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Preliminary considerations of the forest canopy consumer subsystem

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Abstract

A food chain beginning with herbaceous materials produced in the forest canopy is delineated as a subsystem. A conceptual model of energy flow through this subsystem includes assumptions and definitions relating to components of the canopy food chain, processes by which energy is transferred, and the energy pathways. From this conceptual model, it is observed that the canopy food chain is directly coupled to other consumer subsystems through common predators and through the detritus component. Besides the direct relationship through the food base to primary production, this subsystem may also influence the plant system by its effects on the sites of plant hormone production and on the fate of mobile nutrients in the ecosystem.

Introduction

In the past, modeling efforts concerning consumers have been centered on population dynamics, while more recently energetics have been receiving attention. Our considerations of consumers will also concern energy transfer. We will focus on the couplings between consumers and other parts of the ecosystem. These couplings may be direct (i.e., involve energy transfer to or from a consumer) or indirect (i.e., involve the influence of one component on energy transfer between other components of the ecosystem). The major subdivisions of the ecosystem are discussed by Overton (1972).

To facilitate our understanding of the consumer system, it would be convenient to subdivide it into a hierarchical set of units and observe the couplings between them and their couplings with other ecosystem components. If our units are to be subsystems, then the most logical divisions would occur around groups of components with high degrees of interconnections. The majority of linkages with a subsystem's components should occur within the subsystem; couplings to components of other subsystems should be comparatively rare. The classic way to define consumer subsystems has been by trophic levels; however, for our purpose this division may not be the most meaningful one. By basing the division of the consumer system on trophic level designations, the direct linkages with regard to energy flow occur between the subsystems and only indirect linkages, such as competition, occur within them. We hypothesize that a better subdivision of the consumer system could be made by defining the subsystems as food chains on the basis of a stratification of their primary food base.

The first division in our hierarchy will be into grazing and detritus food chains. The grazing food chain includes primary consumers feeding on plant material and a series of secondary consumers that prey on the herbivores and on each other. To further subdivide this food chain, the food base is stratified into forest canopy herbaceous material, woody material, forest floor herbaceous material, and roots. Food chains are defined by the food material eaten by the primary consumers in the chain. Likewise, the detritus food chain which recycles detritus to lower grades of detritus is divided according to particle size. The two resulting food chains use fine or coarse detritus as their primary food sources. By uncoupling these six food chains (four grazing and two detritus) with regard to their food bases, the first order consumers are reasonably unique to a particular food chain subsystem, while common predators couple the subsystems together.

The purposes of this paper will be to define the forest canopy food chain and to develop a conceptual model of it as an example of the type of preliminary consideration which is a prerequisite to mathematical modeling.

The forest canopy food chain forms a subsystem that begins with herbaceous material produced by trees and follows it through its many transfers to detritus. The food base is primarily photosynthetic tissue, needles and leaves of trees; however, buds, young twigs, immature cones, and seeds will also be included, since consumption of these foods is an interrelated process. For present considerations, we will confine our concern to an old-growth, coniferous forest canopy. Successional changes, epidemic outbreaks, and environmental gradients will not be included in our discussions. It is assumed that variations in energy flow from year to year are not appreciable, so there are periods of short-term stability. The conceptual model we will propose is a description of this type of stable condition.

Our discussion will consist of four parts: the components of the subsystem, the processes involved in energy transfer, energy pathways, and the interconnections between this and other food chain subsystems as well as the subsystems defined by Overton (1972) in this symposium. In each section we will present a set of assumptions and definitions that represent our notion of this subsystem. The set will form our conceptual model.

Components

The components of a subsystem are the locations of energy storage and vehicles of energy transfer along the food chain. Components are defined by ecological function rather than taxonomic criteria. However great species diversity might be in a forest canopy, functional roles are common to many species, enabling them to be regarded as a few large populations. To avoid the pitfall of overgeneralization about the superpopulations, a brief discussion of the variations of behavior relevent to energy transfer of our components is included.

Primary consumers are the key links in the food chains, diverting energy produced by the plants into the animal system. In the forest canopy most consumers are insect grazers which feed mainly on new tissue from expanding needles or leaves (Keen 1952). The feeding stage either hatches or emerges near a feeding site, so that food finding initially is not a problem. Many of them feed gregariously when larvae are small, but disperse to feed singly later. The main dissemination phase, however, is the adult where females seek out new feeding sites for oviposition. The feeding period occurs primarily in the spring and early summer with resting phases (pupae, eggs, or overwintering larvae) beginning in late August or early September. A second group of primary consumers includes insects with sucking mouth parts. They act as physiological sinks and remove dissolved nutrients from the xylem sap (Way and Cammell 1970). Only one significant vertebrate foliage feeder has been reported in the forest canopy—the red tree mouse *(Phenacomys longicaudus)* (Maser 1966). It eats needles of Douglas-fir *(Pseudotsuga menziesii)* leaving the central xylem strand. Small branches are cut and carried to the nest where they are consumed.

Plant reproductive tissues are also consumed. Immature cones are attached mainly by cone and seed feeding insects; some feed exclusively on the seeds, while others feed on the cone preventing seed development. Mature seed may be consumed prior to dissemination by certain birds and squirrels. These omnivorous birds use seeds as a primary food source during the winter; they remove undisseminated seeds while the cones are still attached to the tree (Isaac 1943). Squirrels cut cones and extract the seeds on the ground; the subsequent fate of the seeds is considered as part of another food chain subsystem which utilizes forest floor herbaceous material.

Predators and parasites constitute the next links in the food chain. Small invertebrates are consumed generally by other invertebrates. Parasitic forms may feed on larvae, pupae, or eggs of the host. Often several generations of parasites are produced for every single host generation; hyperparasitism of several degrees is possible. Predaceous invertebrates include both spiders and insects. Some, as the orb-spinning spiders, wait for mobile forms to be trapped, while others move about actively in search of food and feed on nearly any invertebrate they can capture (Graham 1952).

During the mating and nesting season, omnivorous birds feed on insects with egg hatch often being correlated with peak insect abundance (Lack 1954). Very small larvae are usually not eaten since they are inconspicuous and many would be required to satisfy a bird's energy needs. Flycatchers, which are not abundant in the winter, breed in the forest canopy and feed mainly on adult insects. Other insectivorous birds search the foliage for the larger larvae. Predation of adult birds is rare, but nest predators may be found consuming both eggs and young nestlings. Other predatory birds are also rare components of the forest canopy; however, the spotted owl *(Strix occidentalis)* is an important predator of vertebrate foliage feeders (Nussbaum 1972[1]).

The components of the forest canopy food chain are restricted to those animals that can complete at least the feeding stages of their life cycles above the shrub stratum. In our considerations of the forest canopy, we have restricted ourselves to endemic population conditions and have not considered the large numbers of defoliators found in some areas. The actual population densities found under "normal" circumstances is not known for the old-growth stands, and estimates of these densities will be a subject of future research. We will consider herbivores to be predator limited and predators to be food limited. All components will be assumed to be balanced with respect to immigration and emigration except for seasonally migrating birds.

In summary, we have designated nine superpopulations or components in the forest canopy food chain subsystem: grazing insects, sucking insects, vertebrate foliage feeders, seed and cone insects, omnivorous birds, parasitic invertebrates, predaceous invertebrates, nest predators, and other predatory birds. Energy flow will be followed between these components; possible transfers within them will not be considered explicitly.

Processes

Certain processes are essential for the transfer of energy, and we have defined five main processes for the food chain subsystems: consumption, elimination, respiration, assimilation, and death. The definitions we use may not be the same as those found in ecological literature, but our definitions are consistent with the purpose of defining direct couplings within and between the food chains and other subsystems of the ecosystem.

The concept of consumption is often equated with ingestion; however, the importance of consumers may not be measured by what they ingest alone. Shelter building and wasteful feeding behavior may result in far greater death of the food resource than the amount ingested. Hence consumption will include ingestion as well as other activities of the animals that result in the loss of life of their food. All forms of waste production by animals after the food is ingested is included in the process of elimination. Thus, energy lost as a result of indigestion, metabolic wastes, or losses of integument will be transferred to detritus via elimination. Assimilation is defined as individual secondary production. It is the process by which energy from one trophic level is incorporated into the tissue of the next. The process of respiration includes the energy loss to the atmospheric sink as the result of maintenance metabolism and of work. Death includes mortality losses as a result of factors other than consumption by another component of a food chain. Both the

[1] Personal communication.

processes of death and elimination result in the production of detritus, but they must be considered separately since they differ in their consequences to the food chain components. Elimination does not affect the potential activity of a component, whereas, death may.

The purpose of defining these five processes is to identify the means by which components are directly coupled with each other or with other subsystems of the ecosystem. Each one is influenced by indirect couplings. For example, feeding behavior, population age structure, and energy demands are indirect couplings between the feeding population and the process of consumption. Nutritional quality of the food may influence the processes of assimilation and elimination. These indirect couplings may be thought of as informational transfers and may be as important to the system as the direct couplings.

Energy Pathways

The general energy pathway is diagrammed in figure 1. The boxes are used to show sites of energy storage. They are associated with a set of variables which are used to describe the site. The consumed tissue compartment is a hypothetical site but is included to separate the processes of consumption and assimilation. Circles are used to indicate the processes which are employed to transfer energy between sites. Solid arrows mean true flows of materials or energy (direct couplings), while dotted arrows and diamonds indicate lines of influence (indirect couplings) from an energy storage site to a process.

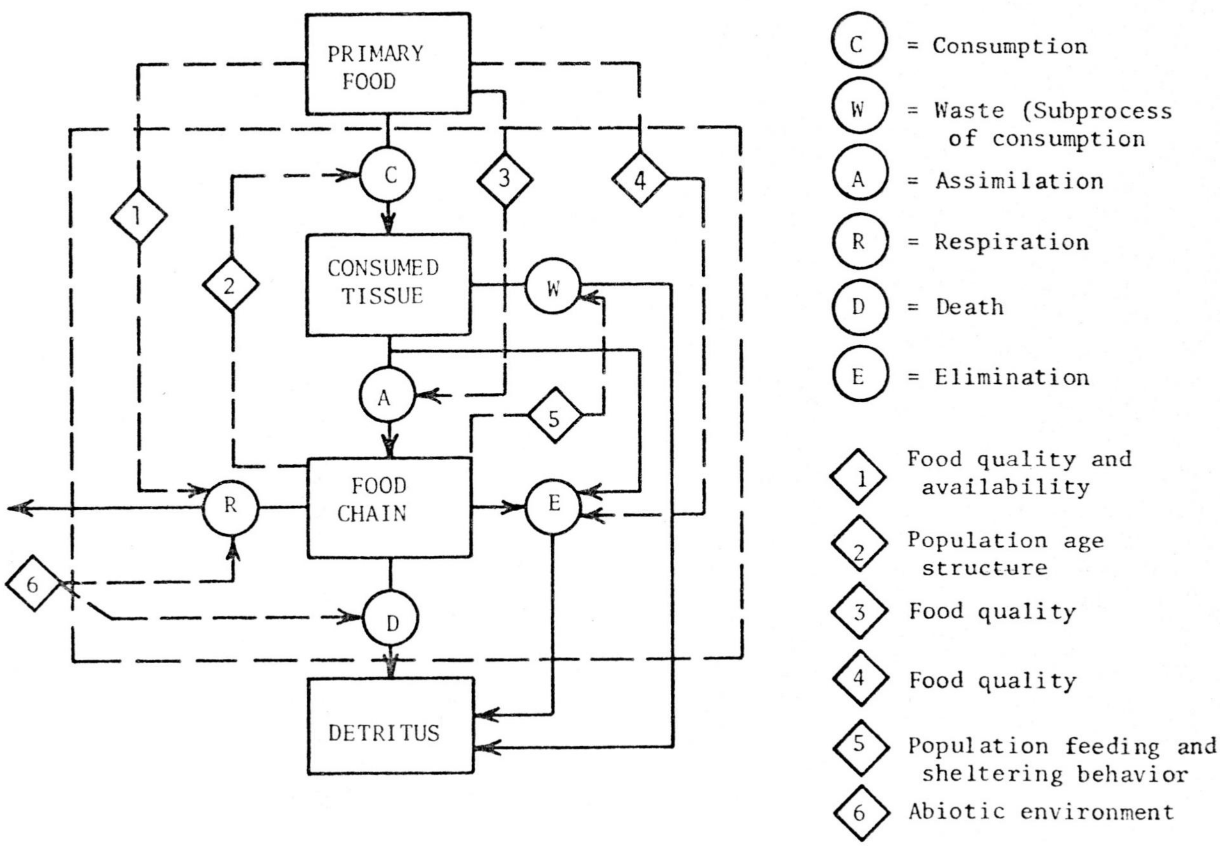

Figure 1. Basic energy pathway through food chain subsystem. See text for explanation of symbols.

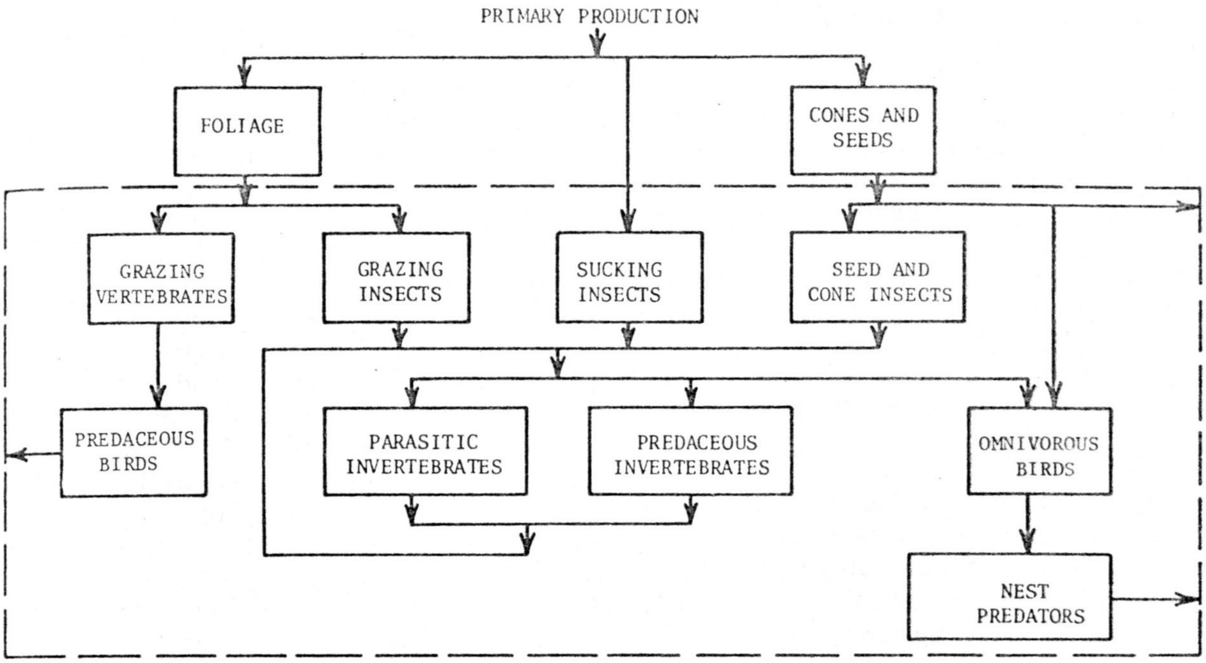

Figure 2. The major energy pathways between components of the forest canopy food chain.

The paths of energy (fig. 2) may be followed beginning in the spring when the buds of the conifers swell and insect herbivores emerge and feed. While they are small, the grazing and sucking insects are preyed upon by other invertebrates. Later they are preyed upon by birds that switch from conifer seeds to insect larvae during their breeding season. Energy leaves the system in the form of food for predators in other food chains, migrating birds, detritus, and heat. The amounts of energy following these routes is not known yet. Consumption rates, relative densities of consumers, food quality variability, assimilation efficiencies, and migration habits are also not known for most of the consumers. These problems will require further research before the model may be quantified. The two diagrams and the definitions and assumptions that were outlined in the preceding sections represent our current conceptual model of the canopy food chain.

Interconnections with Other Subsystems

The conceptual model presented here of the forest canopy consumer subsystem may be used to describe possible interrelations between it and other subsystems. By definition, this subsystem contains consumers that feed primarily in the forest canopy; therefore, we would not expect it to be tightly coupled to other food chains. However, since the food base defines the subsystem and, in the case of the canopy food chain, herbivores are more specific in food habits than the carnivores, it is evident that direct couplings will probably result from the feeding behavior of the secondary consumers. For example, adult insects from other subsystems may serve as food for flycatcher birds which live primarily in the canopy. Predaceous invertebrates from the forest floor feed upon canopy species when they move to the floor for overwintering or pupation. The food chain with primary consumers that feed on fine detritus is coupled to this subsystem through the detritus output, and the canopy food chain may influence the energy flow rates within the detritus food chain by the quality of its detrital outputs.

Besides these connections with other food chain subsystems, the canopy consumers are closely linked to the primary production system. The consumers are influenced by the quantity and quality of herbaceous material produced by the trees. However, the influence of the canopy food chain on primary production is more subtle. Although consumption of foliage or cones is not considered to be at a rate to affect production in the old-growth canopy of the model, the preferential consumption of new needles and expanding cones may affect the nutrient capital of the trees. These consumption sites are physiological sinks, and mobile nutrients are actively moved to them from senescent foliage and storage sites (Sweet and Wareing 1966). The loss of these sinks may mean the return of certain nutrients to the soil solution rather than their retention by the trees (Rafes 1970). Also, consumption of bud tips reduces the sites of growth hormone production; this hormone is necessary for cambial division, and local deficiencies may result from the gregarious feeding habits of some herbivores (Kozlowski 1969). These indirect couplings may prove to be the most significant role of the food chain subsystems in the old-growth forest.

Summary

The consumer system is composed of a series of grazing and detritus food chains. The primary consumers are thought to be reasonably unique to each food chain, and direct energy transfers between the food chains occur via common predators. The processes of energy transfer that link the components of the food chains with each other and the rest of the ecosystem are: consumption, assimilation, elimination, respiration, and death. Indirect links are formed by informational transfers which influence energy flows.

The forest canopy food chain includes the primary consumers that feed on herbaceous material produced in the canopy and the series of related predators. This food chain is directly linked to primary production by consumption of herbaceous materials, to the other food chains by common predators, and to the detritus component through production of detrital material. Primary production influences the food chain processes by variations in nutritional quality, spatial arrangement, and quantity of material produced. The influences of the food chain on primary production are more subtle. Preferential feeding habits of many canopy grazers affect the number of sites of plant hormone production and the fate of mobile nutrients in the ecosystem.

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