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CANOPY INVERTEBRATE COMMUNITY RESPONSE TO DISTURBANCE AND CONSEQUENCES OF HERBIVORY IN TEMPERATE AND TROPICAL FORESTS

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Abstract.—Arboreal invertebrates represent a diverse and functionally important component of forest ecosystems. Many invertebrates respond rapidly and dramatically to changes in environmental conditions, making these organisms potentially useful indicators of forest condition. Canopy arthropods also significantly affect canopy structure and ecosystem processes such as primary productivity, nutrient cycling and hydrology.

Few canopy studies have been designed to address environmental issues such as how changes in land use affect biodiversity or how changes in canopy biodiversity affect functional integration of forest ecosystems. Assessment of canopy invertebrate responses to environmental change and their consequences for ecosystem processes requires manipulative experimental approaches with random replication of independent treatment plots to meet requirements of statistical analyses. This paper describes experimental approaches for evaluating effects of environmental change on canopy arthropod diversity and species abundances and effects of herbivores on ecosystem processes. These studies have indicated similar functional interactions in taxonomically distinct temperate and tropical forest canopies.

Arboreal invertebrates are important components of forest canopies. They represent the bulk of biodiversity and fill important functional roles ranging from affects on tree growth, survival and foliage surface area to regulation of evapotranspiration and nutrient cycling processes (Mattson & Addy 1975, Seastedt & Crossley 1984, Schowalter et al. 1986, Schowalter 1994a). Invertebrate capacity for rapid and dramatic population responses to environmental change affects rates and directions of ecological processes and often seems to conflict with forest management goals. Nevertheless, canopy invertebrates remain a poorly understood ecosystem component, due largely to taxonomic complexity, difficulty of access, and the scarcity of integrated manipulative studies needed to evaluate the breadth and significance of responses or effects.

Approaches to studying canopy invertebrates have varied widely, depending on research objectives. Most of the available research on canopy invertebrates has addressed either their diversity or the natural histories of economically important species, especially during population outbreaks. Few studies have been designed to demonstrate effects of environmental change on diversity, community structure and function, or effects of invertebrate population change on ecosystem processes, despite the importance of such information to appropriate management of forest ecosystems. The dramatic population fluctuations of many species are potentially useful indicators of changing forest condition ("health"), but their utility requires evaluation of responses to specific environmental changes. Assessment and protection of forest health also must address canopy invertebrates as regulators of various ecosystem processes.

This paper describes experimental approaches for evaluating effects of environmental change on invertebrate populations and changes in invertebrate populations for ecosystem processes. Such studies have indicated similar functional interactions in taxonomically distinct temperate and tropical forests and significant effects of herbivores on nutrient cycling processes.

Invertebrate Responses to Environmental Change

A major environmental issue facing ecologists is the effect(s) of environmental changes, including climate change and disturbances such as fire, storms or forest fragmentation, on species abundances and biodiversity. Demonstrating effects of environmental changes on biodiversity or populations of key species requires that canopy research progress from simple, often unreplicated, species inventories to hypothesis testing using replicated experimental (manipulative) treatments. Replicates must be independent and sufficiently dispersed over the landscape to represent variation in canopy conditions. Stationary platforms (including cranes, balloons, etc.) in canopies represent a single independent site, regardless of the number of samples taken from the platform, and therefore do not represent variation in canopy conditions over landscapes or among treatments unless comparable sampling across a network of such structures provides site replication (Hurlbert 1984).

The choice of sampling methods to measure

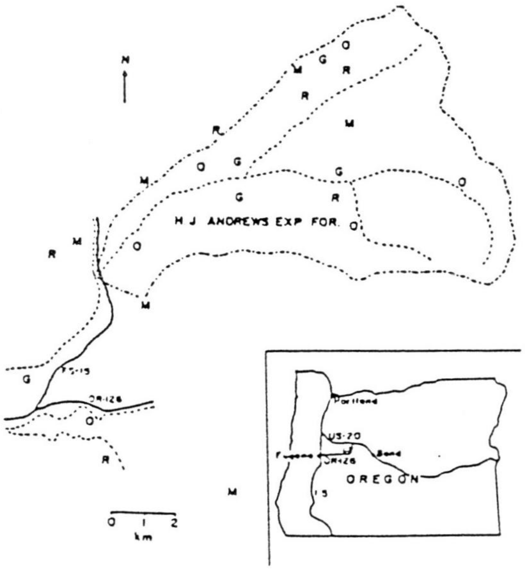

FIGURE 1. Treatment replication at the H.J. Andrews Experimental Forest in western Oregon. O = Old-growth, M = natural mature Douglas-fir, G = partial harvest/green retention, and R = regenerating plantations of Douglas-fir.

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invertebrate population size is critical to comparative studies. Most widely used and convenient invertebrate collecting techniques (e.g., window traps, malais traps, sticky traps) collect the greatest diversity of flying insects but do not indicate the source of these insects nor local population density and are sensitive to forest structure and other factors affecting flying insect behavior. Hence, they indicate only relative changes in population status (Southwood 1978). Sessile or flightless invertebrates, which often are numerically and functionally important, are underrepresented by these techniques. Fogging tree canopies with pyrethoids better represents the fauna associated with a particular canopy but still underrepresents sessile folivores (Majer & Recher 1988). Fogging also may be difficult or inappropriate in particularly tall trees or in canopies that resist invertebrate fallout. Branch bagging tends to underrepresent highly mobile species but best represents sessile folivores and other resident species that are the most important functional components in forest canopies (Crossley et al. 1987, Majer & Recher 1988, Schowalter 1989, 1994b). Furthermore, branch bagging provides for standardization of invertebrate intensities (numbers/kg sample) for comparison among tree species and forest types and permits calculation of invertebrate densities (#/ha) or biomass (Schowalter & Crossley 1987, Schowalter 1989, 1994b).

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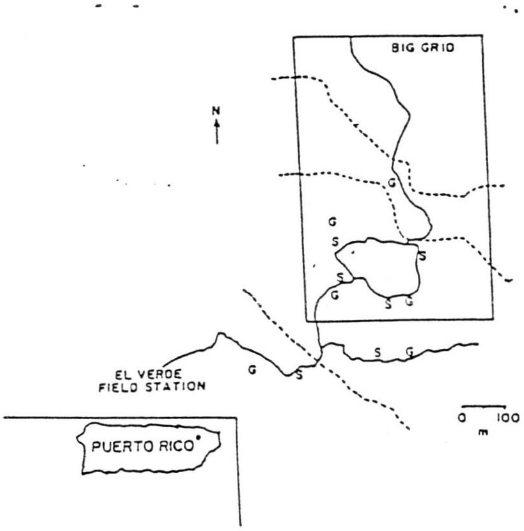

FIGURE 2. Treatment replication at the Luquillo Experimental Forest in Puerto Rico. G = gaps formed by treefall caused by Hurricane Hugo in September 1989, and S = intact forest that suffered defoliation and branch breakage, but no treefall, during the hurricane.

I used branch bagging to compare canopy invertebrate diversity and abundances among disturbance treatments in three distinct forest types: temperate wet forest at the H.J. Andrews Experimental Forest Long Term Ecological Research (LTER) site in western Oregon (44°N,122°W), temperate deciduous forest at Coweeta Hydrologic Laboratory LTER in North Carolina (35°N, 83°W), and tropical wet forest at the Luquillo Experimental Forest LTER in Puerto Rico (18°N, 65°W) to assess responses to disturbance (Schowalter & Crossley 1987, Schowalter 1989, 1994b). The data base for this study includes 36 site-yrs at the Andrews Forest (FIGURE 1), including 12 site-yrs each in old-growth and regenerating plantations (Schowalter 1989 and unpubl. data), and six site-yrs each in mature and partially-harvested old-growth stands (Schowalter unpubl. data); and 36 site-yrs at Luquillo (FIGURE 2), including 18 site-yrs each in intact forest and regenerating gaps (2, 3 and 5 yrs post-hurricane) (Schowalter 1994b and unpubl. data). In addition, eight site-yrs are available for Coweeta, including five site-yrs in mature forests and three site-yrs in regenerating forests (1, 2 and 13 yrs post-clearcut), but these treatments are poorly replicated (Schowalter & Crossley 1987).

The Andrews Forest has a maritime climate with wet, cool winters and dry, warm summers. Temperature averages 8.5°C, and precipitation averages 230 cm with 70% falling as rain between November and March. Vegetation is dominated by old-growth (450 yr old) coniferous forest, with

Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, and western hemlock, *Tsuga heterophylla* (Raf.) Sarg., accounting for 70% of the biomass (Grier & Logan 1977), and 150 yr old mature *P. menziesii* forest. Clearcut and partially-harvested stands have been created during the past 50 yrs.

Coweeta has a continental climate, with average temperature of 13°C and average precipitation of 180 cm evenly distributed throughout the year. Vegetation is dominated by mixed deciduous hardwoods, especially oaks, *Quercus* spp., and hickories, *Carya* spp., which account for 75% of foliage biomass (Schowalter et al. 1981). Black locust, *Robinia pseudoacacia* L., and red maple, *Acer rubrum* L., are major early successional dominants.

Luquillo has a tropical seasonal climate with average temperature of 23°C and average precipitation of 370 cm, with 20–25 cm per mo from January to April and 40 cm per mo the remainder of the year. Vegetation below 600 m is dominated by mixed evergreen tropical hardwoods, especially *Dacryodes excelsa* *Manilkara bidentata* and *Sloanea berteriana* which account for about 60% of biomass (Scatena et al. 1993). *Cecropia peltata* L. is a major early successional dominant.

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Disturbance type, scale and intensity differed somewhat among study plots at the three forested sites. The effect of clearcut harvesting was studied at Coweeta and the Andrews Forest; hurricane (Hugo) disturbance was studied at Luquillo. Disturbed patch sizes were 10–20 ha at Coweeta and the Andrews Forest, 1000–1500 m 2 at Luquillo. Clearcutting and replanting conifers at the Andrews Forest represented the most severe disturbance. Clearcut harvest at Coweeta was followed by sprouting from stumps and roots. Hurricane (Hugo) disturbance at Luquillo opened irregular patches of canopy with some surviving trees within canopy openings; regeneration occurred ~~primarily~~ as sprouting from broken or fallen trees. Partial harvest at the Andrews Forest represented a disturbance treatment similar to hurricane disturbance at Luquillo. Undisturbed canopies were >60 yrs old at Coweeta and Luquillo, 150 yrs old (mature) to 45 yrs old (old-growth) at the Andrews Forest.

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Mature forest canopies at Coweeta and Luquillo reached about 20 m in height and were most conveniently sampled from the ground using a long-handled insect net fitted with a closeable plastic bag. This technique permitted sampling at 8–12 m heights, about mid-canopy. The bag was slipped quickly over a foliage-bearing branch (about 60 cm long), closed and clipped from the tree (Schowalter 1994b). Canopies at the Andrews Forest reached 50 m in mature conifers and 65–75 m in old-growth forests. Canopy dominant trees were rigged with ropes to provide canopy access. Branches were bagged by hand at upper, middle, and lower crown levels of these trees. Canopies of regenerating trees in disturbed forests were 2–4 m in height during the first two years following disturbance at Coweeta and Luquillo and in 10–20 year old plantations at the Andrews Forest. At all three sites, the same tree species were sampled in all treatments for comparison.

Arthropods and plant material were separated in the lab. Arthropods were identified to the lowest rank possible. However, broader taxonomic combinations within functional groups often were necessary because numbers of many species and families were insufficient for statistical comparison of abundances. Plant material was pressed, dried at 50°C, weighed and leaf area measured using a leaf area meter. All invertebrate data were standardized to number per kg plant material and transformed as necessary, usually to natural logarithm, for statistical analyses. Shannon-Wiener diversity indices were calculated from species abundances. Abundances of individual taxa and functional groups were compared among disturbance treatments using ANOVA. Community structure was compared using multivariate techniques.

Canopy communities at the three sites were taxonomically distinct but showed similar functional organization, i.e., relative abundances of chewing and sap-sucking herbivores, specialist and generalist predators, and detritivores. Species diversity and overall invertebrate biomass increased, as expected, from Andrews to Luquillo. However, Shannon-Wiener diversity was similar among tree species at the Andrews and Luquillo sites (TABLE 1), indicating that invertebrate diversity may be a function of plant diversity.

Disturbance severity significantly affected canopy communities. Regenerating forests at all three sites showed significantly elevated abundances of at least some sap-sucking arthropods, likely due to their rapid reproduction and exploitation of rapidly growing foliage with high nutrient translocation rates (e.g., Dixon 1985), and significantly reduced abundances of some defoliating arthropods, probably due to changes in host chemistry and abundance (e.g., Coley et al. 1985, Schowalter & Turchin 1993), and predators and detritivores, probably due to reduced access to prey and exposure to desiccation (e.g., Kruess & Tscharntke 1994). These results indicate both taxonomic and functional responses to disturbance and reveal potential indicators of changing forest conditions. Multivariate analyses confirmed that regenerating forests generally sup-

TABLE 1. Shannon-Wiener diversity in wet temperate forest (H. J. Andrews Experimental Forest, western Oregon) and wet tropical forest (Luquillo Experimental Forest, Puerto Rico) trees.

Wet Temperate Forest	
Pseudotsuga	
Regenerating plantations	0.7
Partially harvested old-growth	2.4
Natural mature	2.6
Old-growth	2.8
Tsuga	
Old-growth	1.8
Wet Tropical Forest	
Casearia	
Standing forest	2.2
Gap	2.2
Cecropia	
Standing forest	1.6
Gap	1.8
Dacryodes	
Standing forest	2.0
Gap	2.2
Manilkara	
Standing forest	2.1
Gap	1.7
Sloanea	
Standing forest	2.1
Gap	2.0

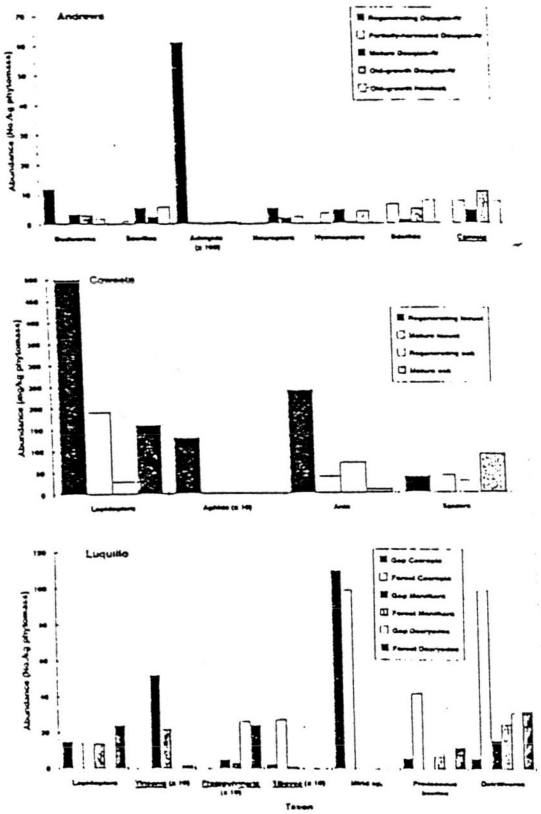

FIGURE 3. Arthropod taxa showing significant differences in intensities (No. or mass/kg phytomass) between canopy treatments at the H. J. Andrews Experimental Forest in western Oregon, Coweeta Hydrologic Laboratory in western North Carolina, and Luquillo Experimental Forest in Puerto Rico.

ported canopy communities distinct from other treatments. Partial harvest and retention of some overstory canopy at the Andrews maintained populations of most species characterizing undisturbed canopies whereas clearcutting did not (FIGURE 3).

The most dramatic responses at all three sites were those of certain species of Homoptera (FIGURE 3). Aphids and associated ants showed dramatic increases in abundance during the first two years following clearcutting at Coweeta (Schowalter & Crossley 1987). Adelgids (especially the Cooley spruce gall adelgid, *Adelges cooleyi*) showed a 500-fold increase in abundance in regenerating (10–20 yr old) plantations (Schowalter 1989 and unpubl. data). Two scale insect species (*Vinsonia stellifera* and *Protopulvinaria pyriformis*) and a mirid species (Heteroptera) showed elevated populations in gaps during the first three years following Hurricane Hugo in Puerto Rico (Schowalter 1994b and unpubl. data). However, a cicadellid (*Sibovea coffeacola*) was relatively more abundant on cecropia seedlings in intact forest.

Defoliating herbivores, especially Lepidoptera, generally were more abundant in undisturbed forests (FIGURE 3). However, some members of this functional group appear to be particularly responsive to host tree density. At the Andrews Forest, Lepidoptera (especially western spruce budworm, *Choristoneura occidentalis*) and sawflies (the only two defoliator taxa at this site) were most abundant (and foliage losses highest) in relatively pure plantations and natural mature stands of *P. menziesii* (FIGURE 3).

Predators and detritivores (including the oribatid mite, *Camisia carrolli*, at the Andrews) showed significantly reduced abundances following disturbances at the Andrews and Luquillo, but not at Coweeta (FIGURE 3). Detritivore responses likely reflect desiccation of the invertebrates themselves or their detrital and microbial resources in exposed canopies. The sensitivity of these groups to disturbance may have important consequences for conservation of biodiversity, regulation of herbivore populations, and ecosystem processes in forest canopies (e.g., Kruess & Tscharntke 1994)

Foliage losses to herbivorous insects appeared to be related to tree species abundance at the

TABLE 2. Estimated densities (no./ha × 1,000) of major arthropod taxa and functional groups in forest canopies in the western Cascades of Oregon. $N = 6$ for all treatments. Note that densities for intact old-growth forests are the sum of densities for old-growth Douglas-fir and hemlock.

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Group (taxon)	Douglas-fir				Hemlock
	Regenerating	Partial harvest	Mature	Old-growth	
Herbivores					
Defoliators	15	12	170	70	38
W. spruce budworm	11	1	59	30	7
Sawflies	0	2	93	24	24
Sap-suckers	5,600	1,100	4,100	1,700	4,600
Kellogg scale	7	180	390	200	300
Pine needle scale	0	320	790	110	3,800
Black pineleaf scale	26	460	2,200	870	72
Adelgids	5,600	100	300	390	300
Giant conifer aphids	33	66	220	34	0
Predators	67	130	960	660	290
Carpenter ants	5	1	0	4	0
Coleoptera	8	5	0	25	16
Neuroptera	0	1	90	20	10
Lestodiplosus	15	13	93	87	28
Hymenoptera	0	8	81	6	17
Bdellid mites	0	15	22	50	33
Anyphaenids	14	17	95	130	16
Aranids	11	15	240	117	59
Philodromids	1	20	140	76	35
Salticids	10	27	100	117	30
Detritivores	1	230	830	590	460
Psocoptera	0	12	35	45	24
Camisia	0	17	76	110	120
Oribatid sp. 3	0	34	25	38	35
Oribatid sp. 4	0	23	79	29	36
Oribatid sp. 5	0	61	420	250	210
Podurids	0	77	170	96	11
Miscellaneous	3	20	190	96	80

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Andrews and Luquillo (Schowalter 1994b and unpubl. data), as predicted by the resource concentration hypothesis (e.g., Kareiva 1983, Schowalter & Turchin 1993). Foliage loss at the Andrews was highest in dense mature Douglas-fir and lowest in sparse partially-harvested Douglas-fir. Foliage loss at Luquillo was higher in standing trees for the later successional species and higher in gaps for the early successional species. Foliage loss to herbivores generally was low (<10%) at all three sites during the study periods.

The quantitative data obtained in these studies permitted calculation of population sizes for assessment of species viabilities. Arthropod intensity (No. or mass/kg foliage) multiplied by foliage biomass (kg/ha) yields estimates of arthropod population density or biomass (Schowalter & Crossley 1987, Schowalter 1989). Data on foliage biomass by canopy treatments at the Andrews (S. Acker unpubl. LTER data) permitted calculation of arthropod densities for that site (TABLE 2). Canopy detritivores and some predator taxa would ~~would~~ not maintain viable populations over a landscape composed largely of regenerating plantations, but such a landscape would be more vulnerable to herbivore outbreaks than would more diverse forests (TABLE see also Schowalter & Turchin 1993).

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HERBIVORE EFFECTS ON ECOSYSTEM PROCESSES

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A second environmental issue facing ecologists is the importance of biodiversity for ecosystem function and stability. Key processes, such as nitrogen fixation, litter decomposition, pollination or seed dispersal, will not occur if key species influencing these functions are absent. Greater cooperation between systematics and community/ecosystem ecologists is necessary to increase our understanding of the importance of biodiversity to ecosystem function. Research on the functional importance of biodiversity might be particularly warranted in forest canopies because

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of their functional importance in forest ecosystems.

Forest canopies are major interfaces between atmospheric and biotic processes. The canopy is the site of photosynthesis and also intercepts light, wind and precipitation, thereby providing the energy and resource base for the ecosystem as well as regulating local and regional temperature and humidity, hydrology (including erosion), wind speed, and nutrient acquisition and cycling. Canopy flora and fauna influence these processes by increasing photosynthetic area and interception (e.g., epiphytes) or reducing foliage area and interception, but stimulating nutrient flows (e.g., herbivores).

Canopy invertebrates play important functional roles in the canopy system but few studies have provided convincing data on the magnitude or range of canopy invertebrate effects on ecosystem processes. Functional importance is complex for invertebrates which often represent different functional roles at different life stages. For example, immature Lepidoptera often are important defoliators whereas adults are important pollinators. Herbivory generally is accorded a negative role, largely because of its interference with production of plant resources, but herbivores also reduce foliage and/or plant density and stimulate nutrient cycling (Seastedt et al. 1983, Schowalter et al. 1991), perhaps alleviating water or nutrient limitations. Future research should address the breadth of canopy invertebrate effects on ecosystem processes.

Methods for measuring and manipulating invertebrate populations is critical to accurate assessment of roles. Appropriate measurement of abundance, as discussed above, is necessary to achieve representative treatment levels. Method of manipulation also affects results. For example, mechanical defoliation as a surrogate for herbivory does not simulate herbivore feeding processes, foliage fragmentation and gut passage, or effects of feces and herbivore tissues in the litter (e.g., Baldwin 1990, Schowalter & Sabin 1991). Insecticidal reduction of herbivore abundance introduces the confounding fertilization effect of many insecticides unless appropriate controls are included to account for the fertilizer effect.

Schowalter et al. (1991) treated Douglas-fir saplings as experimental microcosms. Abundances of endemic herbivores were manually manipulated (removal and addition) during a three-year period at the Andrews Forest. Herbivore effects on plant production, nutrient turnover and litter decomposition rates were compared among treatments. Sap-sucking generally had negligible effects on these processes, but did significantly increase potassium turnover. Up to 20% foliage removal by the defoliator did not reduce plant production, but significantly doubled the amount of water and litter reaching the forest floor and significantly increased turnover of nitrogen, potassium and calcium from foliage to litter. Decomposition of bulk litter was not significantly affected, but litter affected by herbivory was not sufficient in quantity for testing. These results support data from a one-year study by Seastedt et al. (1983) who used carbaryl to reduce foliage loss from 4–10% to 1–2% in red maple and black locust at Coweeta. These data suggest that defoliator effects on nutrient turnover and soil fertility should be considered in assessing impacts on forest resources. Defoliator-enhanced water and nutrient flow to the forest floor may alleviate drought effects. However, these effects likely depend on rates of water and nutrients flow relative to plant capacity to use these nutrients (e.g., Swank et al. 1981, Lovett & Tobiessen 1993) and on effects of environmental changes and unmeasured feedbacks operating over longer time periods.

Long-term compensatory growth has been observed in defoliated stands of older trees, compared to undefoliated stands, although these studies did not involve manipulation of herbivore abundance, and in some cases results might have been confounded by other factors (Wickman 1980, Alfaro & MacDonald 1988, Alfaro & Shepard 1991, Trumble et al. 1993). These data suggest that enhanced soil moisture and/or nutrient cycling and diversification of vegetation increase forest health and productivity over longer time periods than those spanned by typical studies.

Defoliation also contribute~~d~~s to biodiversity. Schowalter & Sabin (1991) reported, from the above study of Douglas-fir saplings, that three litter arthropod species were significantly more abundant under defoliated Douglas-fir saplings, compared to undefoliated saplings, suggesting defoliator effects on unmeasured food resources or litter temperature and moisture. These three species were relatively more numerous during the drier spring and summer when other litter arthropod taxa were reduced or absent.

Canopy opening also provides resources for understory plants, competing canopy trees, and associated fauna. Wickman (1980) documented increased growth of ponderosa pines intermixed with defoliated white fir, and Davidson (1993) reviewed a number of studies showing herbivore and granivore effects on plant succession.

The roles played by a variety of canopy species must be studied experimentally if the functional importance of canopy biodiversity is to be understood and applied to forest management. The distinct adaptive strategies of various species make complete redundancy of functional roles unlikely. Rather, changing environmental conditions will result in species replacement among functional group members with different ranges of tolerance, thereby ensuring the maintenance of ecosystem processes.

CONCLUSIONS

Growing concern over effects of environmental change for biodiversity and functional importance of biodiversity in forest ecosystems requires that canopy research progress from case studies to designed experiments that test hypotheses. Canopy invertebrates are a diverse and functionally important group. Many species show dramatic changes in population size as a result of changing environmental conditions. Hence, more data are needed on canopy invertebrate responses to environmental change, including those induced by alternative ecosystem management options, and effects on ecosystem processes critical to forest health and productivity. Sufficiently replicated manipulative treatments of canopy conditions or invertebrate populations are necessary for statistical analyses of invertebrate responses to environmental change and effects on ecosystem processes.

The data from experimental studies of invertebrate responses to disturbances in temperate and tropical canopies show that Homoptera and Lepidoptera might be particularly useful indicators of environmental change. Changes in abundances of these common herbivores can significantly affect primary productivity, nutrient cycling and hydrology. The sensitivity of predators and detritivores to canopy disturbance suggests that these taxa may be most threatened by exposure and/or desiccation due to widespread forest fragmentation, canopy opening, and climate change. However, more research is necessary to relate response levels to changes in particular factors.

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