15. Canopy Arthropods and Their Response to Forest Disturbance

T.D. Schowalter and D.A. Crossley, Jr.

Most ecological studies of forest canopy arthropods have focused on population dynamics. These studies have contributed much to our understanding of population responses to changes in environmental conditions. Moreover, advances in population theory have indicated the importance of understanding the dynamics of species assemblages. Population irruptions do not result simply from changes in abiotic or host conditions, but also reflect competitive interactions within guilds and predisposing changes in host or predator conditions affected by other guilds (Schowalter 1985). Bark beetle population irruptions, for example, may result from host stress aggravated by defoliator populations (Berryman and Wright 1978).

The nature of interactions within and between arthropod guilds and the effects of those interactions on primary productivity have suggested regulatory roles (Mattson and Addy 1975; Odum 1969; Patten and Odum 1981). Schowalter (1981, 1985) advanced the cybernetic view of ecosystems by proposing that the state of predator–prey interactions varies as a function of ecosystem carrying capacity. Resource subsidy promotes prey population growth while resource stress promotes predator population growth. This view also casts succession as a consequence of regulatory responses to delayed disturbance, i.e., as a succession of associations adapted to decreasing disturbance frequency, rather than as a goal-oriented community strategy. However, few studies have documented changes in arthropod assemblages resulting from changes in environmental conditions. Forest canopy arthropods have been particularly difficult to study because of their taxonomic complexity and difficulty of access to them.

Studies of canopy arthropod assemblages at Coweeta have produced an extensive data set documenting assemblage structure across a wide range of ecosystem states. In this chapter, these data are used to assess the magnitude of canopy arthropod responses to changing environmental conditions, to evaluate the relative importances of factors influencing arthropod responses, and to identify mechanisms of regulation.

Canopy Arthropod Responses to Disturbance

We have compiled data from four watershed-level studies representing 8 watershed-years. Included are four studies of canopy arthropods in mature canopies (Chapter 14 this volume, H. Peturssen and Crossley unpubl. data; Risley 1983; Schowalter et al 1981c), one study of arthropods in first and second-year regrowth (Schowalter et al. 1981c), and one study of arthropods in 13-year-old regrowth (Risley 1983). Arthropod mass intensities (mg/kg foliage) on three late successional dominants (chestnut oak (*Quercus prinus* L.), red maple (*Acer rubrum* L.), hickory (*Carya* spp.), and three early successional dominants (dogwood (*Cornus florida* L.), tulip poplar (*Liriodendron tulipifera* L.), and black locust (*Robinia pseudoacacia* L.) across this successional gradient are presented in Tables 15.1 through 15.6. Canopy arthropod guild structure

Table 15.1. Arthropod Mass Intensities (mg/kg Foliage) on Chestnut Oak (*Quercus prinus*) at Coweeta Hydrologic Laboratory, North Carolina

	Watershed Age (yrs)			
Guild	1[a] (mg/kg)	2[a] (mg/kg)	13[b] (mg/kg)	>60[c] (mg/kg)
Phytophages				
Aphids and aleyrodids	10	3	19	3 (3)
Other sap-suckers	89	41	27	111 (29)
Caterpillars	21	34	397	160 (70)
Tree crickets	268	6	60	110 (130)
Beetles	146	14	41	140 (131)
Leaf miners	1	0	6	4 (4)
Flower-feeders	0	0	61	23 (15)
Bark and wood borers	1	2	0	35 (34)
Omnivores				
Ants	81	60	91	9 (8)
Predators				
Beetles	0	0	3	9 (19)
Lacewings	3	0	2	1 (1)
Flies and wasps	4	6	5	5 (4)
Assassin bugs	7	0	246	29 (23)
Spiders and phalangids	9	45	84	90 (70)
Others	16	22	26	25 (33)
Total	656	233	1068	723 (130)

[a] Data from Schowalter et al. (1981c).
[b] Data from Risley (1983).
[c] $\bar{x} \pm$ SD. Data from Crossley et al. (this volume), H. Peturssen and Crossley (unpublished data), Risley (1983), and Schowalter et al. (1981c).

Table 15.2. Arthropod Mass Intensities (mg/kg Foliage) on Hickories (*Carya* spp.) at Coweeta Hydrologic Laboratory, North Carolina

	Watershed Age (yrs)			
Guild	1[a] (mg/kg)	2[a] (mg/kg)	13[b] (mg/kg)	>60[c] (mg/kg)
Phytophages				
Aphids and aleyrodids	25	7	2	5 (4)
Other sap-suckers	159	66	133	82 (49)
Caterpillars	2	47	196	117 (85)
Tree crickets	0	333	251	27 (32)
Beetles	35	3	72	48 (46)
Leaf miners	0	0	1	0
Flower-feeders	0	1	14	18 (9)
Bark and wood borers	0	89	0	19 (9)
Omnivores				
Ants	36	43	22	13 (8)
Predators				
Beetles	0	0	2	3 (2)
Lacewings	0	0	3	4 (5)
Flies and wasps	1	1	2	3 (2)
Assassin bugs	50	11	49	11 (15)
Spiders and phalangids	40	3	90	58 (25)
Others	18	4	73	32 (30)
Total	366	605	910	453 (147)

[a] Data from Schowalter et al. (1981c).

[b] Data from Risley (1983).

[c] $\bar{x}$ ± SD. Data from Crossley et al. (this volume), H. Peturssen and Crossley (unpublished data), Risley (1983), and Schowalter et al. (1981c).

Table 15.3. Arthropod Mass Intensities (mg/kg Foliage) on Red Maple (*Acer rubrum*) at Coweeta Hydrologic Laboratory, North Carolina

	Watershed Age (yrs)			
Guild	1[a] (mg/kg)	2[a] (mg/kg)	13[b] (mg/kg)	>60[c] (mg/kg)
Phytophages				
Aphids and aleyrodids	33	13	6	5 (5)
Other sap-suckers	94	61	36	52 (24)
Caterpillars	15	14	550	80 (54)
Tree crickets	21	1	0	71 (133)
Beetles	96	15	47	65 (59)
Leaf miners	1	0	4	7 (8)
Flower-feeders	31	13	21	18 (15)
Bark and wood borers	5	23	0	32 (34)
Omnivores				
Ants	273	26	2	5 (3)

(Continued)

Table 15.3. *(Continued)*

	Watershed Age (yrs)			
Guild	1[a] (mg/kg)	2[a] (mg/kg)	13[b] (mg/kg)	>60[c] (mg/kg)
Predators				
Beetles	22	18	7	1 (1)
Lacewings	0	1	0	2 (2)
Flies and wasps	9	61	7	13 (9)
Assassin bugs	6	0	2	18 (21)
Spiders and phalangids	29	19	183	76 (61)
Others	15	27	14	13 (6)
Total	650	292	879	468 (100)

[a] Data from Schowalter et al. (1981c).

[b] Data from Risley (1983).

[c] $\bar{x}$ ± SD. Data from Crossley et al. (this volume), H. Peturssen and Crossley (unpublished data), Risley (1983), and Schowalter et al. (1981c).

Table 15.4. Arthropod Mass Intensities (mg/kg Foliage) on Dogwood (*Cornus florida*) at Coweeta Hydrologic Laboratory, North Carolina

	Watershed Age (yrs)			
Guild	1[a] (mg/kg)	2[a] (mg/kg)	13[b] (mg/kg)	>60[c] (mg/kg)
Phytophages				
Aphids and aleyrodids	0	1	1	1 (0)
Other sap-suckers	110	162	49	77 (48)
Caterpillars	37	10	1022	319 (381)
Tree crickets	47	6	39	2 (3)
Beetles	3	12	27	100 (122)
Leaf miners	2	0	0	1 (1)
Flower-feeders	4	6	55	31 (42)
Bark and wood borers	0	113	1	66 (93)
Omnivores				
Ants	7	1	4	6 (10)
Predators				
Beetles	2	5	5	20 (30)
Lacewings	0	0	1	4 (6)
Flies and wasps	3	31	5	65 (110)
Assassin bugs	0	21	44	55 (73)
Spiders and phalangids	78	117	76	90 (51)
Others	8	4	11	51 (21)
Total	301	489	1390	831 (325)

[a] Data from Schowalter et al. (1981c).

[b] Data from Risley (1983).

[c] $\bar{x}$ ± SD. Data from Crossley et al. (this volume), H. Peturssen and Crossley (unpublished data), Risley (1983), and Schowalter et al. (1981c).

Table 15.5. Arthropod Mass Intensities (mg/kg Foliage) on Tulip Poplar (*Liriodendron tulipifera*) at Coweeta Hydrologic Laboratory, North Carolina

	Watershed Age (yrs)			
Guild	1[a] (mg/kg)	2[a] (mg/kg)	13[b] (mg/kg)	>60[c] (mg/kg)
Phytophages				
Aphids and aleyrodids	226	106	105	19 (15)
Other sap-suckers	135	93	37	50 (26)
Caterpillars	469	395	90	81 (93)
Tree crickets	80	0	392	1 (2)
Beetles	7	2	25	100 (99)
Leaf miners	2	6	0	3 (6)
Flower-feeders	2	10	26	51 (84)
Bark and wood borers	0	108	0	31 (49)
Omnivores				
Ants	14	12	14	17 (10)
Predators				
Beetles	27	0	7	15 (19)
Lacewings	0	2	1	4 (7)
Flies and wasps	4	33	14	12 (6)
Assassin bugs	0	0	42	22 (23)
Spiders and phalangids	33	25	276	93 (47)
Others	16	22	11	14 (8)
Total	1042	814	1040	520 (234)

[a] Data from Schowalter et al. (1981c).
[b] Data from Risley (1983).
[c] $\bar{x}$ ± SD. Data from Crossley et al. (this volume), H. Peturssen and Crossley (unpublished data), Risley (1983), and Schowalter et al. (1981c).

showed a surprising degree of stability upon clearcutting at Coweeta. Mass intensities of most guilds showed no more change as a result of clearcutting than as a result of climatic and edaphic variation between years and watersheds.

The most pronounced responses to clearcutting appeared to be decreased caterpillar and spider biomass and significantly increased aphid and ant biomass on most tree species. Changes in mass intensities following clearcutting were relatively small and apparently compensatory (i.e., little change in total mass) on the late successional tree species (Tables 15.1 through 15.3) but were dramatic and variable on the early successional tree species (Tables 15.4 through 15.6). Aphid and ant mass intensities were significantly and positively correlated following clearcutting, but not in mature canopies (Schowalter et al. 1981c). Following clearcutting, aphid mass intensities increased one to two orders of magnitude on tulip poplar, due to population increases of *Macrosiphum liriodendri* Monell, and on black locust, due to population increases of *Aphis craccivora* Koch (Tables 15.5 and 15.6, Figure 15.1). Ant response was most conspicuous on black locust, where we observed ants feeding on extrafloral nectaries and on aphid and membracid honeydew. Aphid and ant responses were conspicuously absent on dogwood (Table 15.4) despite the abundance and apparency of this species, which codominated the clearcut with black locust (Boring et al. 1981).

Table 15.6. Arthropod Mass Intensities (mg/kg Foliage) on Black Locust (*Robinia pseudoacacia*) at Coweeta Hydrologic Laboratory, North Carolina

	Watershed Age (yrs)		
Guild	1[a] (mg/kg)	2[a] (mg/kg)	>60[b] (mg/kg)
Phytophages			
Aphids and aleyrodids	999	1548	14 (15)
Other sap-suckers	108	205	180 (95)
Caterpillars	822	196	190 (80)
Tree crickets	22	0	340 (480)
Beetles	79	34	79 (62)
Leaf miners	4	4	4 (3)
Flower-feeders	4	54	19 (12)
Bark and wood borers	9	58	14 (19)
Omnivores			
Ants	235	247	38 (36)
Predators			
Beetles	36	10	7 (10)
Lacewings	4	0	13 (11)
Flies and wasps	6	5	15 (2)
Assassin bugs	21	0	1 (1)
Spiders and phalangids	35	41	40 (34)
Others	20	81	46 (62)
Total	2404	2483	1108 (259)

[a] Data from Schowalter et al. (1981c).

[b] $\bar{x}$ ± SD. Data from Crossley et al. (this volume), H. Peturssen and Crossley (unpublished data), and Schowalter et al. (1981c).

Data from a 13 year old watershed undergoing thinning of black locust by the locust borer, *Megacyllene robiniae* (Forster), suggest a sharp increase in abundance of caterpillars and spiders on other tree species (Tables 15.1 through 15.5). Unfortunately, data for black locust during this thinning period are not available.

The changes in arthropod mass intensities on individual tree species following clearcutting were reflected in arthropod biomass at the ecosystem level (Table 15.7). The increases in aphid and ant biomass following clearcutting were statistically significant ($p < 0.02$) (Schowalter et al. 1981c); decreases in caterpillar and spider biomass were not ($p > 0.05$). Notice that differences between the first and second years were much larger as biomass than as weight intensity.

Changes in population dynamics also were observed following clearcutting. Aphid biomass in mature deciduous forests typically peaks in the spring and fall during periods of active nitrogen translocation to and from foliage sinks (Figure 15.2; see also Van Hook et al. 1980). By contrast, aphid biomass continued to increase during the summer on the clearcut watershed (Figure 15.2), presumably because of continued nitrogen translocation in rapidly growing shoots, especially of black locust (Schowalter 1985), and declined earlier in the fall, suggesting that regrowth foliage translocated less N prior to leaf fall.

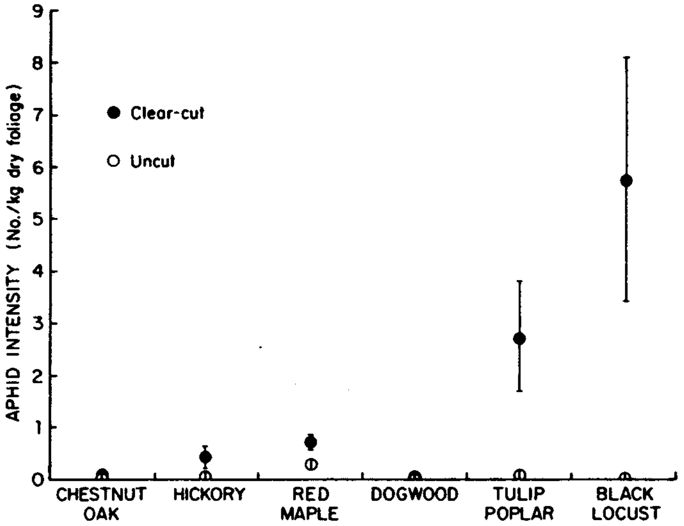

Figure 15.1. Aphid intensities ($\bar{x}$ + SE) in 1977 on chestnut oak (*Quercus prinus*), hickory (*Carya* spp.), red maple (*Acer rubrum*), dogwood (*Cornus florida*), tulip poplar (*Liriodendron tulipifera*), and black locust (*Robinia pseudoacacia*), in a mature forest (WS 2) and an adjacent first-year clearcut (WS 7) at Coweeta Hydrologic Laboratory, North Carolina.

Table 15.7. Canopy Arthropod Biomass (g/ha) in Clearcut and Mature Deciduous Forests at Coweeta Hydrologic Laboratory, North Carolina

	Watershed Age (yrs)		
Guild	1[a] (g/ha)	2[a] (g/ha)	>60[b] (g/ha)
Phytophages			
Aphids and aleyrodids	121	702	24 (6)
Other sap-suckers	141	482	253 (64)
Caterpillars	105	276	322 (153)
Tree crickets	30	24	207 (166)
Beetles	63	62	186 (167)
Leaf miners	19	5	11 (5)
Flower-feeders	77	201	54 (37)
Bark and wood borers	13	126	133 (84)
Omnivores			
Ants	49	153	23 (7)
Predators			
Beetles	14	78	19 (24)
Lacewings	1	2	20 (20)
Flies and wasps	72	45	33 (19)
Assassin bugs	9	175	58 (15)
Spiders and phalangids	43	332	189 (56)
Others	12	82	43 (13)
Total	769	2745	1577 (218)

[a] Data from Schowalter et al. (1981c).

[b] $\bar{x}$ ± SD. Data from Crossley et al. (this volume) and Schowalter et al. 1981c).

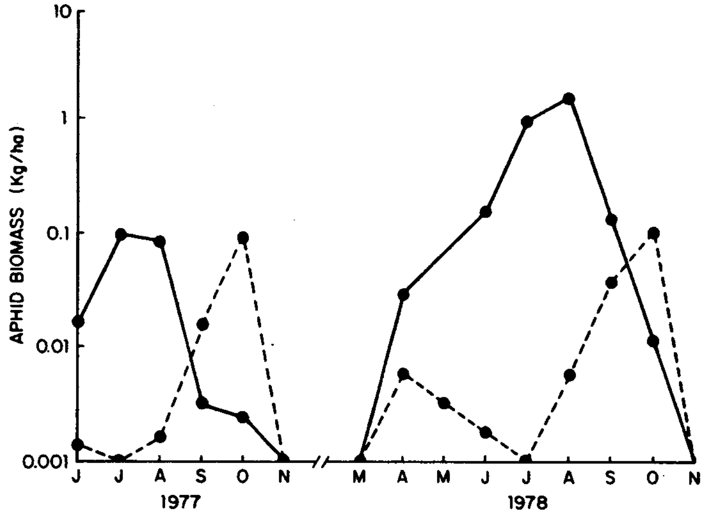

Figure 15.2. Seasonal trends in aphid biomass during 1977 and 1978 in a mature forest (WS 2, ---) and an adjacent clearcut (WS 7, –) at Coweeta Hydrologic Laboratory, North Carolina. [Reproduced from Schowalter (1985) with permission of Academic Press, Inc.]

Factors Influencing Arthropod Responses to Disturbance

The canopy arthropod data from Coweeta can be used to evaluate the relative importances of canopy microclimate, architecture, and nutritional quality as factors influencing arthropod responses to disturbance. These factors have been shown to significantly influence arthropod population dynamics (Mattson 1980; MacMahon 1981; Schowalter et al. 1981b). Clearcutting dramatically altered these environmental variables. Canopy depth and height above the soil surface were greatly reduced, placing the canopy within the influence of the hot, dry conditions prevailing at the soil surface (Seastedt and Crossley 1981). Canopy architecture was altered in at least one additional way as habitat structure changed from woody material with dispersed, growing shoots to clumped, succulent shoots. The relative abundances of host species shifted from oaks and hickories to dogwood and black locust. Nutritional quality was changed as nutrients became relatively more available to the reduced plant biomass and were actively translocated to foliage sinks over an extended period, as shoot elongation and foliage production continued through the summer. Although the influence of these factors on canopy arthropods was not assessed directly, indirect approaches can be used to evaluate relative importances.

Canopy microclimate and architecture appeared to have relatively little effect on arthropod assemblage structure. If either of these factors had a primary effect, we would expect similar arthropod assemblages among the regenerating tree species, which had similar phenologies and architectures and, presumably, similar microclimates. Instead, dramatic differences in arthropod assemblages were observed among the tree species. For example, compare aphids and ants on dogwoods and black locust which assumed canopy dominance following clearcutting (Tables 15.4 and 15.6). Furthermore, arthropod mass intensities in mature forests showed considerable variation between years and watersheds (Tables 15.1 through 15.6) despite relatively constant canopy microclimate and architecture.

This assessment is not intended to suggest that individual arthropod species were not affected by changes in canopy microclimate and architecture. Rather, our data indicate that, at the guild level of resolution, any effect of these factors was masked by compensatory responses among arthropod species or by responses to other factors.

The observed responses of canopy arthropods to clearcutting at Coweeta appeared to be explained best by changes in nutritional factors. This explanation is supported by several lines of evidence. First, the most dramatic arthropod response occurred on black locust, a nitrogen-fixing legume (Table 15.6). Nitrogen availability is known to influence aphid populations (Mattson 1980; Van Hook et al. 1980) and, thereby, to influence ant foraging behavior indirectly (Messina 1981; Schowalter et al. 1981c). Nitrogen availability also directly influenced ant foraging behavior at Coweeta. Black locust shoots on the clearcut produced extrafloral nectaries, which attracted ants in early spring prior to aphid population growth (Schowalter, Crossley and Seastedt, personal observation). Aphid and ant biomass subsequently increased on black locust through positive feedback. Second, fertilization experiments involving 4-year-old black locust (Hargrove et al. 1984) resulted in arthropod responses similar to those observed as a result of clearcutting. Addition of nitrogen–phosphorus–potassium fertilizer resulted in increased foliar nitrogen and phosphorus (but not potassium) concentrations. Hargrove et al. (1984) observed an initial increase in foliage loss to defoliators, but a subsequent decrease due to a combination of a tolerance response (increased foliage production) and a resistance response (reduced foliage consumption). These responses resembled the increased defoliator biomass the first year after cutting, followed by greatly reduced defoliator biomass the second year, especially on black locust (Tables 15.1 through 15.6). Third, an apparent increase in caterpillar biomass coincided with a locust borer population irruption and increased nitrate export on the 13-year-old successional stand (Tables 15.1 through 15.6), suggesting that changes in the nitrogen regime resulting from locust borer activity increased foliage nutritional quality for caterpillars.

These data indicate an important influence of nutritional factors on canopy arthropods and also explain some variations in the pattern of arthropod responses on different tree species. Different nutrient uptake rates between tree species could account for different arthropod responses. The most dramatic and variable arthropod reponses occurred on the early successional tree species, *Cornus* and *Robinia* (Tables 15.4 through 15.6), which showed the most rapid responses to clearcutting. Species specific responses of trees to the altered availability of nutrients following clearcutting altered foliar nutrient pools (Chapter 12) in ways which could elicit differing responses from the arthropod guilds. For example, increased nitrogen can affect sap-suckers positively and defoliators negatively, while increased potassium can have the opposite effect (Bogenschütz and König 1976), depending on the nutrient allocation pattern of the plant (Schowalter 1985).

The conspicuous absence of aphid and ant responses on dogwood is particularly intriguing (Table 15.4). The failure of aphids to respond suggests that dogwood's nitrogen budget was not affected by clearcutting. The failure of ants to respond suggests nonrandom foraging influenced by aphid abundance. However, the apparent absence of ant response on tulip poplar, which did support increased aphid populations, and also ant attraction to extrafloral nectaries on black locust suggest that nutritional factors were involved as well. Thus, indirect evidence indicates that nutritional factors were the primary stimuli influencing canopy arthropod responses to clearcutting at Coweeta.

Regulatory Effects of Canopy Arthropod Responses

Schowalter (1981, 1985) developed a cybernetic model of ecosystems in which changes in host allocation of available resources trigger consumer responses which tend to regulate net primary productivity (NPP) and protect ecosystem carrying capacity (Figure 15.3). This model advances ecosystem theory beyond earlier cybernetic models (Mattson and Addy 1975; Odum 1969; Patten and Odum 1981) in several ways.

First, the individual is clearly the unit of selection. Ecosystem stability is not a community goal, but rather a consequence of increased fitness accruing to individuals which, in addition to other adaptive attributes, interact in ways that contribute to persistence in a temporally-variable environment.

Second, changes in resource allocation pattern, resulting from changes in resource availability at each trophic level, are identified as the mechanism which communicates the current state of the system throughout the food web and triggers feedback responses. Underexploitation and consequent reduction of ecosystem carrying capacity can be remedied by rapid growth and reproduction of vigorous individuals aided by mutualistic interactions; disruptive overexploitation can be controlled by selective cropping, often by the same species functioning as mutualists under more favorable conditions.

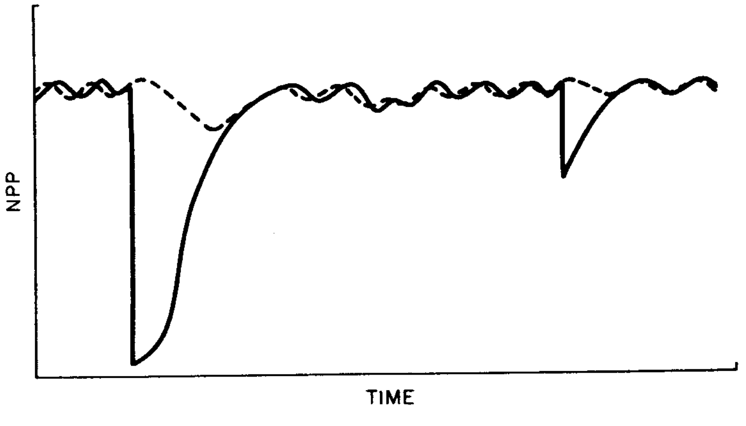

Figure 15.3. Trends in ecosystem net primary production (—) and ecosystem carrying capacity (---) through time. Reduced carrying capacity immediately after disturbance is due to dissipative forces (e.g., leaching and erosion) uncontrolled by biota.

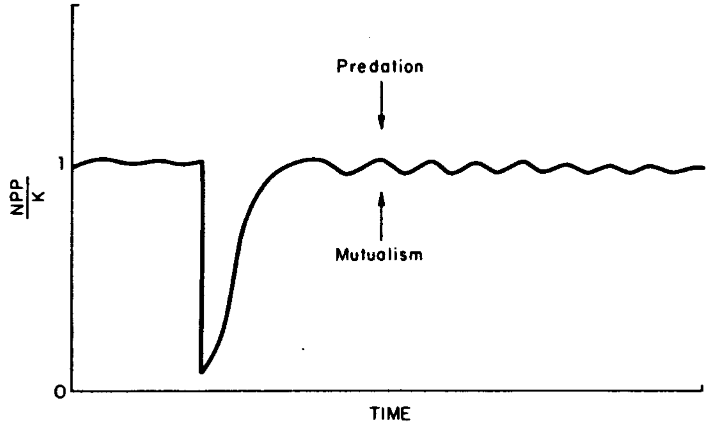

Figure 15.4. Hypothesized mechanism by which species interactions dampen deviation in the ratio between ecosystem net primary production (NPP) and ecosystem carrying capacity (K). Mutualistic interactions stimulate production and accelerate recovery when NPP falls below carrying capacity (NPP/K < 1). Predation in response to increasing host competitive stress reduces NPP at NPP/K > 1. The efficiency of species interactions increases as community development increases the strength of species interactions.

Finally, the most significant advance in ecosystem theory is provided by casting succession not as a goal-oriented strategy, but as a consequence of delayed disturbance. Disturbance frequency selects for species adaptive strategies which also influence rates of resource accretion or export (Grime 1977). Hence, ruderal species characterizing frequently-disturbed ecosystems are highly productive and tend to minimize resource export, often through mutualistic interactions (Figure 15.4). Stress-tolerant species characterizing infrequently-disturbed ecosystems are less productive and tend to prevent overexploitation of resources through predatory interactions (Figure 15.4). The spatial-temporal framework of disturbance maintains species associations representing the range of resource utilization strategies within the ecosystem. Succession occurs because ruderal associations adapted to frequent disturbance colonize disturbed sites. If disturbance does not recur in time to prevent overexploitation and rejuvenate the disturbance-adapted, competition-intolerant association, the plants become stressed, vulnerable to herbivores, and replaced by competition- or stress-tolerant associations adapted to less-frequent disturbance. Although competitive interactions could eventually accomplish species replacement, consumer responses to host stress are viewed as providing more efficient regulation by accelerating replacement and adjustment of NPP to carrying capacity.

Data from canopy arthropod studies at Coweeta support this model. The apparent sensitivity of key guilds to changes in host nutritional quality reflecting changes in ecosystem carrying capacity (Schowalter et al. 1981c) indicates a mechanism for regulating NPP. A clearly disturbance-adapted species assemblage with strong mutualistic interactions became predominant after clearcutting. A relatively high ecosystem carrying capacity (K $>$ NPP) inherited from the preceding community promoted rapid growth. Productivity was enhanced by stimulation of plant growth (especially of black locust) by nitrogen-fixing microorganisms (Boring et al. 1981), stimulation of nitrogen-fixation by aphids (Petelle 1980), and stimulation of aphid productivity, and perhaps plant protection, by ants (Schowalter et al. 1981c; Tilman 1978; but see Fritz 1983). Cycling of nitrogen, potassium, sodium, and perhaps phosphorus, was accelerated by canopy arthropod feeding (Hargrove et al. 1984; Schowalter et al. 1981c; Seastedt et al. 1983).

Rapid growth by the colonizing association eventually should result in overexploitation of resources (K < NPP) despite soil nutrient retention and nitrogen accretion. Such a situation could explain the irruptions of locust borer and defoliator populations which reduced NPP, increased nitrate and potassium mobilization (Schowalter and Crossley 1983; Schowalter et al. 1981a), and which appear to be accelerating a successional transition from the ruderal community to a more stress-tolerant community (sensu Grime 1977).

Finally, periodic overexploitation of resources is likely to continue in mature forests as a result of fluctuating environmental conditions (Figure 15.3). We have observed fall cankerworm [*Alsophila pometaria* (Harris)] population irruptions initially reducing NPP, but subsequently increasing mobilization and availability of nutrients (especially nitrogen), and, ultimately, increasing NPP (Swank et al. 1981). Such regulation might be enhanced by the differing sensitivities of different arthropod guilds to different types or intensities of environmental change (Bogenschütz and König 1976; Schowalter 1985).

Conclusions

Studies of canopy arthropod assemblages at Coweeta support a hypothesis that host resource allocation pattern and consumer response constitute the mechanism for cybernetic control of NPP in temporally-variable environments. We recognize the need for increased resolution of canopy arthropod assemblage structural and functional interactions. If the functional interactions between species represent mechanisms for cybernetic control of NPP, then increased species diversity and community connectivity should contribute to ecosystem stability only to the extent that redundancy ensures an adequate response. Furthermore, the relative importances of mutualistic, competitive, and predatory interactions at any point in time should indicate the instantaneous direction and amplitude of deviation of NPP from ecosystem carrying capacity (Figure 15.4). Consequently, the instantaneous abundance of particular taxa does not necessarily indicate ecological importance. Regulation can be accomplished most efficiently by small, inexpensive (in terms of resource needs) biomass, which can be rapidly multiplied (e.g., as in insects) and amplified through indirect effects (e.g., stimulation of nitrogen-fixation). Increased understanding of canopy arthropod assemblages and responses to changes in environmental conditions will contribute to ecosystem management strategies.

1332

Reprinted from

W.T. Swank and D.A. Crossley Jr.

Ecological Studies, Vol. 66: Forest Hydrology and Ecology at Coweeta

---

Printed in the United States of America

Springer-Verlag
New York Berlin Heidelberg
London Paris Tokyo