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CANOPY FOOD CHAIN
IN A CONIFEROUS FOREST WATERSHED

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ABSTRACT

The internal structure and external couplings of the canopy food chain are examined to quantify the pattern of energy distribution in an old-growth Douglas-fir watershed. The food chain has been divided into nine functional groups: grazing vertebrates, grazing insects, sucking insects, seed and cone insects, predaceous birds, parasitic invertebrates, predaceous invertebrates, omnivorous birds, and nest predators. Surveys of the watershed fauna have shown that these functional groups are complex and may contain large numbers of species. For example, the five invertebrate groups may include as many as 450 species.

Modeling techniques are employed to compute total annual consumption and secondary production for two functional groups, grazing insects and omnivorous birds. The estimates are based on field density records, published data, and simplifying assumptions. The annual consumption by grazing insects on the watershed is estimated to be 42.5 kg/ha or about 1.6% of total primary production. The omnivorous bird population consumes 6.2 kg/ha while on the watershed; about 75% of their diet consists of insects. The consumption rates and mean standing crop values are similar to those reported for other forests. At current population levels, this food chain represents only a minor pathway in the total watershed energy flux.

INTRODUCTION

The canopy food chain is a subsystem within the forest ecosystem. The internal structure and external couplings of this subsystem have been examined as part of an integrated research effort to quantify the pattern of energy distribution in an old-growth Douglas-fir watershed. This watershed is designated number 10 in USDA Forest Service studies and is located at the H. J. Andrews Experimental Forest on the west side of the Cascade Range in Oregon. The distribution of biomass within the vegetation subsystems is described by Grier et al. (1974) in this volume. Other descriptions have been made by Fredriksen (1972). This paper discusses the role of the canopy food chain as a user of energy.

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FOOD CHAIN STRUCTURE

In 1972 the conceptual structure of the canopy food chain was presented (Strand and Nagel 1972). Figure 1 shows the main routes of energy transfer between the functional groups in the postulated structure. Since then, two survey projects were begun to examine the bird and invertebrate populations. The bird surveys were coordinated by Dr. Ronald Nussbaum. They were located in several sites, some in the intensively studied watershed and others in similar stands. The invertebrate survey was the responsibility of Drs. William Nagel and Gary Daterman. Their sampling sites were in several forest types and stand ages. The purpose of these surveys was to identify the important animal types and to observe the relative diversity of types. Grazing vertebrates were not sampled, but they have been the subject of previous investigation (Maser 1966).

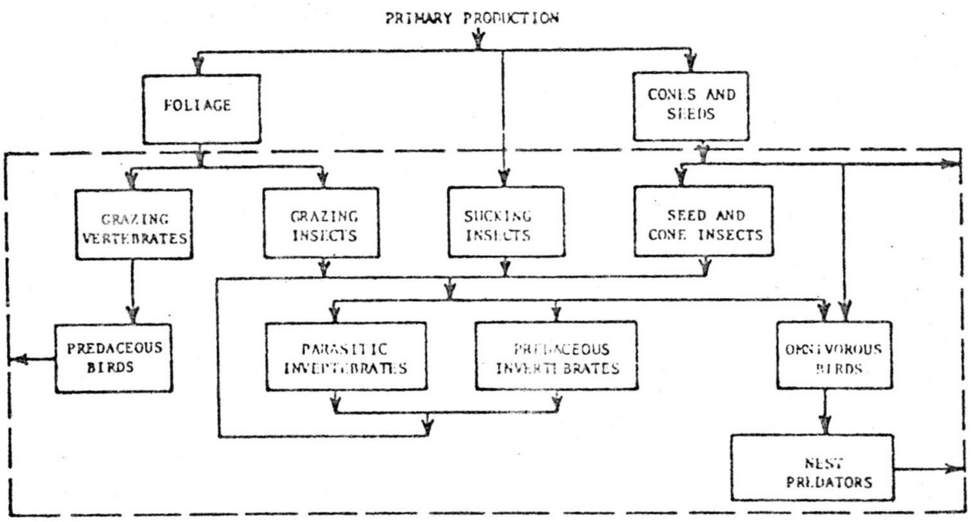

Figure 1. The major energy pathways between components of the forest canopy food chain (from Strand and Nagel 1972).

More detailed papers on sampling techniques and results of surveys will be presented later, but some preliminary results show the complexity of this food chain. Table 1 shows the distribution of taxa found in the various functional groups of invertebrates. About 65% of the species captured potentially dwell in the canopy. The sampling methods included rotary nets; window, sticky, and pitfall traps; and foliage beating. The bird survey observed 23 species in 11 stand types and as many as 15 species in one location. At watershed 10, seven species of omnivorous canopy birds were found. Densities of breeding birds and migration dates were also recorded (Table 2). From these observations, representative taxa were named for each functional group (Table 3). These representatives are listed to illustrate both the prevalent types and general life habits.

Table 1. Number of species of invertebrates captured in three Douglas-fir stands (W. P. Nagel, pers. commun.).

Invertebrate	No. of species	
Herbivores feeding on:		
Any plant	166	
Herbs	6	
Trees and shrubs	63	
Lower plants	24	
		259
Predators *		150
Parasites feeding on:		
Invertebrates	94	
Vertebrates	1	
		95
Saprophytes feeding on:		
Plant material	78	
Animal material and feces	14	
		92
General scavengers:		100
	Total	696

Table 2. Breeding birds observed at the intensively studied watershed in 1972 (R. A. Nussbaum, pers. commun.).

	Arrival begins (month/day)	Departure complete (month/day)	Breeding birds (indiv./ha)
Chestnut-backed chickadee	a		1.98
Golden-crowned kinglet	a		2.22
Hammond's flycatcher	5/7	9/22	0.68
Hermit warbler	4/28	8/15	1.60
Steller's jay	a		0.34
Western flycatcher	5/4	9/8	1.36
Western tanager	4/10	9/28	0.42

[a] Year-round residents.

Table 3. The canopy food chain.

Functional group	Principal representative
Grazing vertebrate	Red tree mouse
Grazing insects	Leaf beetles (Chrysomelidae)
Sucking insects	Adelgidae
Seed and cone insects	Douglas-fir midge
Predaceous birds	Spotted owl
Parasitic invertebrates	Wolf spiders (Lycosidae)
Omnivorous birds	Golden-crowned kinglet
Nest predators	Black raven

ENERGY USE

Birds

To determine the energy distribution among some of the food chain members, modeling techniques were employed. Because density estimates were available only for the omnivorous birds, they were the first group to be examined. They were modeled in two groups, the breeding adults and the young of the year. An equation for daily consumption per individual adult bird was derived from equations by R. A. Nussbaum (pers. commun.) and from a set of assumptions. The assumptions are as follows: (1) Assimilation balances respiration. (2) Respiration is a function of ambient temperature, body size, and bird activity. (3) Digestive efficiency is constant (0.70).

Daily consumption is calculated by:

$$C = a_1 a_2 W^{a_3} \qquad (1)$$

where C = daily consumption per individual (grams dry wt), a_1 = activity factor (a_1 is 2.0 during the breeding season, and 1.4, otherwise), a_2 = temperature factor (a_2 = -0.008T + 0.39), and a_3 = body weight exponent (a_3 = 0.003T + 0.53) where T = daily mean temperature, and W = adult weight (grams dry wt). This relationship is illustrated in Figure 2.

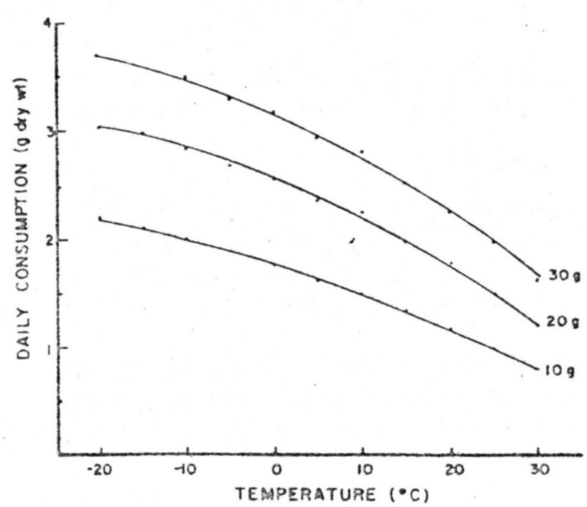

Figure 2. The modeled relationship between daily consumption and temperature for adult birds weighing 10, 20, and 30 g.

Equations for juvenile birds were derived by assuming that: (1) birds follow a prescribed growth curve; (2) energy derived from assimilation goes either to maintain the prescribed growth rate or to basal and activity metabolism; and (3) digestive efficiency is constant (0.70).

The expressions used to compute daily consumption are:

$$S_i = b_1 - b_2 \exp -b_3 i, \quad (2)$$

$$G_i = S_i - S_{i-1}, \quad (3)$$

$$M_i = a_1 a_2 S_i^{a_3}, \quad (4)$$

$$C = M_i + fG_i, \quad (5)$$

where S_i = body weight of an individual on the ith day after hatching, b_1, b_2, b_3 = parameters of the growth equation that are unique for each species, G_i = weight gain on the ith day, M_i = metabolic energy requirements, a_1, a_2, a_3 = parameters same as those in equation (1), C = daily consumption per individual (grams dry wt), and f = consumption for growth conversion factor (= 1.14). The growth and consumption curve for a juvenile western tanager is illustrated in Figure 3.

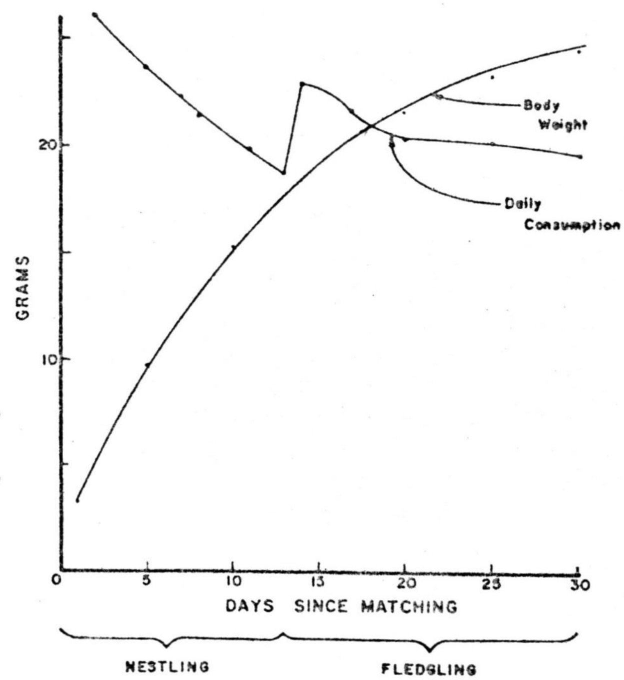

Figure 3. Juvenile growth and consumption by the western tanager at constant temperature of 16°C.

The total annual consumption while at watershed 10 was computed for the seven bird populations found there. Temperature data from the watershed, observed migration dates, bird densities, and survival rates were used in the computation. Also, the proportion of insects in the diet was estimated for each season and annual totals were computed. Insects composed 75% of the diet of the bird population; the other 25% was mostly seeds (Table 4).

Table 4. Annual consumption by the canopy bird population while in residence at watershed 10 (R. A. Nussbaum, pers. commun.).

	Days at watershed 10 per year	Annual consumption (kg/ha) Insects	Total
Chestnut-backed chickadee	365	1.7	2.1
Golden-crowned kinglet	365	1.7	1.8
Hammond's flycatcher	112	0.2	0.2
Hermit warbler	88	0.3	0.3
Steller's jay	365	0.2	1.2
Western flycatcher	100	0.3	0.3
Western tanager	145	0.3	0.3
Total		4.8	6.2

Insects

Although the survey did not record densities of the invertebrates, estimates of production and consumption of grazing insects were made using the bird model consumption estimate. To make these predictions, the following assumptions were made:

1. Of the insects eaten by the omnivorous birds, 35% are canopy grazers. This is the percentage

of grazers found in all samples taken by window traps, foliage beating, and rotary net from an old-growth Douglas-fir stand (W. P. Nagel, pers. commun.

2. The birds consume 20% of the annual production of the grazing insects. Birds consume about 1% of the spruce budworm population during epidemic periods and as much as 50% during endemic periods (Morris et al. 1958).

3. Growth efficiency of these insects is 0.20. This is the median value given by Waldbauer (1968) for a number of species of grazing insects.

The annual consumption by grazing insects is computed to be 42.5 kg/ha and annual production is 8.5 kg/ha.

ENERGY BUDGET

To illustrate the distribution of energy, a partial energy budget for the canopy food chain was constructed (Figure 4). The values used in the budget were computed in the previous section or estimated from other studies. The relationship between the mean standing crop and annual production was derived by simulation (M. A. Strand, MS in preparation). For grazing insects, the mean standing crop represents 15% of total production and for birds it is 125%. Nonassimilated energy was assumed to be 56% of consumption for the insects (Waldbauer 1968) and 30% for birds (R. A. Nussbaum, pers. commun.). Respiration was computed by subtraction.

The grazing insects are probably the major foliage consumers in the canopy food chain. Table 5 shows the percentage of annual production and standing crop of trees that this consumption represents. The data for the vegetation mass are from the paper by Grier et al. (1974). Although the percentage of foliage production that is consumed is very high, the other percentages compare favorably with those reported for forests by other authors (Table 6). A younger forest, for example the 40-year-old stand at the Thompson site (Grier et al. 1974), would have sustained only a 2% loss of foliage production with the same rate of consumption. The standing crop of the insects and the birds estimated in this paper are nearly the same as those reported by Ovington (1962) for other forests (Table 7).

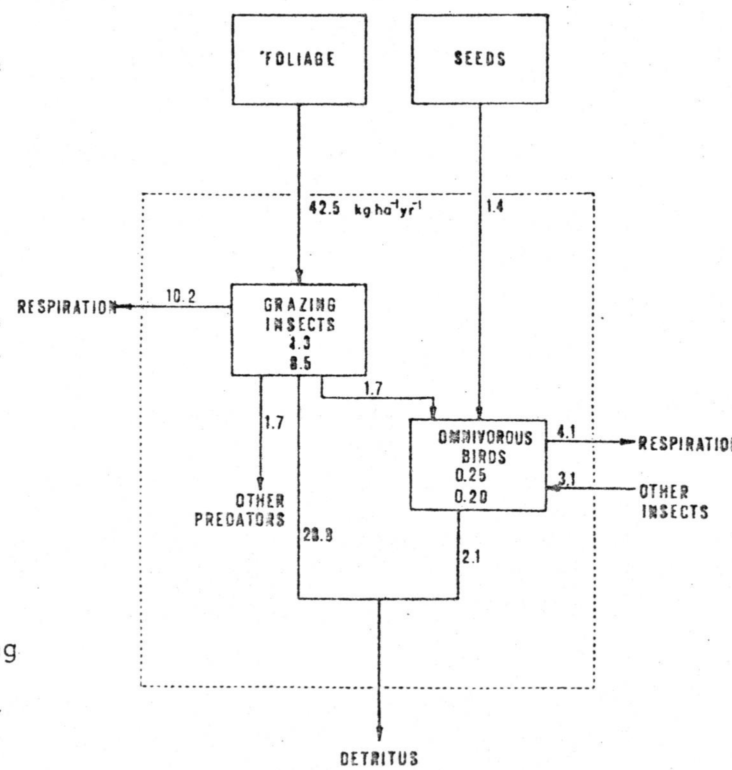

Figure 4. The energy flux through two functional groups in the canopy food chain. Under "grazing insects" and "omnivorous birds," the first number indicates mean standing crop during spring and summer, and the second number indicates annual secondary production; both are in kilograms per hectare.

Table 5. Estimated percentage of plant standing crop and production consumed annually by grazing insects.

	Standing crop (%)	Primary production (%)
Foliage	0.5	102
Aboveground	0.008	1.8
Total	0.007	1.6

Table 6. Primary consumption as a percentage of primary production in various communities.

Community type	Percentage consumed	Authority
Prunus mixed forest	2.5[a]	Bray 1964
Acer-Fagus forest	1.7[a]	Bray 1964
Fagus forest	1.5[a]	Bray 1964
Liriodendron forest (model)	2.6[b]	Reichle et al. 1973
Old field	20[c]	Odum et al. 1962
Salt marsh	7[c]	Teal 1962

[a]Net aboveground primary production. [b]Net foliage production. [c]Net primary production.

Table 7. Standing crops of animals in various forests reported by Ovington (1962) and the estimated values for watershed 10.

Animal	Standing crop (kg/ha)	Forest
Canopy insects	1.3	Douglas-fir (WS 10)
	0.1-5.0	Scotch pine
	0.01-2.0	Corsican pine
Birds	0.25	Douglas-fir (WS 10)
	0.48[a]	Spruce
	1.17[a]	Beech mixed
	1.15[a]	Oak mixed

[a]Fresh weight.

At current population levels, the canopy food chain uses a relatively small amount of the net energy entering the watershed. Some members, however, have the capacity for extreme population fluctuations that can make them major energy users. Keene (1952) lists 14 species of grazing and sucking insects that have been reported as economic pests in Douglas-fir forests. The complete defoliation of watershed 10 would mean a loss of leaves equivalent to 335% of one year's primary production, and the influences would go far beyond the mere loss of tissue (Rafes 1971, Grison 1971). The canopy food chain at present population levels represents a small energy pathway, but it is potentially a major factor in the distribution of energy in the forest ecosystem.

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