

15

THE ORGANIZATION OF ENERGY AND MATTER IN PLANT AND ANIMAL COMMUNITIES

Plant and animal communities are assemblages of individuals that live together in an ecologically organized manner. Individuals in a community have requirements that are met by the resources in the physical area that encompasses that community. As the community develops, interrelationships develop between individual plants, plant species, individual animals, animal species, and between plants and animals.

Many of the interrelationships between organisms are unique to the developed community. Some relationships are species dependent—in some cases obligatory. For example, the lichens that grow on the branches of trees in a dense coniferous forest are composed of both fungi and algae, which depend on each other for their existence, and the lichen as a whole depends on the conditions imposed on it by the dense coniferous overstory. The lichens may be attached to several different tree species, and several different species may be attached to a single tree.

The organization of communities can be described in many different ways. Taxonomic structure is a common way to describe it, especially through time inasmuch as different species are found in different successional stages. Different species have different morphologies, giving communities different appearances. The appearance of a community changes owing to phenological changes such as the falling of leaves, and the chemical composition of the different species varies with time also. A fundamental characteristic of an organized group of organisms is the flow of energy and matter through the group, beginning with solar energy and continuing through photosynthesis (primary production), ingestion (primary consumption), synthesis (secondary production), reingestion (secondary consumption), and decomposition resulting in the dissipation of energy.

15-1 TAXONOMIC RELATIONSHIPS

Plant communities contain members from different taxonomic groups. Oosting (1956) stresses the description of plant communities on the basis of their composition and structure. If two communities had identical taxonomic composition, they would have a maximum (1.0) *coefficient of similarity*. If they had no species in common, the coefficient of similarity would be zero. This kind of comparison shows that communities on similar soil and topography, with similar water resources, and in close physical proximity have high coefficients of similarity if they are of similar ecological age. Thus a maple-basswood forest in one location is quite similar in many respects to a maple-basswood forest in another area.

Animals, especially primary consumers, are closely tied to plant communities because of food resources. The coefficient of similarity can be applied to these animal populations. Some animals are found in rather specialized plant communities (spruce grouse, for example, are found only in rather mature coniferous forests), while others are much less selective in terms of plant-community characteristics. A white-tailed deer is an example of the latter type; it is found in a variety of plant communities ranging from grassland to coniferous forests.

15-2 MORPHOLOGICAL RELATIONSHIPS

Gross morphological characteristics of plants are well known to everyone. Leaves are the primary location for photosynthesis. The stems are supporting structures, as well as "pipelines" for the movement of water and absorbed nutrients to the leaves and for the movement of the products of photosynthesis from the leaves to the fruits and roots. The roots serve as anchors and are also metabolically active inasmuch as the growing tips absorb water and soil nutrients. Photosynthetic products, translocated to the roots, are the sources of energy for root metabolism. The reproductive structures take a variety of forms in plants, but all serve to concentrate enough energy in a small amount of matter (the seed) so that the life cycle can begin again under favorable conditions.

Different kinds of plant and animal communities have different appearances because of the life-form of their members. Tundra communities contain low-growing vegetation, without a great deal of taxonomic diversity. The prairie is another type of community with low-growing vegetation; the entire community is confined to a vertical height of a few feet. Variations in prairie communities relate to hydrologic and other physical factors. In general, the greater the amount of water available to a prairie community, the greater the vertical height of that community. This results in the following morphological classification of prairie types: tall-grass prairie, mixed prairie, and short-grass prairie. The distribution of prairie types from east to west in the prairie states generally follows the moisture gradients.

Deciduous forest communities have a distinctive morphology that includes layers of vegetation. The upper layer, made up of tree crowns, is the canopy. Beneath the canopy is the subcanopy, which is made up of shrubs and young trees (saplings) that have not yet reached the height of the canopy. Below the

canopy and subcanopy is the understory, composed of herbaceous plants and tree seedlings that adapt to the conditions imposed on them by the canopy and subcanopy.

The vertical morphology of a deciduous forest community changes seasonally with the emergence and fall of leaves. In the spring, the canopy is a rigid, woody structure with a fairly low density, permitting sunlight to penetrate. The understory responds with a variety of fast-growing, short-lived flowering plants. These plants generally complete their life cycles before the canopy reaches maximum density. When the leaves are on the trees, the canopy is dense, shading the lower levels of the community. The understory is fairly quiescent at that time of the year.

A coniferous community has a more stable morphology. The loss of leaves (needles) takes place throughout the year, so seasonal differences in canopy characteristics are not marked. The density of mature coniferous canopies is usually great enough to prevent the growth of a diverse understory, resulting in a much simpler community morphology.

The size and distribution of trees in a forest community can be estimated by the use of standard methods. Square or circular plots are used as sample areas, and an estimate of the total number of plants in a community can be obtained by multiplying the number in a sample area by the quotient obtained by dividing the total area by the sample area. Using this method, several community characteristics can be described with the following terms:

Basal area: The area of a cross section of a tree trunk, generally taken at $4\frac{1}{2}$ feet above the ground.

Diameter, breast high (dbh): The diameter of a tree trunk at $4\frac{1}{2}$ feet.

Density, absolute: The number of trees of a given species in the sample plots.

Density, community: The total number of trees of each species per unit land area.

Density, relative: The number of individuals of a given species in relation to the total number of individuals of all species.

Dominance, absolute: The sum of the basal areas of individual trees of a given species in the sample plots.

Dominance, absolute mean: The average basal area of the individuals of a given species in each plot.

Dominance, community: The sum of the basal areas of individuals of a given species throughout the entire community.

Dominance, relative: The basal areas of a given species in relation to the basal area of all species, which can be expressed as a simple ratio or as a percentage.

Frequency, absolute: The number of plots in which a given species is found.

Frequency, relative: The number of plots containing a given species compared with the total number of plots sampled, which can be expressed as a simple ratio or as a percentage.

Frequency, relative community: The number of individuals of a given species in the sample plots as a percentage of the total number of individuals of all species.

The basal area can be found by measuring the circumference of a tree at a height of $4\frac{1}{2}$ ft with a tape that is marked for reading basal area directly (in square inches or square centimeters);¹ or the basal area can be calculated by measuring either the circumference or the diameter of the trunk at a height of $4\frac{1}{2}$ ft and using equations (15-1) and (15-2).

$$BA = \pi \left(\frac{C}{2\pi} \right)^2 \quad (15-1)$$

$$BA = \pi \left(\frac{D}{2} \right)^2 \quad (15-2)$$

The use of circular or rectangular plots for determining the number and distribution of trees is a straightforward mathematical technique, but it is frequently filled with statistical complications owing to the nonrandom distribution of trees in a forest. The location of the sample plots may be randomly determined or systematically determined, and the decision of which method to use should be based on the purpose of the sampling and on the general characteristics of the vegetation. Grieg-Smith (1964) discusses these considerations and many others in quantitative plant ecology in considerable detail.

There are several other methods for the determination of the distribution of trees in a forest. The inefficiency in using the large sample plots necessary in tree stands has resulted in the development of plotless sampling techniques. These are described further by Grieg-Smith (1964) and include the following:

1. *Closest individual method*: The distance from the sampling point to the nearest tree is measured.
2. *Nearest neighbor method*: The distance from the sampling point to the nearest tree is measured.
3. *Random pairs method*: A line from the sampling point to the nearest tree is first described, followed by a line perpendicular to the first line and through the sampling point. The distance from the tree nearest the sampling point to the tree closest to the nearest tree but on the other side of the second line (the one perpendicular to the first line) is measured.
4. *Point-centered quarter method*: The distance from the sampling point to the nearest tree in each quarter is measured, using a previously determined orientation of the quarters.

The calculation of density from the distances measured using these methods is based on a calculation of the mean area surrounding the trees described by the linear measurements. Grieg-Smith (1964, p. 49) states that the mean linear value obtained by using the first two methods is one-half the square root of the mean area. He discusses research on this that evaluates the applicability of the factor 2 (one-half) in the calculation, concluding that no single factor can be

¹Basal-area tapes can be made by the student.

applied to allow for bias in the sample of distances. This is likely true for all four methods, although 0.8 is stated as the correction factor for the third method. The fourth method may be the most accurate; the mean of all distances measured is equal to the square root of the mean area. Thus the area surrounding each tree (the mean of all trees in the stand) can be calculated with equation (15-3).

$$\bar{A} = \bar{D}^2 \quad (15-3)$$

where

\bar{D} = average distance from points to trees

The density of trees per acre can be determined by equation (15-4).

$$\text{Density per acre} = \frac{43560}{\bar{A}} \quad (15-4)$$

where

\bar{A} = mean area (ft²) surrounding the trees in the stand

The frequency of occurrence and the dominant characteristics can be calculated as in the sample plot methods; the plotless sampling technique results in the same data but for plots of variable size.

There are very practical problems in using these approaches in the field. Trees are not all single bole structures, but often have sprouts at the base. This is especially true of some species in second-growth areas. *Tilia americana* (basswood) is an example of a tree that sprouts profusely. Some trees live together in groups called clones. *Populus* (aspen) is such a tree; a "mother" tree may have several offspring that have grown from shoots off the sprawling roots of the parent tree, resulting in a very bunched distribution. There often is a fairly symmetrical shape to the clone, with the parent tree in the center and progressively shorter, younger trees toward the periphery.

There can be similar problems in applying these techniques to herbaceous vegetation. Typically, large plots or plotless sampling are applied to the trees, smaller plots to saplings (1" diameter at ground level to 4" dbh), and still smaller plots to seedlings (less than 1" diameter at ground level), shrubs, and herbaceous vegetation. The same type of sampling problems appear in each case, since many shrubs are clonal, sapling distribution is often related to the distribution of parent trees, and herbaceous vegetation is often clumped. This is especially true on the prairie where many species grow as "bunchgrass," or in clumps that may or may not form continuous mats of vegetation.

These sampling techniques, along with others described in the plant ecology references listed at the end of the chapter, are useful for describing community structure in terms of the parameters measured. Frequently, these parameters are not the pertinent factors in an animal-plant-environment relationship, however. Dominance based on the basal area of the bole may be of less significance than the dominant effect of canopy characteristics on the penetration of energy and

the synthesis of matter into living tissue in the understory. There is a danger in using such general approaches because they may direct attention away from the functional relationship between organism and environment, resulting in an inability to perceive in an analytical way the transport of energy and matter through the system.

Animal communities have a morphology that can be described in a manner similar to that for plant communities. Animal communities exist within plant communities, of course, with individual animals usually having a considerable amount of mobility. Some species have a group mobility (migration), resulting in a seasonal movement of an entire group or population from one plant community to another.

One factor that plays a significant role in the distribution of energy and matter in the animal community is the effect of pheromones. These chemical substances, released from one animal, trigger specific reactions from another in the same species. An interesting characteristic of these pheromones is that such minute quantities markedly alter the behavior of members of the population. The expenditure of energy for their emission is miniscule compared with the expenditure of energy that may result from a response to them.

Analyses of the basic matter and energy characteristics of an animal might start with three basic questions: (1) What is its chemical composition? (2) What are its thermal energy characteristics? and (3) Where does the matter and energy come from?

The first question deals with the basic chemical structure of the animal. Elements—primarily carbon, hydrogen, oxygen, and nitrogen—are bound together with other elements found in lesser quantities to form compounds of unique biological capabilities when they are combined in cells, tissues, and organs. Energy is stored as tissue synthesis occurs. Animal products are also formed, including the fetus, milk, and eggs. Some tissue is formed at seasonal intervals, such as feathers, hair, and antlers. The amount of energy necessary for the synthesis of these materials can be quantified and, if considered in terms of time, becomes a dynamic measurement of the cost of life.

An animal's thermal energy characteristics play an important part in its physiological processes. These in turn affect behavior, and behavior can alter thermal characteristics as animals change their posture, activity, habitat, and so forth. Some animals maintain a fairly constant body temperature, whereas others have much more variation. Some are regulated at one level for part of the year and at a much lower level at other times (hibernation). All organisms live in a thermal-energy regime that results in a continual and dynamic exchange of heat energy with its environment.

Where this energy comes from can be answered in one word—food. The processes taking part in the ingestion, digestion, absorption, and utilization of food are very complex. An understanding of these processes is fundamental to an understanding of the productivity of an animal. The productivity of an individual animal is a basic part of the productivity of an animal community within an ecosystem. The productivity of primary consumers is directly related to the

productivity of the plant community. The productivity of secondary consumers is directly related to that of primary consumers, which in turn is related to the productivity of the plant community. Thus there is an n -dimensional series of interrelationships in a plant and animal community. The challenge is that of analyzing significant parts of these relationships so that simple models can be developed that will lead to a greater understanding of the energy, matter, and time interactions that make the system what it is.

The "home range" of an animal generally varies according to the size of the animal. Small rodents such as *Microtus* and *Peromyscus* have home ranges of about an acre in size, whereas large mammals such as moose may range over several miles. There are many reasons for the relationship between body size and home-range size, including morphological ones—a small mammal simply cannot travel fast enough to cover a large home range; but one basic regulatory mechanism present is the distribution of energy and matter in relation to the requirements of the animal. Large mammals such as moose, elk, and deer must have a large supply of resources in order to satisfy their physiological requirements. Superimposed on this energy and matter distribution is the effect of pheromones and other stimuli, which regulate the spacing of animals in a group. These stimuli may at times spread the animals out more than would be necessary to stay within the energy and matter limits of the resources. They may limit gregariousness that would cause an overuse of the resource supply, allowing the populations to be successful over a long period of time.

Animals that are gregarious during part or all of the year are usually quite mobile members of the animal community. Waterfowl congregate on the wintering grounds, and move as a group to feeding areas. Caribou move long distances in herds; elk migrate, congregating in wintering areas; and white-tailed deer often move to yarding areas in the winter and disperse in the spring. Snow conditions in these yards often confine the animals to limited areas, resulting in a rapid depletion of the food resource. The energy and matter balance is upset because the animals are confined, not only to specific yarding areas but to trails within the yards.

Physical characteristics of the habitat influence the distribution of animals within a community. In very homogenous habitats, territories may tend to be more regular in shape. In habitats with much variability in physical and biological features, territories conform to these features to some extent. Tree-nesting birds, for example, are found in plant communities of the right ecological age to include the right kinds of trees. Birds nesting in herbaceous vegetation are associated with plant communities of that type. These plant communities may be dependent on some physical feature—such as the distribution of cattails around a marsh, which provides nesting cover for red-winged blackbirds.

The morphology of the physical and biotic components of a habitat is often apparently very slightly different for closely related animals living in the habitat, but it may have more distinct ecological differences in both time and space. MacArthur (1958) has shown that ecological differences exist for five species of warblers that live in northeastern coniferous forests. These five species behave

in manners that expose them to different kinds of food. Some feed in the crowns of trees, others in the lower reaches. Some feed on the periphery, and others in the interior of the crowns. The timing of changes in food requirements is such that peak requirements are slightly out of phase. Thus the members of the animal community utilize different aspects of the plant community and its physical and biological features. The *effective, functional* organization is different for different species and the roles of various community characteristics should only be evaluated in relation to the community members.

15-3 CHEMICAL RELATIONSHIPS

Since the distribution of energy and matter is a fundamental regulatory mechanism in the formation of plant and animal communities, it is useful to consider the distribution of chemicals (matter) that are the source of energy and matter for the metabolism of community members. The chemical characteristics of a plant community are related in part to the morphological characteristics of the community. Energy is stored in plant structures, with different amounts in different structures. Matter is distributed throughout the plant, with some plant parts serving specifically as storage organs.

The energy and matter cycle in plants occurs as a result of photosynthesis with the source of energy being the sun. The products of photosynthesis are used by the plant to synthesize its own tissue and are stored in the plant as a source of energy for subsequent plant growth (germinating seeds). These products, both in the leaves and seeds, are consumed by herbivores (primary consumers), who in turn synthesize their own body tissue with its particular energy and matter configuration.

The differences in the chemical morphology of plant parts result in different levels of usefulness to a primary consumer. Detailed data are lacking on the energy and matter distribution in wild plants, but values for corn illustrate this distribution pattern. A mature corn plant has the approximate energy and matter morphology shown in Figure 15-1. Note that the grain contains the highest protein and the highest digestible energy. This is because the grains are storage organs, whereas the other plant parts, such as the cobs and stem, are structures for mechanical support. They have rigid cell walls that provide structure, but they are not as nutritionally useful to a primary consumer as the grain is because the energy and matter is resistant to the action of digestive enzymes. The grain, however, contains sugar, starches, and proteins that are more readily available, except for the protective, highly lignified pericarp on the kernel.

The *presence* of nutrients such as protein must be carefully distinguished from the *availability* of nutrients in the plant parts. Digestible-protein data for cattle [data from Crampton and Harris (1969)] show that 46% of the protein in the aerial part of the plant is digestible; none of the protein in the cob is digestible; 28% of the protein in the husks is; and 76% of the protein in the grain is digestible. Thus the grain not only contains the highest percentage of crude protein but a distinctly greater amount of it is digestible by cattle. This illustrates that the

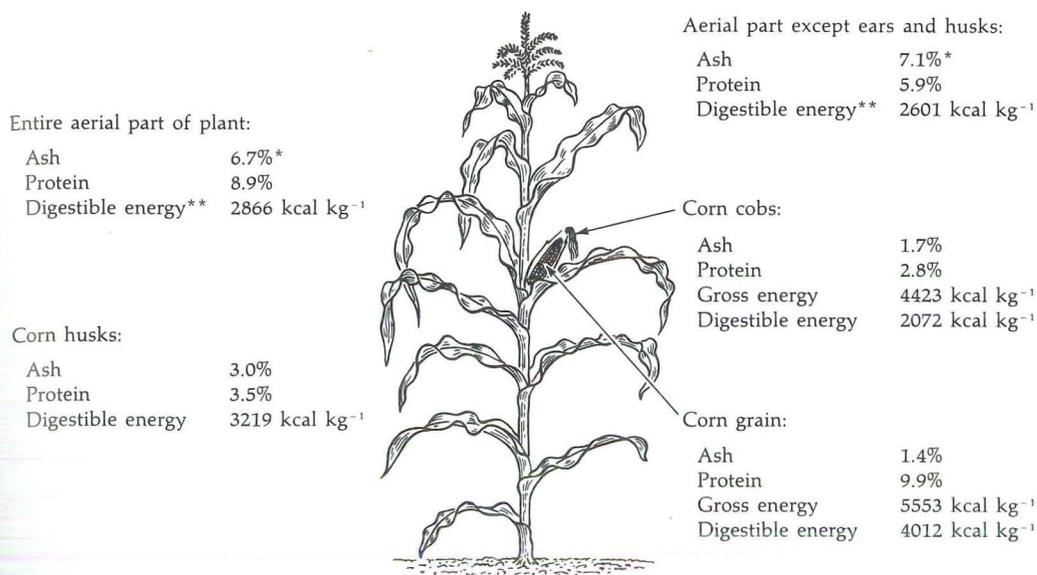


FIGURE 15-1. The energy and matter morphology of a corn plant: * indicates percentages based on dry weight; ** indicates digestible energy for cattle. (Data from Crampton and Harris 1968.)

nutrient content of plants is of little significance by itself; the plant and animal must be considered together when evaluating the distribution of energy and matter in relation to productivity.

One other consideration will illustrate this point further. The protein content of corn grain is 10%, with 75% of the protein digestible by cattle. The absorption, metabolism, and synthesis of protein within the animal is a function of factors additional to digestibility. The *net* protein is of greatest significance because it represents the balance between the synthesis of protein in animal tissue and protein (nitrogen) extraction from the animal. Corn is deficient in the amino acid *lysine*, however, and as a result it is not a good single source of protein. Other forage containing lysine is necessary to make the amino acids in corn of greatest value to the animal. Since wild animals cannot very likely compensate for such kinds of deficiencies in their diets any more than domestic cattle can, it is clear that the analytical ecologist must pursue the animal-environment relationship to considerable depth if he is going to understand functional relationships in their entirety. Such subtle characteristics may have great ecological significance, especially when productivity is in a precarious balance.

The preceding discussion of chemical relationships showed how energy and matter is distributed within single plants. These combine to form a community distribution. Dense tree crowns form canopies that reduce photosynthetic activity in the subcanopies and at ground level. Some species have large numbers of suckers that are nourished by the parent tree. These individuals can survive in the subcanopy in part because they have a source of energy—the parent tree—that

illustrate the importance of these changes. The fall of acorns, for example, results in a sudden abundance of food for ground-dwelling deer. The abundance of this food may have a significant effect on the amount of fat deposition in the deer prior to winter, which is important to winter survival. The development of corn in farmers' fields can have a dramatic effect on the food habits of racoon. The fall of leaves markedly alters the optical characteristics of the canopy, resulting in greater visibility for some kinds of predators and prey. These changes have an effect on the mechanical and thermal characteristics of the canopy as well; a sparse canopy intercepts less snow, has less effect on the reduction of wind, and is less effective as a barrier to the heat-sink effects of a cold night sky.

Changes in the chemical phenology of plants are as marked as changes in the morphological phenology. They are more subtle, however, and have not received as much attention from ecologists as have the more obvious morphological characteristics. Changes in the protein content of Kentucky bluegrass (*Poa pratensis*) as the plant goes from the immature stage to the mature stage range from 17.3% (dry-weight basis) to 3.3%, respectively (Figure 15-2). The continual decline in protein content is accompanied by a concomitant decline in digestibility (by cattle), indicating that the nutritional usefulness of this forage plant actually deteriorates more than the crude-protein levels indicate.

Seasonal changes in the distribution and characteristics of energy and matter in plants owing to the processes of translocation and maturation occur also in alfalfa and timothy. In the immature stage, alfalfa has a protein content of 24.5%. This drops to 20.5% in prebloom, 19.3% in early bloom, 17.8% in midbloom, and 15.9% in full bloom [data from Crampton and Harris (1969)]. The data on timothy hay show the same trend since the protein content goes from 16.9% to 8.9% to 6.2% when cut in the immature, full bloom, and mature stages, respectively.

The rapid decline in protein content has considerable ecological significance. The timing of these changes in relation to the timing of the birth of deer fawns is of interest because fawns begin nibbling leaves shortly after birth. If the fawns are born at a time when both the protein content and the protein digestibility

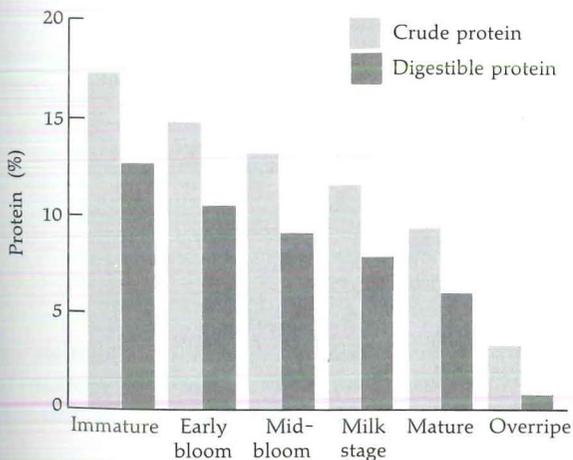


FIGURE 15-2. Protein content of Kentucky bluegrass at different stages of maturity. (Data from Crampton and Harris 1969, pp. 517-519.)

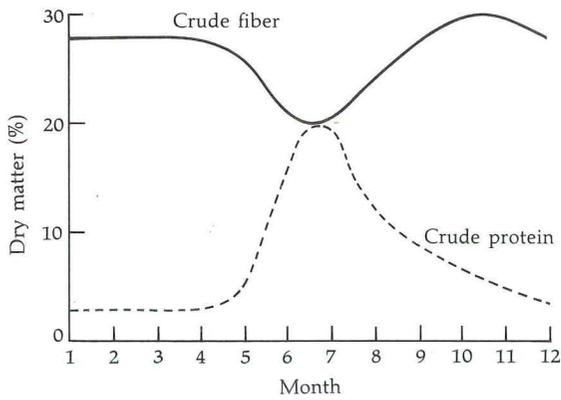


FIGURE 15-3. Seasonal variation in crude fiber and crude protein content of reindeer pasture. (Data from Steen 1968.)

is high, considerably more nutritive value can be derived from the plants. A month later the same forage species might have only half as much useful protein, resulting in a subtle deterioration in the range quality unless the fawn can compensate by selecting later-maturing species.

Changes in the chemical composition of plants occur continually, but at different rates at different physiological ages throughout the annual cycle. Steen (1968) shows the annual variation in the percentage of crude protein and crude fiber on reindeer pasture, illustrating the rapidity of the changes during the growing season (Figure 15-3). A similar graph by Kubota, Rieger, and Lazer (1970) for browse plants in Alaska is shown in Figure 15-4.

Chemical differences between species and between seasons for aspen, willow, blueberry, and grass on the Cache la Poudre Range in Colorado are reported by Dietz, Udall, and Yeager (1962). Protein, ash, and phosphorous percentages were higher in the spring than in the fall, and the fat, crude fiber, nitrogen-free extract, and calcium percentages were higher in the fall (Figure 15-5). Thus there is a shift from higher protein values during the growing season to higher fat and carbohydrate values in the fall when the plant is mature and the cell-wall fraction has increased.

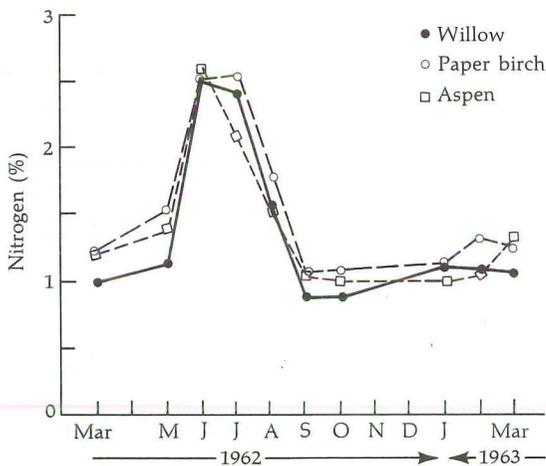


FIGURE 15-4. Seasonal changes in concentration of nitrogen in leaves and twigs of three Alaskan browse plants. (Data from Kubota, Rieger, and Lazer 1970, *J. Wildlife Management*.)

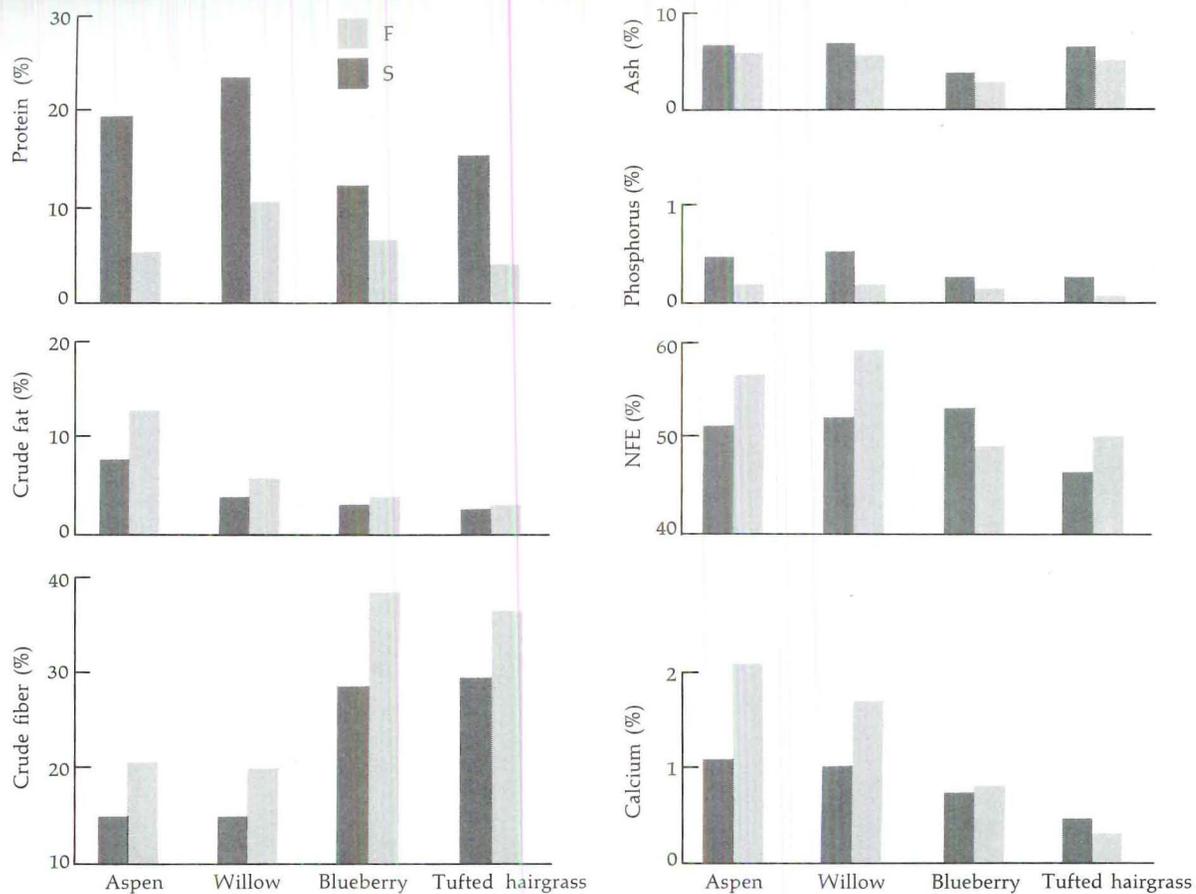


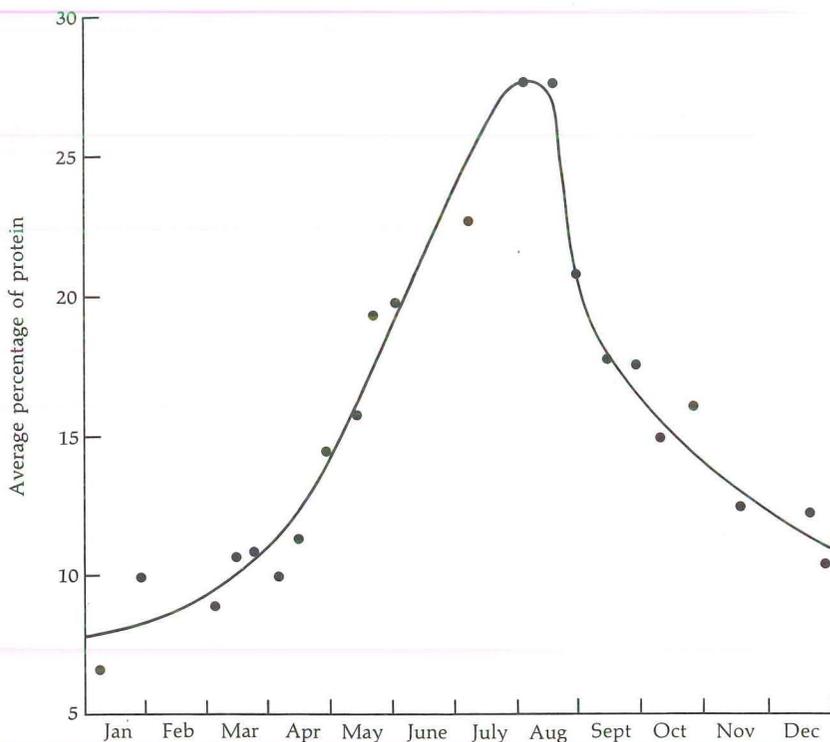
FIGURE 15-5. Seasonal and species differences in the chemical analyses of forage. (Data from Dietz, Udall, and Yeager 1962.)

Differences between seasons can be attributed to variations in the weather conditions that affect plant growth. These differences are greater for herbaceous plants than for woody species. The prairie, for example, can vary greatly from year to year because of differences in rainfall, solar radiation, and temperature.

It was pointed out earlier that the characteristics of the range cannot be evaluated in an ecologically realistic manner without an analysis of the animal characteristics as well. Ingestion, digestion, and nutrient metabolism were discussed in Part 3. Variation in the chemical characteristics of the range may also be reflected in the rumen content of animals on the range; the percentage of protein in the rumen of elk clearly coincide with the seasonal variation in the protein content of range plants (Figure 15-6).

Animals exhibit a chemical phenology as changes in body composition take place during growth and seasonally. The deposition of fat, for example, is a seasonal physiological function common to many animals. Rodents that enter hibernation have an accumulation of brown fat that is metabolized during hibernation. A lactating female deer has a lower fat content than a nonlactating animal, because the nutrient assimilation in the former is directed toward the synthesis of milk rather than fat. White-tailed deer reach their heaviest weights in the fall, with a decline beginning in November. The decline is greatest for males owing to their activity during breeding. Much of this weight loss can be attributed to

FIGURE 15-6. Seasonal changes in the percentage of protein in elk rumens. Note the close similarity between this pattern and the protein content of the range shown in Figures 15-3 and 15-4. (Data from McBee 1964.)



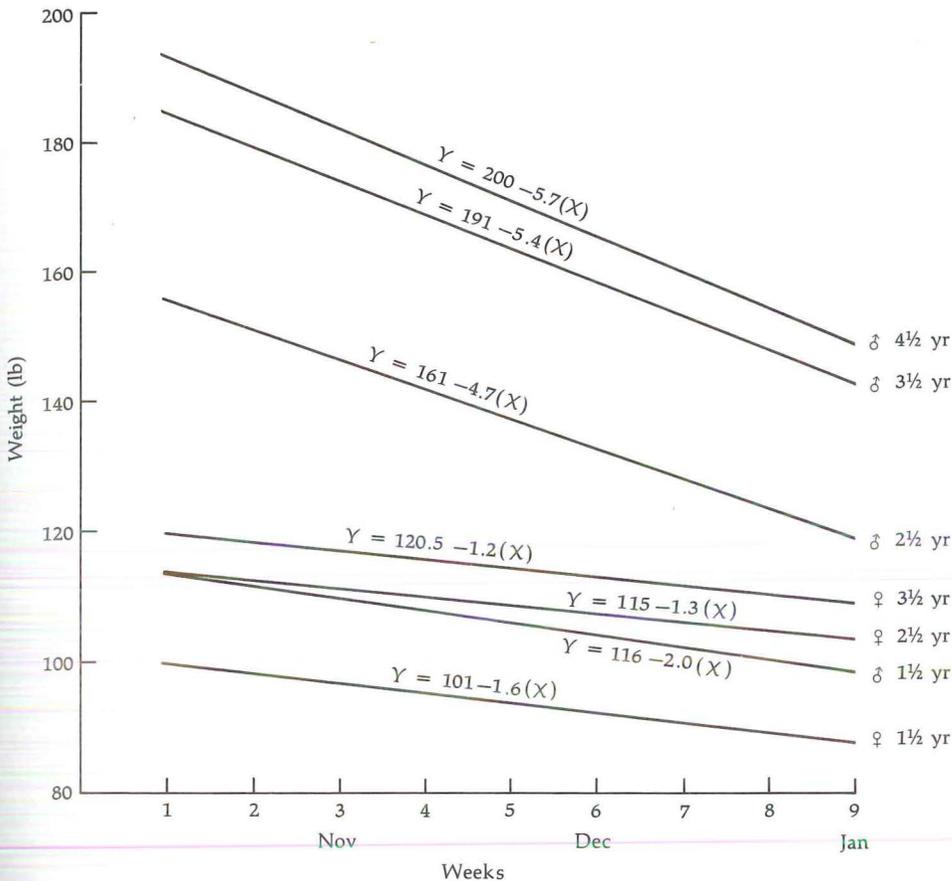


FIGURE 15-7. Weight loss of deer in November and December. (Calculated from data in Siegler 1968.)

the mobilization of body fat. The data in Figure 15-7 indicate a distinct difference in the weight losses between sexes and ages, with a more rapid loss for the older males. The older females hold their weight fairly well, perhaps even gaining during November and December if sufficient forage is available. Regression equations are in Appendix 5.

Minerals are mobilized on a seasonal basis for particular physiological functions. Antler growth is a seasonal phenomenon in white-tailed deer, normally occurring during the period from March to September. The deposition of calcium and phosphorus for antler growth occurs as a rich blood supply covers the antlers in a vascular tissue called "velvet." Some of the phosphorus comes from the ribs (Whelan, personal communication).

Many similar types of mobilization can be demonstrated for laboratory animals as the body shifts its physiological attention from one growing point to another. The occurrence of the redistribution of body components by free-ranging animals during the annual cycle is largely unknown. Its ecological significance in terms of productivity and even survival warrants further consideration.

Both plants and animals make provisions for survival during periods in which resources are unavailable or in short supply. This has been discussed with reference to the storage of the products of photosynthesis in seeds and fruits for later use as a source of energy for germination. The fat reserve of a hibernating animal functions in a similar manner inasmuch as it becomes a source of energy when ingestion processes are not active.

The requirements of animals for energy, protein, and other nutrients used in body-tissue maintenance and productivity are fairly regular over the annual cycle. The need for thermal energy to maintain homeothermy is a function of the thermal regime imposed on the animal by weather conditions and by its physiological condition. Weather conditions are regular on a long-term basis (the seasonal cycles) but irregular on a short-term basis, because of day-to-day weather fluctuations. The animal's physiological condition is fairly regular; seasonal shifts in metabolism and reproduction relate to such stimuli as daylength.

The bioenergetics of willow ptarmigan (*Lagopus lagopus*) over the yearly cycle illustrate the sequential occurrence of energy-demanding activities such as seasonal changes in weight, molt, egg laying, thermoregulation, and gross activity (West 1968). The spring molt begins two months before egg laying starts, and in females, the molt is interrupted during egg laying. Weight losses occur after egg laying and midway through the molt. West found that the birds in experimental pens were active during each of the 24 hours of daylight in the summer (College, Alaska), with a very small amount of activity in the long winter night. Additional energy requirements need to be considered for a bird in the field, including the cost of food gathering, migration, courtship behavior, incubating eggs, raising young, escaping from predators, responding to weather conditions, and others. West's article forms an excellent basis for the development of an analytical model describing the energetics of a free-ranging animal, and students are encouraged to continue within this framework for other species.

A similar bioenergetic model of a beaver (*Castor canadensis canadensis*) population has been described by Novakowski (1967). He shows that the energy supply cached for winter use when the colony was confined under the ice was not sufficient for the energy requirements of the colony, calculated on the basis of the number and weight of animals in each colony. This suggests that energy conservation is necessary, possibly including reduced activity, periods of dormancy, huddling, insulation by the lodge and fur, and fat deposition. The younger animals, both kits and yearlings, gained weight during the winter, whereas the older animals did not. An analysis of the energetics of beavers of different weights, with a consideration of the roles of different members of the population in the social structures, is basic to an understanding of the population dynamics and ecological organization of the beaver colony.

SUCCESSION. Plant communities that are undisturbed by the activities of man undergo natural successional changes. These changes are affected by physical factors, such as soil characteristics, rainfall, topography, and radiant energy, and biological factors that result from interactions between members of the plant

community. This natural succession follows certain patterns that are predictable within the limits of variation in the physical factors from year to year.

Primary succession occurs as plants invade an area that has not supported life before in its present physical state. The bedrock exposed as a result of earthquakes, areas covered with volcanic ash, and so forth, are examples of potentially large-scale physical areas. On a smaller scale, overburden due to mining operations, exposure of the substrate owing to general removal, and local erosion over bedrock results in the exposure of physical substrates that have not supported life previously.

The plants that invade these areas are called pioneer plants. They include lichens that can grow on bare rock, which in turn contribute to a chemical and physical breakdown of the rock surface, preparing a substrate that is suitable for higher plants such as mosses. These modify further the rock-plant interface, resulting eventually in sufficient substrate that the higher seed plants can invade. Many higher plants invade newly exposed soil substrates directly without going through the sequence of lichen, moss, and higher plants. Floods, for example, redistribute soil that may be invaded directly by higher plants.

The disturbance of organisms in a developed community results in secondary succession. Fire, for example, can cause the destruction of a stand of mature trees. Soon after, herbaceous and woody plants invade the area, resulting in a new stand of young trees and an understory abundant in herbaceous plants. *Epilobium angustifolium* (fireweed) is a common herbaceous invader, and aspen (*Populus sp*) is a common woody invader, along with other trees and shrubs.

Plant succession occurs from an aquatic to a terrestrial substrate, as well as from virgin terra. A body of water, such as a pond, may support the growth of phytoplankton, and as these organisms die there is an accumulation of detritus on the pond's bottom that becomes a substrate for higher plants. At the same time, a mat of plants may be growing from the shore out into the water, resulting in a "floating bog" formation that encroaches on the open water. In time, the mat may cover the entire water surface unless it is destroyed by wind or some other natural force. As this occurs, rings of vegetation are also forming from the shore to the upland surrounding the water (Figure 15-8). Many examples of various stages of bog succession may be found, particularly in the northern part of the United States.

A succession of animals occurs concomitant with plant succession. Members of the grouse family illustrate this very well. Prairie grouse, such as the prairie chicken (*Tympanuchus cupido*), live on the prairie and do not tolerate dense canopies. If the shrub stage encroaches on the prairie, the habitat becomes more suitable for sharp-tailed grouse (*Pedioecetes phasianellus*). As a forest develops, particularly in the early stages of succession that include aspen trees, ruffed grouse (*Bonasa umbellus*) become more predominant. Finally, as the forest approaches a coniferous climax (the last stage in succession in any area, dependent on climatic condition), spruce grouse (*Canachites canadensis*) are natural members of the community (Figure 15-9). Similar trends in species distribution through successional stages can be observed for song birds, small rodents, rabbits and hares, and big game.



FIGURE 15-8. Successional stages from open water to the upland hardwood stand.

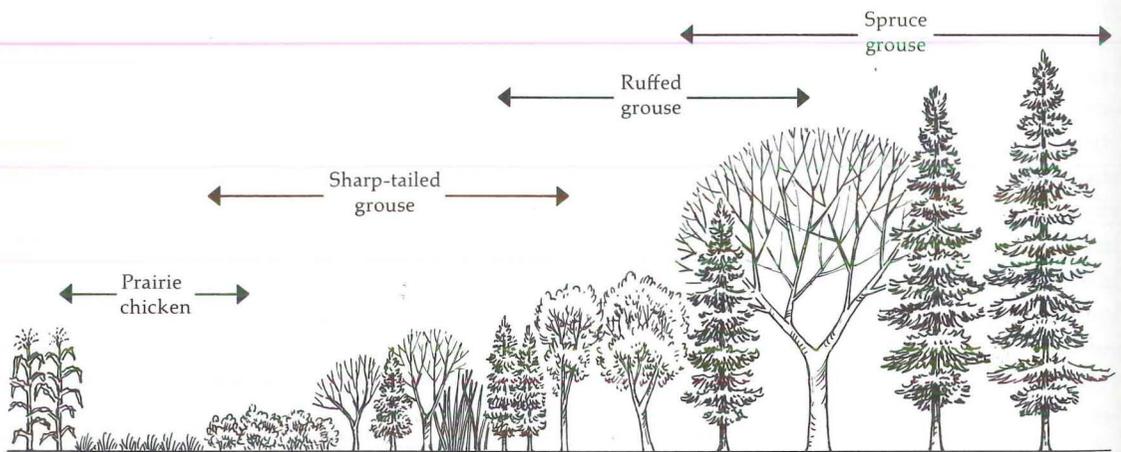


FIGURE 15-9. The relationship between prairie-to-forest succession and grouse species.

15-5 A PLANT-PRODUCTION MODEL

A GEOMETRIC MODEL. A geometric model of a plant is developed most easily if the plant is strikingly symmetrical. White pine (*Pinus strobus*) is such a plant. It is composed of a central axis with primary, secondary, tertiary, and quaternary

whorls (Figure 15-10). The growth and forage production of twelve trees from 2 to 19 years old is shown in Table 15-2. Summation of these data results in a theoretical tree representing the average of measurements taken at identical growing points on different trees and variation in time for each tree.

A geometric model such as this need not be precise if the intent is to test the effect of variation in forage production on the productivity of the consumer. Everyone knows that forage production varies; the critical question for the ecologist is "How does variation in plant productivity affect animal productivity?" The value of a descriptive geometric model is in its mathematical form, which is compatible with computer analysis. Pictures of trees cannot be programmed; tables per se cannot be programmed. It is necessary to find some means to describe the growth over time in order for it to be synthesized with animal productivity in a dynamic way.

FIGURE 15-10. The geometry of a white pine.

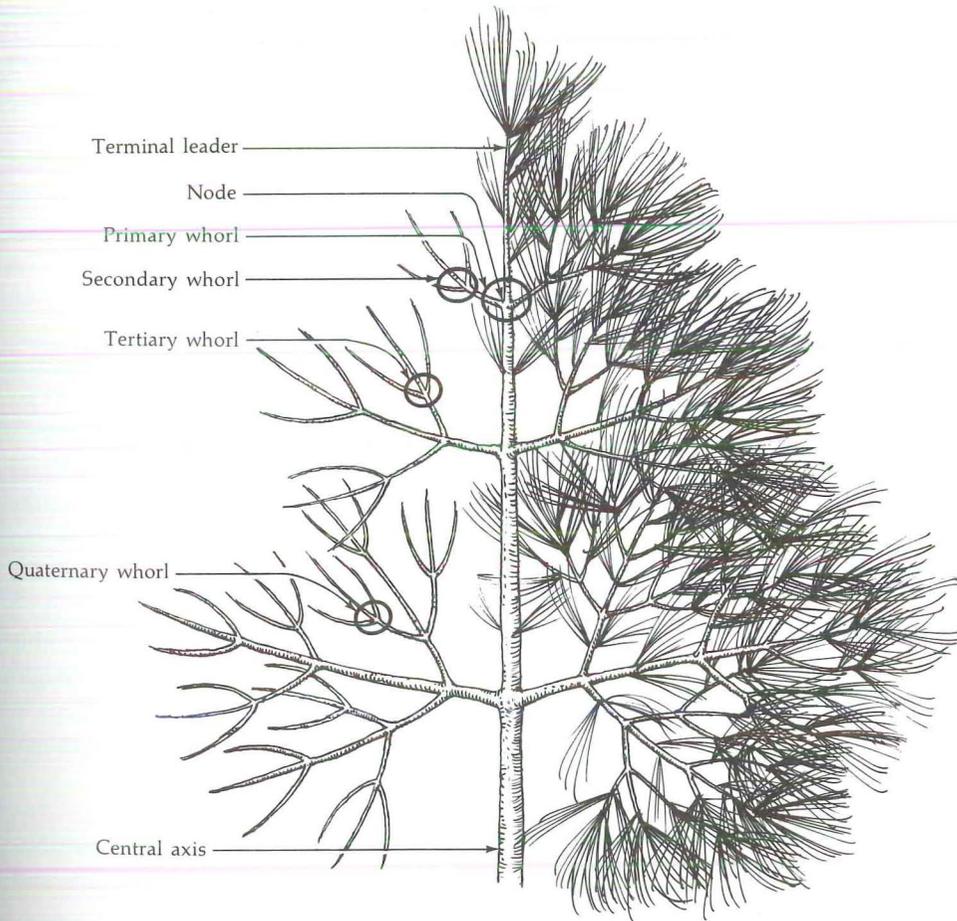


TABLE 15-2 GROWTH AND FORAGE PRODUCTION OF TWELVE WHITE PINE TREES FROM 2 TO 19 YEARS OF AGE

Growth in height	12.7 in yr ⁻¹	32.3 cm yr ⁻¹
Dry weight/length of current annual growth	0.44 g in ⁻¹	0.173 g cm ⁻¹
Total current annual growth in length	969 in yr ⁻¹	2461 cm yr ⁻¹
Total dry weight of current annual growth		425 g yr ⁻¹
Dry weight of current annual forage production (under 6 ft)		350 g yr ⁻¹

A tree, snow, and a primary consumer make a good combination for an analysis of the effect of interaction between chemical energy and forage, mechanical energy required for movement through snow by an animal, and the animal's energy metabolism. These relationships are depicted schematically in Figure 15-11; students are urged to expand on this model by using hypothetical components first, progressing towards greater realism as more data are assembled in successive models that describe the different functions.

The range ecologist and manager may be interested in only a specific aspect of the productivity of a tree or plant community. Deer and elk forage on the twigs of trees, usually the current annual growth (CAG), and it is the production of CAG that has the greatest short-term significance as a winter food supply. A mere estimation of range condition—excellent, good, or bad, for example—is not sufficient for a detailed analysis of animal-range relationships. A forage-production model composed of forage weight and chemical and nutritive characteristics of the forage for different consumers provides a much more realistic base for evaluating range quality.

The weight of CAG in relation to the number of CAG twigs of *Tilia americana* saplings is shown in Figure 15-12. This illustrates a technique for estimating the forage production on a given area, after which the nutritive characteristics can be related to forage production and, ultimately, to the net production of the consumer for maintenance and productive purposes.

The amount of CAG is dependent on many factors, of course, and it is desirable to determine the maximum production possible. The use of a number-weight equation for maximum production, followed by a series of forage reductions at set intervals permits the analysis of the effect of forage production on animal productivity.

A SEASONAL MODEL. A descriptive model of seasonal variations in the distribution of energy and matter is useful for depicting the phenology of plants and

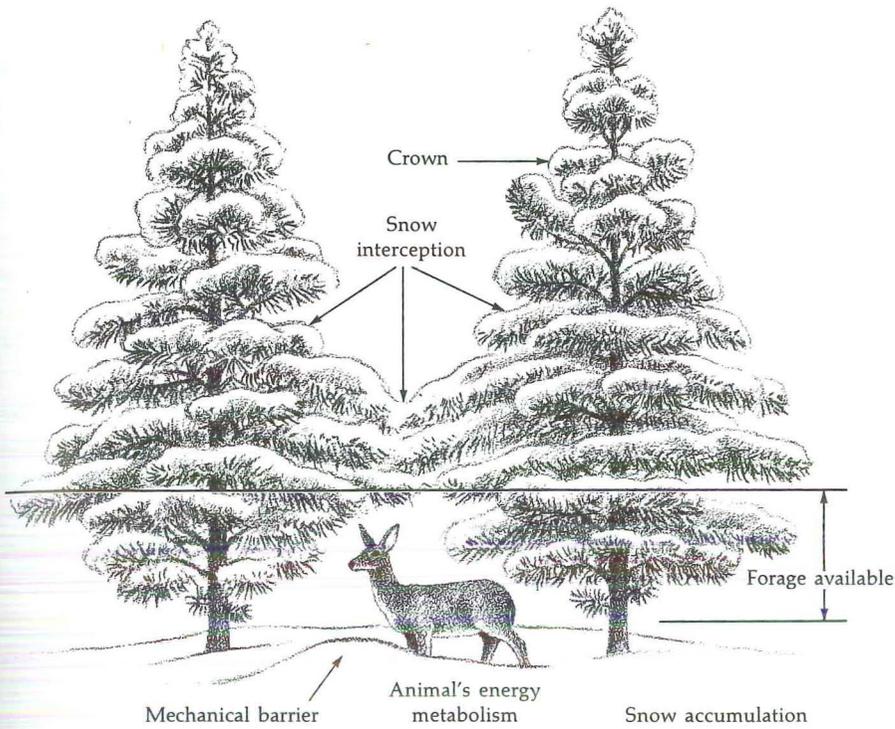


FIGURE 15-11. A simple representation of the interaction between an animal and snow, tree canopy, and forage.

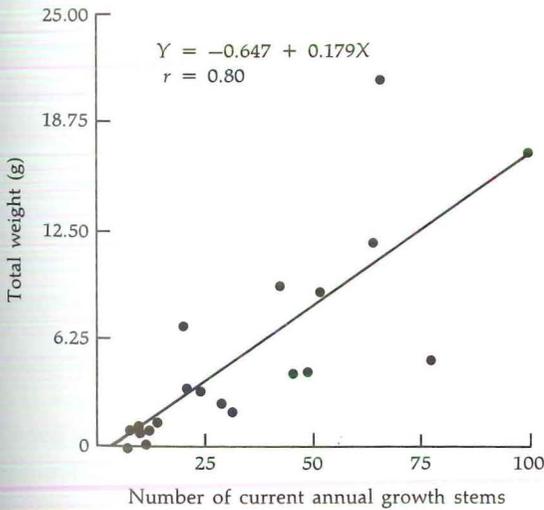
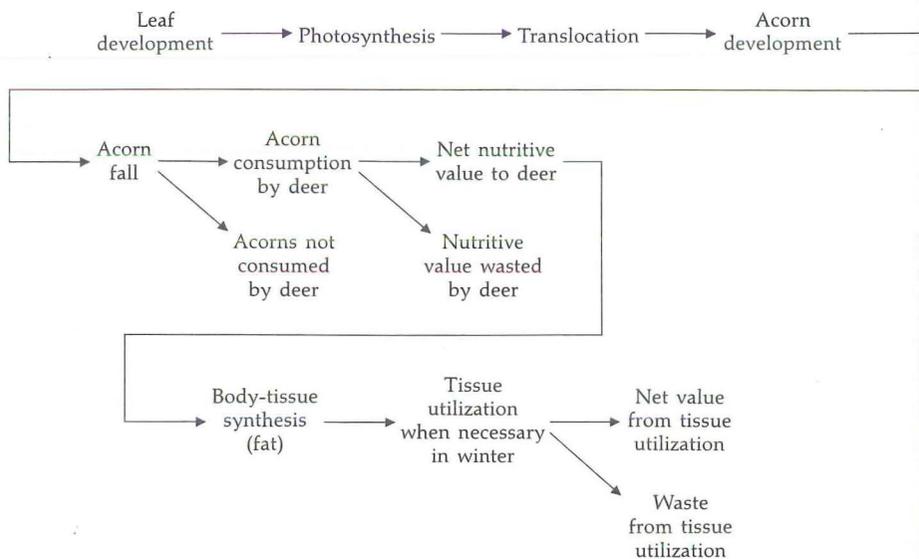


FIGURE 15-12. An illustration of a technique for predicting the weight of forage produced in relation to the number of current growth stems.

its relationship to primary consumers. The regression equation shown in Figure 15-12 could be a part of such a model. Another seasonal effect that could be considered is the growth, development, and fall of oak leaves and acorns. Leaf development must precede acorn development, since the leaves are sites of photosynthesis, which results in the formation of metabolites that can be translocated to the acorn for storage. The fall of leaves and acorns has a marked effect on the distribution of energy and matter. Thermal-energy relationships change owing to the differences in crown density. This was discussed in greater detail in Chapter 6. Chemical-energy distribution changes as the leaves and acorns fall. This results in an abundant supply of acorns for deer, and this may be important for fat deposition, which may be important for survival during the winter.

How is acorn production and fall utilized in a model that includes animal productivity? A working model can be developed first by using nondimensional numbers for acorn production, fall, and utilization by a primary consumer such as deer. A flow sheet is shown in Figure 15-13. Note the order in which the biological processes occur. It is not necessary to have complete information on each of these processes for useful dimensionless models for testing certain mechanisms. Select particular processes for the first model—acorn fall through tissue utilization in winter, for example. Use a linear regression equation to describe the rate of acorn fall (Y) over time (X). This takes the form of $Y = a + bX$. Suppose 100 units of acorns fell over 10 units of time. The specific equation is $Y = 0 + 10X$, where the limit of X equals 10. Suppose deer ate acorns at the rate of one half per unit time for a total of 50 units of time. The specific equation for that is $Y = 75 + \frac{1}{2}X$, where the limit of X is 50. This results in three known

FIGURE 15-13. A flow sheet for acorn production, fall, and utilization by deer.



values for the flow sheet: 100 units of acorns produced, 25 units eaten, and 75 units not eaten. If the net nutritive efficiency is 30%, there would be $25 \times .30$ units available for tissue synthesis, or 7.5, with 17.5 units being nutritive waste. Fat mobilization at a later date might be 80% efficient, making $.80 \times 7.5 = 6.0$ units available from tissue mobilization, with a waste of 1.5 units.

The total efficiency of this acorn-to-deer analysis is 6%, given the dimensionless units above. Keep in mind that all of the numbers used are arbitrarily selected to illustrate the mechanism of this kind of a calculation. Real numbers can be substituted to make the model more realistic. Many variations are possible within the simple framework used, including differences in acorn production, rate of fall, length of time the deer could consume acorns (this could depend on snow accumulation), and net nutritive value of acorns to the deer. Variations in any of these inputs will result in variations in the outputs. These variations could represent errors in measurements or natural variation in biological characteristics, or both.

This model is largely descriptive, especially if it is confined to acorn fall and tissue utilization, because there are no biologically dependent functions in the model. The model could be expanded to include dependent functions, such as photosynthesis = f (radiant energy, leaf surface area, leaf orientation, water absorption, transpiration . . .). The transition from a descriptive type of model to an analytical type can be exceedingly complex because so many more interactions, both direct and indirect, are included. Analytical models are conspicuously absent from the ecological literature, with a few exceptions.

One analytical model relating to plant productivity has recently appeared in *Science*. The model, developed by Dr. Edgar Lemon and his associates at the USDA Laboratory at Cornell University, illustrates the use of analytical data for the description of energy and matter interactions in a monotypic plant community.

A PHYSIOLOGICAL MODEL FOR PREDICTING NET PHOTOSYNTHESIS. The Soil-Plant-Atmosphere Model (SPAM) developed by Lemon, Stewart, and Shawcroft (1971) contains the basic mathematical format used to simulate a simple plant community—a corn field. The various submodels considered in SPAM are shown schematically in Figure 15-14. Note that the model is limited to the soil-surface boundary and the climate boundary surrounding the plant community. The gross structure of the plant community (crop submodel) and the fine structure at the site of photosynthesis (leaf submodel) are both considered. The former (crop submodel) has an effect on the distribution of energy and matter, including the geometric considerations of leaf angle and area distribution, light and wind distribution, and vertical diffusivity of energy and matter. The latter (leaf submodel) includes considerations of basic photosynthetic, metabolic, heat exchange and mass (water-vapor) transport from the leaves. Community behavior is predicted inasmuch as SPAM gives the vertical distribution of the activity of various community processes and vertical fluxes. Thus the vertical radiant-energy flux,

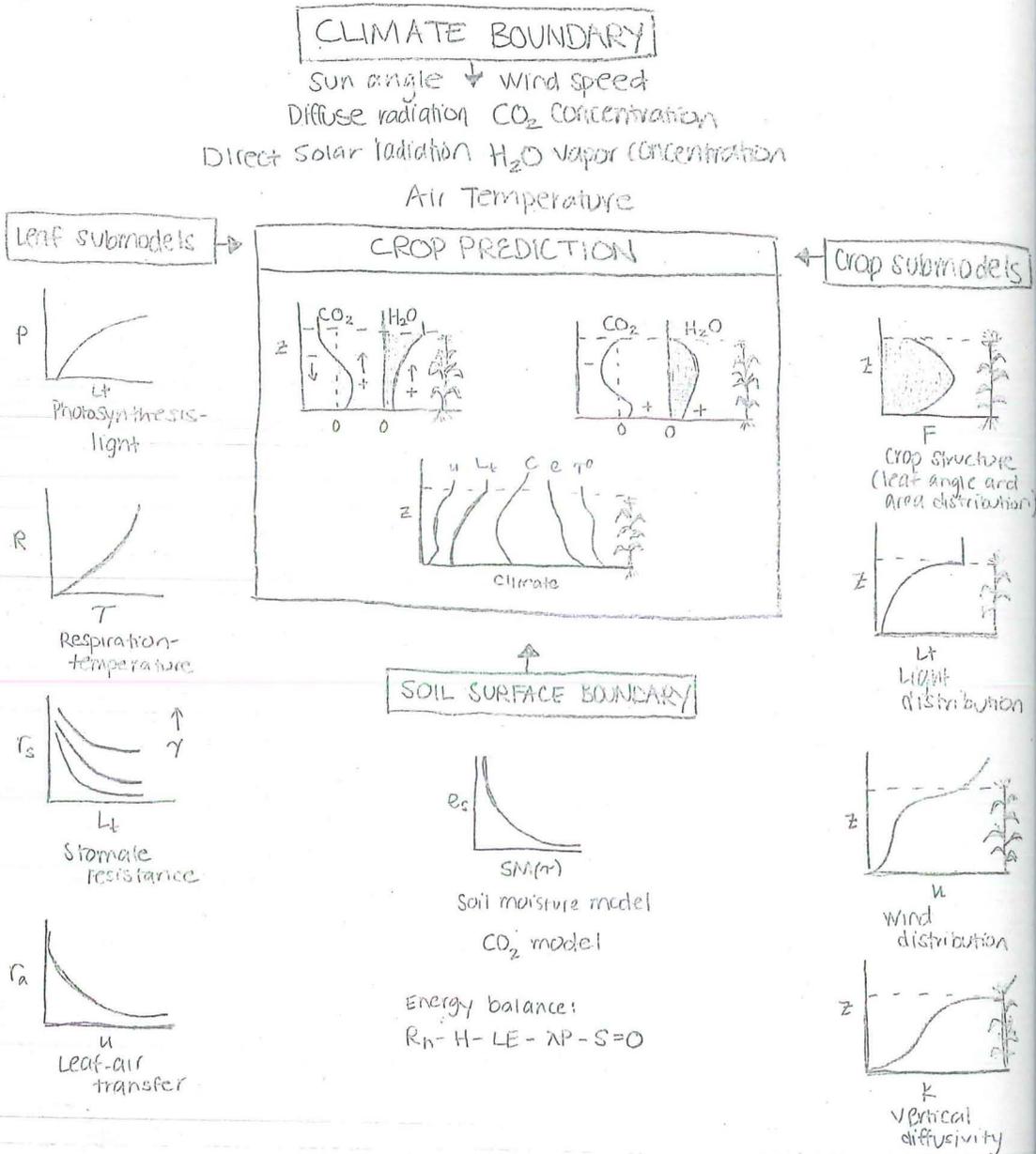
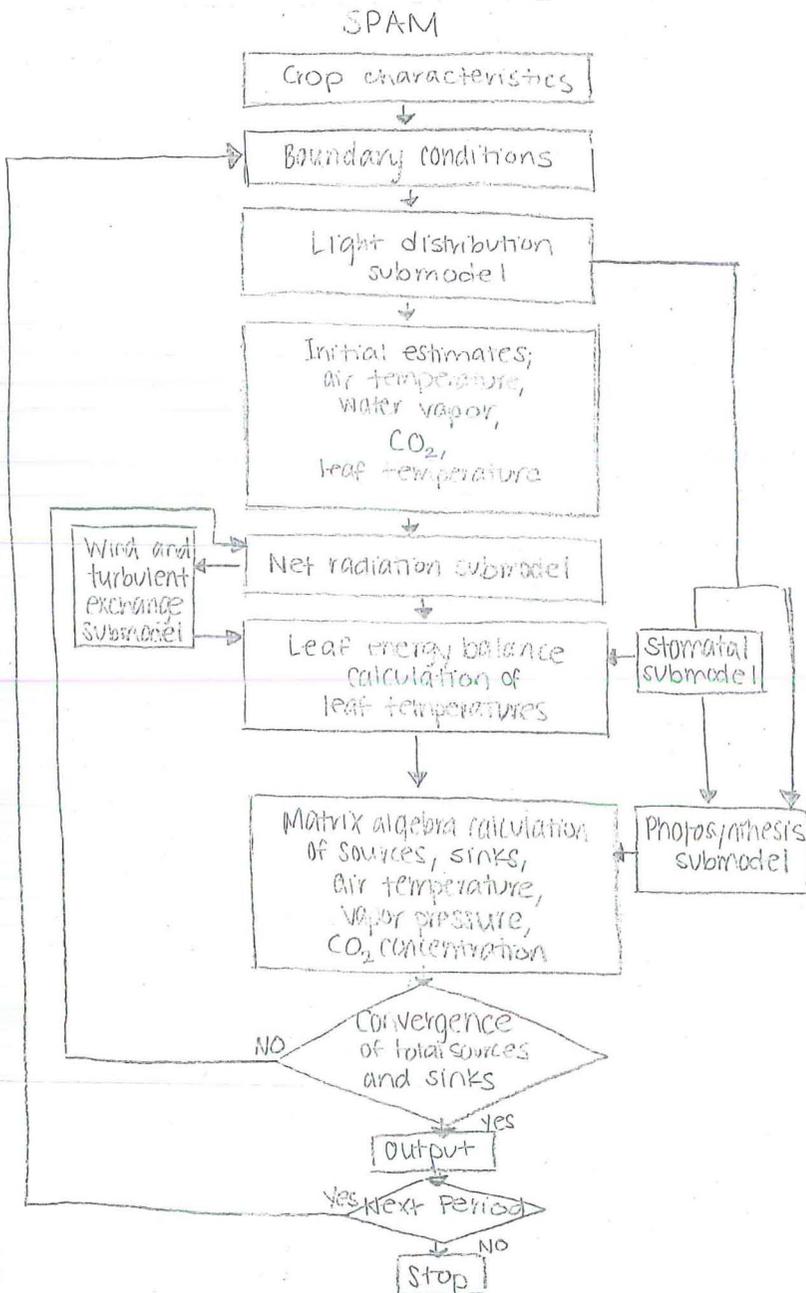


FIGURE 15-14. Schematic summary of a mathematical soil-plant-atmosphere model (SPAM), giving required inputs, submodels, and representative daytime predictions of climate and community activity (that is, water vapor and carbon dioxide exchange). (Adapted from "The Sun's Work in a Cornfield" by E. Lemon, W. Stewart, and R. W. Shawcroft.)

FIGURE 15-15. The general procedure of SPAM, given as a flow diagram. (Adapted from "The Sun's Work in a Cornfield" by E. Lemon, W. Stewart, and R. W. Shawcroft.)



air-temperature profile, wind profile, and profile describing water-vapor concentrations are used in predicting evaporation from the leaf surfaces at various heights. Similar kinds of predictions are made as other factors are considered in the interactions between energy and matter. A flow diagram with these relationships is shown in Figure 15-15.

The importance of these interactions is recognized by Lemon, Stewart, and Shawcroft: "It is obvious that solving the equation of any given part of SPAM is dependent on solving the equation of some other part." Once these interactions can be described, field tests can proceed to find the strengths and weaknesses of the model.

Lemon, Stewart, and Shawcroft have tested their model and find that some relationships were predicted quite accurately whereas others were much less so. The cause of discrepancies between measured values and predicted values must be determined by the analytical ecologist. The authors of SPAM suspect that classical fluid dynamic theory for turbulent boundary flow (such as wind in a plant canopy) is not applicable to tall vegetation that is porous and flexible. Work at the BioThermal Laboratory suggests that deer hair, too, has unique characteristics that affect the transfer of heat energy.

One consideration made possible with SPAM is that of carbon dioxide fertilization on a field scale. Green house fertilization with carbon dioxide has proved successful, but many more variables exist in the field that might reduce the efficiency of this practice. Simulations of different levels of carbon dioxide fertilization showed that high rates of release did not affect the concentration in the photosynthetically active part of the canopy. This is due to the vigorous diffusion processes in the atmosphere. Thus it appears that carbon dioxide fertilization is not a feasible solution for increasing yield. It was concluded, however, that wind plays such an important part in regulating the natural supply of carbon dioxide that the idea of designing crop communities to enhance air flow has merit.

Community structure was shown to have the greatest effect on productivity. This suggests that selective breeding might improve leaf angle, for example, resulting in a higher photosynthetic efficiency. The authors point out, however, that no one structure can be "ideal," but rather varies with climate, crop, latitude, and time of year.

It is interesting that a mathematical model based on extensive field experiments should result in such strong emphasis on community structure. Assuming that this is the case for natural plant communities, as well as a corn community, the student interested in plant ecology has a tremendous opportunity to analyse the structure of natural communities on the basis of energy, matter, and time interactions. This would result in a significant increase in our understanding of plant productivity in natural systems. The modeling and simulation approach requires the use of computer analyses, of course, along with several types of field instrumentation that may not have been used very frequently by plant ecologists in the past. Both gross and fine plant community structures have to be studied in

relation to cellular physiology. These new dimensions only serve to add excitement to the field of ecology; indeed, many conclusions in the literature can be reevaluated with new insights that often lead to interesting new conclusions.

15-6 PERTURBATIONS

OVERGRAZING. Plant communities on the range are dynamic biological units that respond not only to forces imposed on them by natural events but also to the additional pressures of grazing by both wild and domestic animals. The foraging activities of domestic and wild animals cause changes in the floral composition of a plant community. Stoddart and Smith (1955) review the terminology associated with changes in the species composition of the range community, including *climax decreaseers*, *climax increaseers*, and *invaders*. Species that become less abundant under heavy grazing are climax decreaseers; they are likely to be the species most preferred by the grazing animals. Those species that become more abundant under heavy grazing are climax increaseers; they are the species least preferred by the grazing animal. Invaders are species that are originally not present but which become established in the grazed area.

In general, overgrazing reduces the number of native (prior to grazing) plants on an area, with an increase in the number of weeds (unpalatable forbs) in the community. Shrubs can become abundant, too, often resulting in a plant community that is resistant to the effects of grazing because the energy and matter in the plants is largely unavailable to the primary consumers. It is a kind of dynamic nutrient filtration process that leaves only the non-nutrients in the system.

FIRE. Fire is often thought of as a disaster, and indeed it is just that to the forester intent on harvesting mature trees for lumber. The ecological significance of fire is relative to the organisms under consideration, however. Thus a fire in a mature forest is bad for spruce grouse but good for ruffed grouse, bad for caribou but good for deer. The effect of fire is best evaluated within a framework of the successional stages desired. The prairie, a mixture of grasses and forbs, is maintained only when fire or some other perturbation prevents invasion by shrubs. Virgin prairie near Kensington, Minnesota (Douglas County, west-central part of the state), is being invaded by *Symphoricarpus occidentalis*, a low-growing shrub, because fire has been eliminated in one small area and because of overgrazing on an adjacent pasture. *Quercus macrocarpa* (Burr oak), a fire resistant tree, is found in some uncultivated areas along lakes and marshes, with sugar maple (*Acer saccharum*) and basswood found in areas protected from fire by the lakes. One stand of trees on a peninsula extending northward into a shallow lake contains about 80% sugar maple (Moen 1964). This sugar maple community would very likely not be present if the water had not protected it from fire, prior to settlement in that area.

Many other perturbations can occur, including floods, tornadoes, hurricanes, hail storms, and, over long periods of time, glaciation. All of these conditions may result in fairly long-term effects, and although they are interesting from an ecological point of view, they may not be the most important factors in the short-term population fluctuations that cause concern among sportsmen, legislators, and other members of the public whose interests and activities are geared to the present. Thus the resource analyst and manager must balance the theoretical long-term effects with the more immediate, short-term considerations, keeping in mind that in each case certain fundamental principles and physical laws affect the distribution of matter and energy in the ecosystem.

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