*Dendroctonus ponderosa* Hopkins), Bark beetles (*Ips* spp.), red rot of pine (caused by *Dichomitus squalens* (P. Karst.) D. Reid, Schweinitzii root rot (caused by *Phaeolus schweinitzii* (Fr.: Fr.) Pat.), lightning, cattle damage, fluctuating water table, harvesting, strong winds, fire, heavy frosts, and other disturbance agents (Lundquist, 1991a,b, 1993a).

The etiology of canopy gaps can be complex because cause/effect relationships are often not obvious. Two or more disturbance agents commonly interact to cause gaps. Relatively little work has been done on multiple pest complexes (Shaw and Eav, 1993). Preliminary studies in the Black Hills indicated that cause could often be characterized as an interaction between predisposing agents that enhance susceptibility to killing agents, the agents that kill trees, and tree responses that result in canopy gaps (Lundquist, 1993b).

The objective of the study discussed below was to examine how interacting diseases, insects, and other disturbance agents alter canopy structure and coarse woody debris composition. Canopy gaps were chosen

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as a vehicle to examine these interactions because: (1) trees dying in groups are a common indicator of various stress agents; (2) gap sizes can be expressed in both individual tree and landscape scales; (3) gaps affect various commodity and non-commodity forest resources; (4) gaps alter rates and direction of succession in forest ecosystems and (5) a gap is an easily understood concept that bridges several fields of forest study, including pathology, entomology, silviculture, management, and ecology.

2. Materials and methods

2.1. Study sites

This study was conducted in the Black Hills National Forest in west central South Dakota. The Black Hills are the easternmost outlier of the Rocky Mountains. Elevation reaches 2300 m (Froiland, 1990). Forests occur between 1200 m and 2100 m. Precipitation averages about 750 mm year^{-1}, mostly as rain during summer months. *Pinus ponderosa* is the dominant tree species. Other dominant tree species include *Picea glauca* (Moench) Voss, *Populus tremuloides* Michx., and *Quercus macrocarpa* Michx. (Hoffman and Alexander, 1987).

Plots were established in three *Pinus ponderosa* stands, each differing in management history. Plots were located at random, except that they were not placed where major rock outcrops, meadows, or other non-killing agents might have been responsible for lack of canopy. These stands were chosen because they represented some extremes in management activities found in the Black Hills National Forest. The stands were:

2.1.1. Upper Pine Creek Research Natural Area (UPC)

This is a 475 ha area located 8 km west of Mt Rushmore National Monument (T2SR5E Sec 15). This area was set aside in 1932 as a Research Natural Area. Stands within the UPC had not been previously harvested, but wildfires had been excluded (S. Sylva, personal communication, 1993). In an unpublished report (1965), C.E. Boldt (Research Silviculturist, USDA Forest Service) described the area:

> ''Ponderosa pine stands, mostly pure and evenaged occupy approximately 85% of the 1190 acres included within the present boundaries. Inventory data and gross observations both indicate that about half of the acres occupied by pine support typical, dense, immature stands, mostly of small pole and sapling size. Remainder of the pine-stocked acres support mature and overmature stands of sawtimber. Some patches of sawtimber are sufficiently dense and continuous to preclude development of a seedling–sapling understory. However, most of the yellowbark stands are irregularly stocked, because of mortality, and under these stands advance reproduction forms a characteristic, non-uniform second story. Small groups of extremely old veterans are fairly common and, on favorable sites, some of these old-timers have attained truly impressive sizes. Most of the mature and overmature stands show evidence of continuous, selective attack by endemic populations of Black Hills beetles.''

2.1.2. Palmer Creek (PC)

This is an 80 ha area within the Norbeck Wildlife Preserve, approximately 2 km west of UPC (T2SR5E Sec 8). The Norbeck Wildlife Preserve was established in 1920 to protect game animals and birds. Stands were selectively harvested prior to 1960, but more specific details are lacking because management records are incomplete. Currently, harvest of *P. ponderosa* in this area is aimed at enhancing wildlife habitat and vegetation diversity (S.D. Custer, 1994). Timber harvesting options for ponderosa pine stands include: (1) clearcut with intermediate thinning, with density range for thinnings of 30–60% and approximate basal area for thinnings of 70–90%, and (2) two-step shelterwood with intermediate thinning, with density range for thinnings of 30–50% and approximate basal area for thinnings of 70–90% (S.D. Custer, 1994).

2.1.3. Fourcorners (FC)

This is an approximately 40 ha area, 15 km west of the UPC (T2SR3E Sec 7). This area is currently managed for timber production as an even-aged stand using a two-step shelterwood with intermediate thinning (S.D. Custer, 1994). Stands were thinned in 1991.

2.2. Stand characteristics

Comparisons were made among the three sites. Within each site, at least five randomly located variable plots were established using a prism with a basal area factor of 2.5 m^2 ha^{-1}. Species, diameter at 1.5 m, and current condition (living or dead) were determined for all tally trees. Basal area, stem density, and quadratic mean diameter were subsequently calculated for each plot. To determine preharvest conditions, cut stumps were also tallied and analyzed as if stems were still attached using stump diameter to estimate diameter at 1.5 m.

2.3. Gap characteristics

Canopy gap characteristics were summarized for each stand and compared among the three stands. A gap was defined as a canopy opening created by the death or removal of at least one codominant or dominant tree. Each stand was surveyed using 10 m wide parallel strip transects located 90 m apart (Runkle, 1992); i.e. a 10% sample. Six, 1000 m transects were used to sample a 27 ha area at UPC. Six, 300 m transects were used to characterize 9 ha plots each at PC and FC. Gaps whose centers fell on the transect were assessed for cause, frequency and size, and snag and downed wood distribution, as follows:

2.3.1. Gap causes

Each gap was assessed visually by a team of scientists and technicians who conferred in the field in determining causes of each gap. Most team members had had extensive experience with diagnosis and were familiar with symptoms and signs of diseases, insects, and other disturbances known to occur in the Black Hills. Diagnoses were based on obvious symptoms and signs. Best guesses were made as a team where symptoms and signs were not obvious.

Diversity of disturbance pathways in each plot was assessed as pathway richness (number of different pathways) and the Shannon–Weaver Index of General Diversity. The Shannon–Weaver Index was calculated using:

$$H' = -\Sigma(n_i/N)\ \log(n_i/N)$$

where n_i is number of occurrences of pathway i and N is total number of occurrences of all pathways (Shannon and Weaver, 1949).

2.3.2. Gap frequency and size

To determine gap frequency, perpendicular distance from transect center to gap center was noted. Gap density was estimated using distance sampling techniques (Buckland et al., 1993) with strip width truncated at 5 m. Diameter of each gap within the strip was measured by noting the transect distance of the gap's beginning and ending edge at the stem base of edge trees (Runkle, 1992). Mean gap diameter for each stand and for gaps associated with each major disturbance pathway were compared using the Welch Test for groups with heterogeneous variances and unequal sample sizes (Milliken and Johnson, 1984).

The summed diameter of all gaps in which a pathway occurred divided by total diameter of all gaps in the plot was used to assess the relative importance of each disturbance pathway; i.e.:

$$\mathrm{IMPORTANCE}_{a,b,c} = \Sigma(\mathrm{DIAM}_{a,b,c}/\mathrm{TOTDIAM})$$

where $\mathrm{DIAM}_{a,b,c}$ is the diameter of all gaps with pathway a, b, c; TOTDIAM is the diameter of all gaps; $\mathrm{IMPORTANCE}_{a,b,c,}$ is the activity of pathway a,b,c; a is the predisposing factor; b is the killing agent; and c is the tree response.

UPC data were used as a reference with which to compare and contrast pathway importance among plots. Relative importance of each pathway in previously harvested plots was determined by comparing their importance values to the same pathways in UPC using:

$$\mathrm{UPC}_{ij} - [(\mathrm{PC}_{ij} + \mathrm{FC}_{ij})/2],$$

where i and j represent the interaction of a predisposing factor i and a killing agent j, or a killing agent i and a tree response j.

2.3.3. Snag and downed log distribution

All snags, stumps, and downed logs within each gap were scored for decomposition class using diagrams originally developed for spruce/fir forests in the Pacific Northwest (Maser et al., 1979; Thomas et al., 1979), and modified slightly by the author for ponderosa pine in the Black Hills. Snag classes were: 1, living; 2, declining; 3, new dead; 4, old dead; 5, loose bark stage;

Table 1
Relative importance of each disturbance pathway identified in this study. Disturbance pathways are composed of predisposing factors, killing agents, and tree responses. The total importance values for some pathways is above 1.0 because multiple pathways involving the same agents commonly occurred within the same gap

Predisposing	Killer	Response	Importance[a]		
			UPC	Palmer	Fourcorn
Cattle grazing	None/unknown	Standing dead	0	0	0.05
Fire	Bark beetles	Butt snap	0.06	0	0.03
Fire	Bark beetles	Standing dead	0	0.06	0
Fire	Bark beetles	Stem break	0.12	0.02	0.14
Fire	Bark beetles	Tree fall	0.01	0	0
Fire	Bark beetles	Uprooting	0.01	0	0
Fire	Fire	Standing dead	0.01	0	0
Fire	Fire	Stem burn	0.02	0.03	0.07
Fire	None/unknown	Butt snap	0.02	0.11	0
Fire	None/unknown	Standing dead	0	0.26	0
Fire	None/unknown	Stem break	0.04	0.05	0.05
Fire	None/unknown	Tree fall	0.01	0.05	0
Fire	None/unknown	Uprooting	0	0.23	0
Fire	Root rot	Butt snap	0.01	0	0
Fire	Root rot	Stem break	0.02	0	0
Fire	Root rot	Uprooting	0.01	0	0
Fire	Rot/beetles	Butt snap	0.03	0	0
Fire	Rot/beetles	Stem break	0.04	0	0
Fire	Rot/beetles	Uprooting	0.01	0	0
Fire	Wind	Tree fal	0.01	0	0
Fire	Wind	Uprooting	0.18	0	0.54
None/unknown	Bark beetles	Butt snap	0.04	0.28	0.37
None/unknown	Bark beetles	Regen failure	0	0.04	0
None/unknown	Bark beetles	Standing dead	0	0.16	0.92
None/unknown	Bark beetles	Stem break	0.11	0	1.14
None/unknown	Bark beetles	Tree fall	0.05	0	0.05
None/unknown	Bark beetles	Uprooting	0.02	0.05	0.13
None/unknown	Fire	Tree removal	0	0.01	0
None/unknown	Lightning	Shattered stem	0.01	0	3.99
None/unknown	None/unknown	Butt snap	0	0.29	1
None/unknown	None/unknown	Regen failure	0	0.15	0
None/unknown	None/unknown	Stem break	0.01	0.07	0
None/unknown	None/unknown	Tree fall	0.01	0.06	0
None/unknown	None/unknown	Uprooting	0.01	0.18	0
None/unknown	None/unknown	Butt snap	0.06	0	0
None/unknown	Root rot	Standing dead	0	0.10	0
None/unknown	Root rot	Stem break	0.04	0	0
None/unknown	Root rot	Uprooting	0.04	0	0
None/unknown	Rot beetles	Butt snap	0.04	0	0.39
None/unknown	Rot beetles	Standing dead	0.03	0	0
None/unknown	Rot beetles	Stem break	0.10	0	0.51
None/unknown	Rot beetles	Uprooting	0.03	0	0.05
None/unknown	Tree harvest	Tree removal	0.01	1.62	0.11
None/unknown	Wind	Standing dead	0	0.01	0
None/unknown	Wind	Tree fall	0	0.017	0
Shallow soil	Bark beetles	Butt snap	0.05	0	0.01
Shallow soil	Bark beetles	Standing dead	0.01	0.06	0.19
Shallow soil	Bark beetles	Stem break	0.07	0	0.16
Shallow soil	Bark beetles	Uprooting	0.02	0.01	0
Shallow soil	None/unknown	Butt snap	0	0.06	0
Shallow soil	None/unknown	Regen failure	0	0.02	0

Predisposing	Killer	Response	Importance[a]		
			UPC	Palmer	Fourcorn
Shallow/soil	None/unknown	Standing dead	0	0.02	0
Shallow/soil	None/unknown	Stem break	0.01	0	0
Shallow/soil	None/unknown	Uprooting	0	0.06	0
Shallow/soil	Root rot	Butt snap	0.01	0	0
Shallow/soil	Root rot	Standing dead	0.01	0	0
Shallow/soil	Root rot	Stem break	0.01	0	0
Shallow/soil	Wind	Uprooting	0.01	0.03	0
Soil/fire	Bark beetles	Butt snap	0.19	0	0.05
Soil/fire	Bark beetles	Standing dead	0.04	0	0
Soil/fire	Bark beetles	Stem break	0.23	0	0
Soil/fire	Bark beetles	Tree fall	0.02	0	0
Soil/fire	Bark beetles	Uprooting	0.06	0	0
Soil/fire	Fire	Standing dead	0	0	0.04
Soil/fire	None/unknown	Butt snap	0.03	0.02	0.03
Soil/fire	None/unknown	Standing dead	0.02	0.05	0.03
Soil/fire	None/unknown	Stem break	0.03	0	0.19
Soil/fire	None/unknown	Tree fall	0.02	0	0.10
Soil/fire	None/unknown	Uprooting	0.11	0.13	0.20
Soil/fire	Root rot	Butt snap	0.05	0	0
Soil/fire	Root rot	Standing dead	0.01	0	0
Soil/fire	Root rot	Stem break	0.03	0	0
Soil/fire	Root rot	Uprooting	0.02	0	0
Soil/fire	Rot/beetles	Butt snap	0.04	0	0
Soil/fire	Rot/beetles	Stem break	0.04	0	0
Soil/fire	Tree harvest	Standing dead	0	0	0.02
Soil/fire	Tree harvest	Tree removal	0.01	0	0
Soil/fire	Wind	Stem break	0.01	0	0
Soil/fire	Wind	Tree fall	0.06	0	0
Soil/fire	Wind	Uprooting	1.12	0	0.69
Suppression	Bark beetles	Standing dead	0	0.01	0
Suppression	Ice/snow	Tree push	0.01	0	0
Suppression	None/unknown	Regen failure	0	0.03	0
Suppression	None/unknown	Standing dead	0	0.11	0
Suppression	None/unknown	Tree fall	0.01	0.15	0
Suppression	None/unknown	Uprooting	0	0.04	0
Suppression	Root rot	Regen failure	0	0.01	0
Suppression	Root rot	Uprooting	0	0.01	0
Suppression	Weak parasites	Butt snap	0	0.02	0
Suppression	Weak parasites	Regen failure	0	0.78	0
Suppression	Weak parasites	Standing dead	0	0.03	0
Suppression	Weak parasites	Tree fall	0.07	0.53	0
Suppression	Weak parasites	Tree push	0.04	0	0
Suppression	Wind	Tree fall	0.01	0	0
Tree harvest	None/unknown	Butt snap	0	0	0.11
Tree harvest	None/unknown	Stem break	0	0	0.38
Tree harvest	Rot/beetles	Butt snap	0	0	0.10
Tree harvest	Rot/beetles	Standing dead	0	0	0.03
Tree harvest	Rot/beetles	Stem break	0	0	0.10

[a] $\mathrm{IMPORTANCE}_{a,b,c} = \Sigma(\mathrm{DIAM}_{a,b,c}/\mathrm{TOTDIAM})$
where $\mathrm{DIAM}_{a,b,c}$ is diameter of all gaps with pathway *a*, *b*, *c*; TOTDIAM is diameter of all gaps; $\mathrm{IMPORTANCE}_{a,b,c}$ is activity of pathway *a*,*b*,*c*; *a* is predisposing factor *a*; *b* is killing agent *b*; and *c* is tree response *c*.

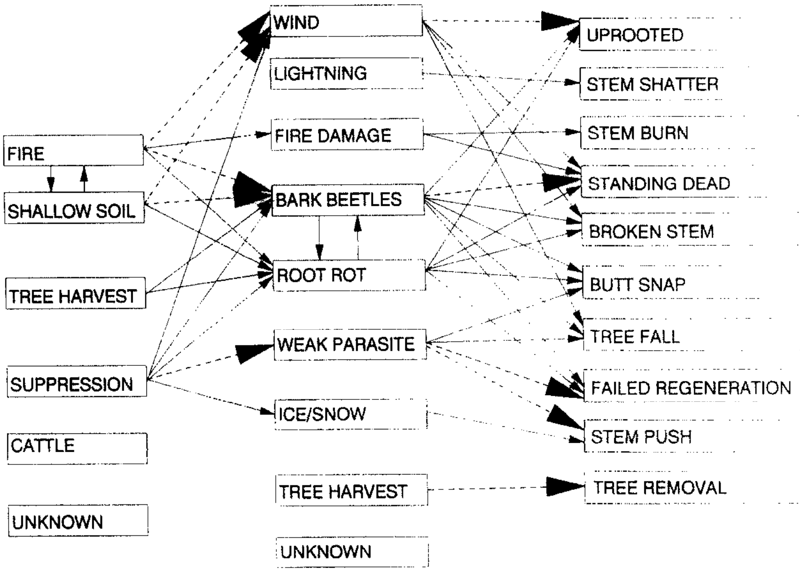

Fig. 1. Relational diagram illustrating the interactions among predisposing agents, killing agents and tree responses observed at Upper Pine Creek Research Natural Area, Palmer Creek, and Fourcorners. Broken arrows with large arrow heads represent pathways enhanced by timber harvesting. Broken and dotted arrows with large arrow heads represent pathways diminished by timber harvesting. Solid arrows represent pathways that are unaffected by timber harvesting.

6, no bark stage; 7, broken stem; 8, butt snap; 9, cut stump; 10, windthrow. Log classes were 1, fresh; 2, old; 3, no bark; 4, half decomposed; 5, mostly decomposed. Data were summarized for each stand and each major disturbance pathway in histograms of decomposition class frequencies, which were compared and contrasted using contingency tables and Pearson's Chi square test of independence (Sokal and Rohlf, 1981).

Relative contribution of individual killing agents to various snag classes was calculated using:

$$\mathrm{CONTRIB}_{ij} = (\mathrm{SNAG}_{ij}/\mathrm{TOTSNAG}) * 100$$

where SNAG_{ij} is the frequency of snags class_{ij} associated with the interaction between killing agent i and snag class j, and TOTSNAG is the total number of snags.

3. Results

3.1. Stand characteristics

Current stand conditions at UPC were 30.3 $\mathrm{m}^2\ \mathrm{ha}^{-1}$ basal area (BA), 29.8 cm average dbh, and 435 stems ha^{-1} (sph) stem density. Current stand conditions at PC were 20.2 m^2 BA, 37.2 cm average dbh, and 190 sph. Estimated pre-harvest conditions at PC were 24.8 m^2 BA and 232 sph, although pre-harvest conditions were difficult to determine because stumps had rotted away or ground cover had overgrown old stumps. Current stand conditions at FC were 14.2 m^2 BA, 36.9 cm average dbh and 130 sph; estimated pre-harvest conditions were 30.3 m^2 BA and 284 sph.

3.2. Gap characteristics

3.2.1. Gap causes

For all sites combined, the most common killing agents were fire, tree harvesting, bark beetles, root rot, wind, and secondary (weak) pathogens. These killing agents were often linked to predisposing factors and specific tree responses. The composition of predisposing factors, killing agents, and tree responses varied among stands. Within individual gaps, various combinations were coupled sequentially or concurrently and, consequently, occurred as disturbance pathways (Fig. 1). Many gaps had more than one pathway. Sixty eight, 45, and 33 different disturbance pathways were identified at UPC, PC, and FC, respectively (Table 1). In UPC, the most active pathways involved combinations of shallow soil, fire, strong winds, ice and snow; and standing dead and uprooting. At PC and FC, the most active disturbance pathways involved shallow soil, fire,

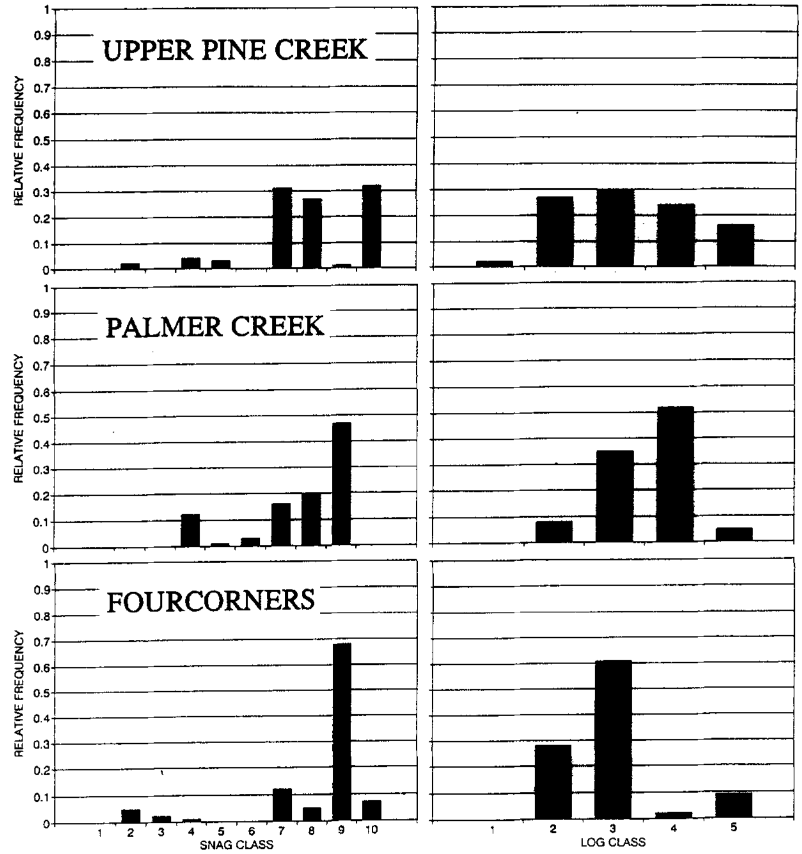

Fig. 2. Frequency class distribution of snag (left column) and log (right column) decomposition classes for Upper Pine Creek Research Natural Area, Palmer Creek, and Fourcorners. For snag and log classes see text.

cattle damage, tree harvesting, bark beetles, strong wind, standing dead, uprooting and tree removal. Disturbance pathway diversity was greater at UPC ($H'=8.77$) than either PC ($H'=4.62$) or FC ($H'=5.07$).

The relative importance of the following pathways increased in harvested stands: bark beetles-standing dead, tree harvest-stump and suppression-weak parasite-failed regeneration (Fig. 1). The importance of the following pathways decreased: soil/fire-wind-uprooted, soil/fire-bark beetles-standing dead and weak parasites-stem push. Other pathways were not significantly altered by harvesting.

3.2.2. Gap frequency and size

Gap frequency (F) was greater at PC (57 gaps ha^{-1}) than either UPC (26 gaps ha^{-1}) or FC (36 gaps ha^{-1}), and these were significantly different ($F=20.73$, $P<0.0003$). Mean gap diameter was greater at FC (average = 17.3 m; S.E. = 0.53) than UPC (average = 13.6; S.E. = 0.68) and PC (average = 11.3; S.E. = 0.63), and these differences were significantly different ($F=21.23$; d.f. = 2; $P<0.01$).

3.2.3. Snag and downed wood distribution

Mean snag frequencies (within gaps) were 211, 183, and 267 snags ha^{-1} at UPC, PC, and FC, respectively. Mean snag frequency per ha did not differ significantly among sites at $P<0.05$. Snag decomposition class frequency distribution significantly differed among the three stands ($\chi^2=2131$; d.f. = 16; $P<0.0001$). Cut stumps comprised the dominant snag class at PC and FC (Fig. 2). Stem snap, butt snap, and uprooting were dominant in UPC, where cut stumps were absent. Mean log frequencies were 214, 211, and 194 ha^{-1} at UPC, PC, and FC. Log frequency per ha at FC did not differ

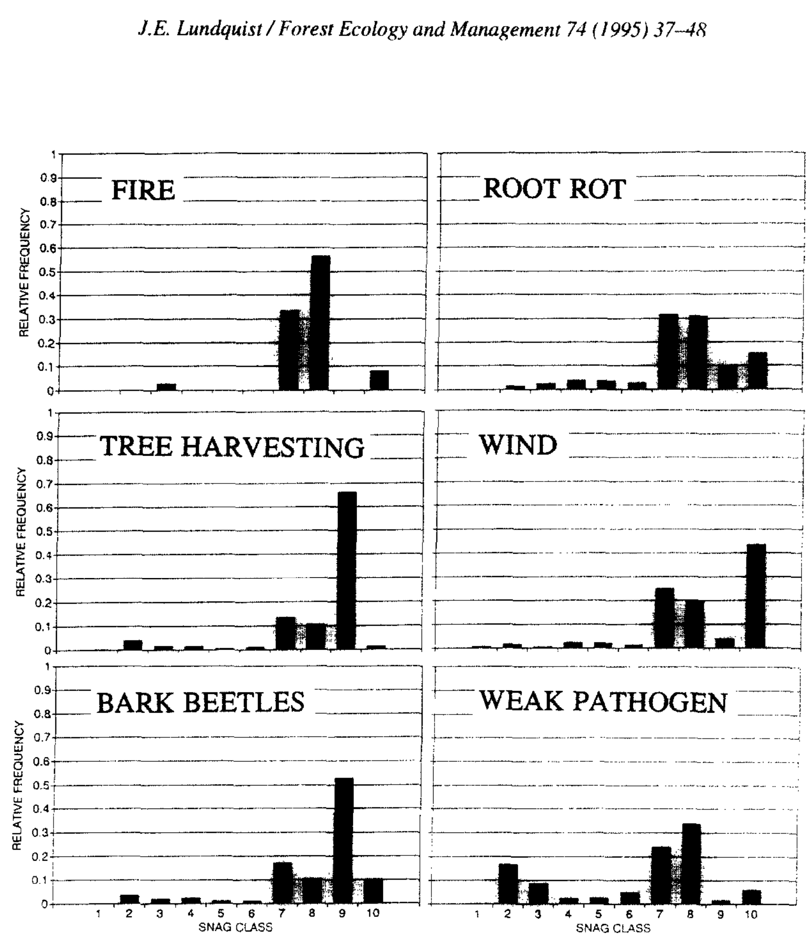

Fig. 3. Frequency class distribution of snags associated with six primary killing agents at Upper Pine Creek, Palmer Creek and Fourcorners combined. For snag classes see text.

significantly among the three sites at the 0.05 level, but log decomposition class frequency distribution differed significantly among all sites ($\chi^2=432$; d.f. $=8$; $P<0.001$).

The six most common killing agents for all sites combined (fire, tree harvesting, bark beetles, root rot, wind, and weak pathogens) differed significantly in snag decomposition distribution ($\chi^2=236$; d.f. $=42$; $P<0.001$) (Fig. 3) and log decomposition distribution ($\chi^2=1422$; d.f. $=28$; $P<0.001$) (Fig. 4).

The relative contributions of killing agents to various snag classes varied among agents and among sites (Table 2). Wind and bark beetles were the greatest contributors at UPC. Tree harvesting and bark beetles were the greatest at FC. At PC, the major contributors were tree harvesting and weak pathogens, although a very large 'unknown' component also occurred.

4. Discussion

4.1. Causes

Under non-epidemic conditions, gap formation involves predisposing factors, killing agents, and tree responses, which are coupled sequentially and concurrently in time and space. A slightly different version of this model was previously presented by Sinclair (1967) for declines of hardwoods. Similar models have been developed since (Manion, 1981; Sinclair and Hudler, 1988; Manion and Lachance, 1992). Many of these models have focused on complex diseases of individual trees. On a community scale or larger, interactions of disturbance agents within tree populations can be even more complex. In this study, relational diagrams were used to capture this complexity.

Cause and effect relationships in forestry are often difficult to prove, even between only two elements

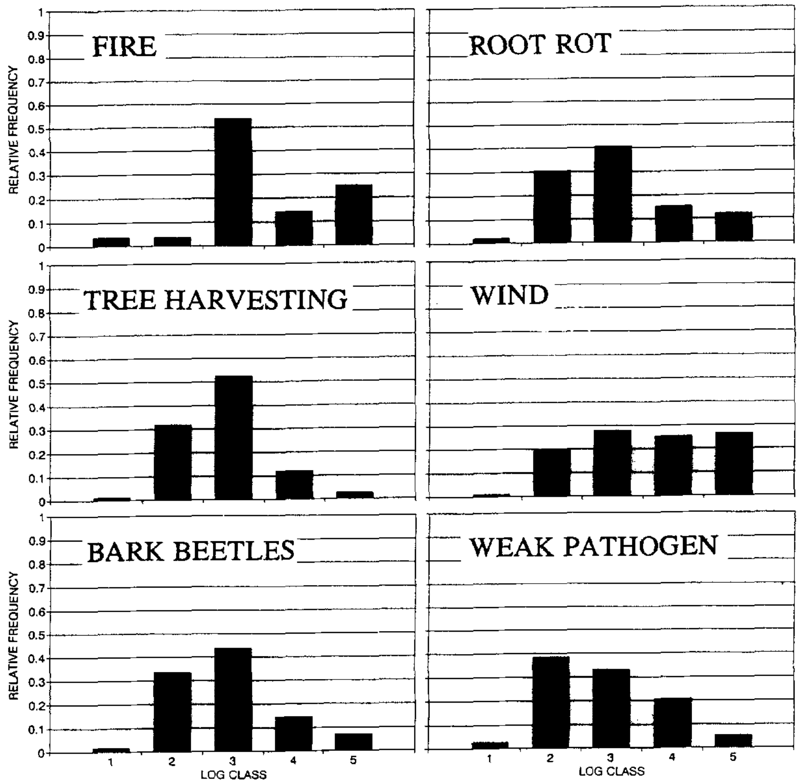

Fig. 4. Frequency class distribution of logs associated with six primary killing agents at Upper Pine Creek, Palmer Creek and Fourcorners combined. For log classes see text.

(Schreuder and Thomas, 1991). Several studies have been done on disturbance interactions (Witter, 1990, Schowalter and Filip, 1993). Modeling cause/effect interactions is difficult because they are unpredictable and chaotic (Lynch, 1990; Liebhold, 1994); many elements can directly or indirectly interact or both (Witter, 1990); and information about prior stresses is often incomplete. Furthermore, several conditions must be met before a causal relationship is proven (Dillon and Goldstein, 1984): (1) elements must show concomitant variation or covariation, (2) elements must show sequential placement in time, and (3) elements must maintain their effect when confounding variables are no longer present. The results presented above are based on observational data, and represent a best estimate of what may have actually caused the gaps.

The relational diagrams presented here offer a simplified version of what more detailed studies would unquestionably describe to be very complex systems. Even the most detailed simulations of such ecological phenomena are only hypotheses. These diagrams, however, help to integrate thinking about impacts of disturbances on ecosystem functions, highlight weak links in our knowledge, and offer a method of quantifying complex interactions (Dillon and Goldstein, 1984). Network models also enable an assessment of the relative contributions of various disturbance pathways.

Results of this study suggest that tree harvesting initiates a systematic sequence of recovery. Initially, bark beetles attack trees stressed by the sudden opening of a stand following thinning, increase the contagion or clumpiness of the stand, and destabilize and suppress trees as they grow larger. The most common predisposing factor at PC involved suppression, a consequence of the tree distribution left after selective tree harvest. Suppressed trees harbor weak parasites and

Table 2
Relative contributions of various combinations of killing agents and snag classes at Upper Pine Creek Research Natural Area, Palmer Creek, and Fourcorners

Class	Relative contribution (%)								
	LITNING	FIREDAM	Cutting	Unknown	BARKBTL	Rootrot	Wind	WKPARA	Ice
Upper Pine Creek									
1	0	0	0	7	21	0	71	0	0
2	0	0	0	0	38	11	48	3	0
3	0	0	0	0	56	21	24	0	0
4	3	0	0	10	34	17	33	3	0
5	0	0	0	4	32	19	36	10	0
6	0	0	0	0	36	0	61	3	0
7	1	1	1	8	35	15	35	6	1
8	1	2	0	7	33	16	33	8	1
9	0	0	55	0	0	0	46	0	0
10	1	1	1	7	28	7	54	3	1
Palmer Creek									
1	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0
3	1	1	18	28	12	2	0	37	0
4	0	0	0	60	0	20	0	20	0
5	0	0	12	63	4	0	0	21	0
6	0	0	19	34	14	6	1	27	0
7	0	0	21	39	13	1	1	34	0
8	1	1	33	35	4	2	2	23	0
9	0	0	0	0	0	0	0	1	0
10	0	0	0	1	0	0	0	0	0
Fourcorners									
1	0	0	0	0	0	0	0	0	0
2	0	0	58	7	36	0	0	0	0
3	0	0	50	4	46	0	0	0	0
4	0	0	41	26	33	0	0	0	0
5	0	0	50	0	50	0	0	0	0
6	0	0	0	0	0	0	0	0	0
7	0	1	39	11	45	0	5	0	0
8	0	2	34	21	43	0	0	0	0
9	0	0	44	6	50	0	0	0	0
10	0	0	7	15	12	0	66	0	0

LITNING, lightning; FIREDAM, fire damage; BARKBTL, bark beetles; WKPARA, weak parasites.

insects and are prone to tree push, caused by wind, tree fall, or the buildup of ice and snow. With time, *Armillaria* sp. colonize the roots of cut stumps and trees killed by bark beetles. These infected trees, scattered among the healthy population, act as focus trees that help maintain bark beetle populations during inter-infestation periods.

Bark beetle distribution at UPC may typify the inter-infestation condition, where beetles maintain themselves in the ecosystem by attacking scattered weak trees (Eckberg et al., 1994). Many investigators argue that focus trees are predisposed by some stress (Eckberg et al., 1994), such as root disease (Cobb, 1988). The most commonly identified root disease of pines in the Black Hills is *Armillaria* root disease (Lundquist, 1991c). The relationship between *Armillaria* root disease and the mountain pine beetle has been previously examined (Hinds et al., 1984; Lessard et al., 1985; Holah, 1994). In the present study, the number of pathways involving both *Armillaria* sp. and beetles was relatively small, probably because this interaction is difficult to diagnose.

Results indicate that unharvested stands are relatively rich in disturbance processes, and that the flow of pathway processes within the disturbance network can be shifted by introducing different combinations of disturbance agents. Tree harvesting, for instance, reduces the richness and relative importance of predisposing factors. Eighty five percent of all disturbance pathways at UPC were connected to some type of predisposing factor, primarily shallow soils and frequent wildfires. In contrast, 46% of the disturbance pathways at PC involved predisposing conditions, and only 14% at FC.

4.2. Snags and logs

Timber harvesting influences the abundance and types of animal using the forest ecosystem. Snag and log abundance and condition impact various non-timber resources, especially wildlife habitat (Maser et al., 1979; Thomas et al., 1979). Timber harvesting clears the forest of snags, but increases downed woody debris and the weak parasites and insects that feed on it. This pattern enhances the habitat of animals that use downed logs, but diminishes the habitat of animals that use snags. The types and distributions of logs and snags in managed stands differ from those caused by the natural mix of disturbance processes. Correspondingly, the types and abundance of animals using harvested stands may differ from the natural composition.

The decomposition sequence of a tree depends on what killed the tree. Results suggest that snag and log decomposition sequences and rates differ among causal pathways. For example, bark beetle-killed trees tended to have more sap rot than trees killed by root rot and often the former broke at the main stem. In contrast, trees killed by root rot tended to have more heart rot, and usually broke at the butt or were uprooted. Obviously, time also plays an important role in determining these distributions. Relatively little has been done on rates of decomposition and decomposition pathways (Harmon et al., 1986). Understanding these relationships might enable the development of predictive models that relate actions of specific mixes of disturbances to impacts on wildlife habitat and other non-timber resources.

This study is descriptive and aims at developing hypotheses to test in subsequent studies. Based on the results presented above it could be stated that the diversity of disturbance pathways influences structural diversity of the forest vegetation, and the abundance and composition distribution of snags and downed logs. In addition, the intensity of management influences the structural diversity of the forest vegetation, and the diversity of disturbance pathways.

5. Conclusion

Interactions among disturbance agents and predisposing factors in *P. ponderosa* in the Black Hills cause an array of tree responses that impact various stand characteristics. How trees die, the frequency and size of the canopy gaps resulting from tree death, and the subsequent mix of coarse woody debris influence wildlife, scenic beauty, recreational and timber values (Hunter, 1990). Little, however, is known about these relationships.

Manipulating natural causal pathways offers many potential tools (in addition to tree cutting alone) for changing stand structure to achieve a desired management condition. However, we will not be able to make effective use of this tool until we know more about how disturbance agents interact within forest ecosystems.

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