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THE CARBON BALANCE OF PLANTS

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INTRODUCTION

There has been considerable recent interest in the assessment of the energy allocation of plants (38, 50, 52). It is likely that through a quantitative understanding of how different plants gain and allocate their resources it will be possible to make predictions as to their success in any given physical environment in combination with any competitor and predator. We are still far from this reality. However, as a contribution toward this goal, this review seeks to gather the available information on the various evolutionary strategies which plants have evolved to gain energy and to account for the numerous ways in which this energy is utilized to meet the demands of the environment, as well as to successfully produce progeny.

To date, studies which have considered allocation have generally been at a rather gross level—e.g., reproductive versus nonreproductive (38), roots versus shoots (117), and photosynthetic versus nonphotosynthetic tissue (86). A study by Harper & Ogden (52) has attempted, however, to account in somewhat more detail for the various sources of energy allocation.

To account in more detail for energy gain in allocation and for its eventual loss through a variety of routes, the approach that will be used here is the capture of carbon by plants and its subsequent diversion into various products which perform a multiplicity of functions. Carbon is the vehicle by which organisms store and transfer energy by chemical binding. This device enables the utilization of a large reservoir of physiological and ecological data into a single coherent body. However, it becomes rather clear that the total information required for any given plant simply does not exist. Thus, this review unfortunately can represent only a composite picture of the generalized routes of carbon movement in plants. It does, however, call attention to the continual partitioning of resources and the multiplicity of carbon pathways. Emphasis is placed on the modes of capture of carbon. Hopefully, this analysis will stimulate studies which will provide, for a given series of biotypes, the total information on carbon gain, use, and loss, so that quantitative models can be derived relating these to short- and long-term environmental influences.

CARBON GAIN

Physiological and biochemical basis.—The principal path of carbon from the atmosphere to the plant is by diffusion of carbon dioxide through leaf stomata into the leaf intracellular spaces and then through the walls of the mesophyll cells to the sites of fixation (carboxylation). The latter transport is in the liquid phase. According to the commonly used electrical analogy, the resistance to transport is composed of two components—the stomatal (R_s) and the mesophyll (R_m) resistances. The mesophyll resistance is determined by liquid diffusion and the efficiency of carboxylation. It has not been possible to distinguish between these physical and biochemical components.

Since the cells of the leaf mesophyll are fully hydrated and their wall surfaces saturated, water will diffuse outwards to the atmosphere via these pores when stomates are open. Water has a shorter diffusional pathway than CO_2 since it does not include a mesophyll resistance. When stomates partially close, the resistance to water transport is affected proportionally to a greater degree than CO_2 .

A consequence of having low resistance pathways for carbon from the atmosphere to the cellular trapping sites is that equally low resistance pathways for the outward diffusion of water are created. These interrelationships result in the evolutionary dilemma of how to enhance carbon gain without excessive water loss. It appears that the physical structures which plants have evolved to trap and fix carbon most often represent a best-possible compromise between efficiency of carbon gain and of preventing water loss. This optimization process will, of course, vary considerably depending upon the relative abundance of water in the habitat. There is one additional dimension to this compromise in that transpirational water loss under certain environmental conditions results in a substantial leaf cooling.

Gates (39) has extensively examined the interrelationships among environment, leaf resistance and dimensions, and leaf temperature. He has shown, for example, that when large leaves restrict water loss under a high radiation load, their temperatures can considerably exceed ambient temperature. The smaller the leaf, under these conditions, the more the leaf temperature will approach air temperature. This relationship illustrates the adaptive advantage of small leaf size in desert evergreen plants.

A survey of the rates of photosynthesis of diverse groups of plants (Table 1) indicates considerable variability in carbon-gaining capacity. A certain amount of this variation has a biochemical basis. There are three distinctive photosynthetic biochemical pathways in higher plants. The pathway which characterizes the majority of the world's plants is termed *the Calvin cycle* (C_3 plants). Plants which have this biochemical pathway differ in their initial photosynthetic products from plants possessing either the C_4 -dicarboxylic acid cycle (C_4 plants) or plants with crassulacean acid metabolism (CAM). C_4 -type photosynthesis is found in a series of unrelated genera and families, including

TABLE 1. Normal maximum photosynthetic values of plants under conditions of light saturation, optimal temperature, water, and normal CO₂ concentration*

	CO ₂ uptake mg CO ₂ dm ⁻² hr ⁻¹
Herbaceous plants	
Cultivated plants with Calvin cycle	20-35
Plants with C ₄ -dicarboxylic acid cycle	30-70
Herbs from sunny habitats	15-60
Herbs from shaded habitats	4-16
Succulents	4-12
Woody plants	
Deciduous broad-leaved plants	10-25
Evergreen broad-leaved trees	10-16
Ericaceae and semi-arid sclerophyllous shrubs	4-12
Evergreen conifers	4-12

* From Sestak, Catsky & Jarvis (113).

grasses of tropical origin as well as a number of dicotyledonous families, such as the Chenopodiaceae, Amaranthaceae, and Zygophyllaceae, characteristic of hot, arid regions (24). Plants with C₃ and C₄ photosynthesis may occur together in the same genus (10, 115).

C₄ plants differ biochemically and physiologically from C₃ plants in a number of features, including the absence of photorespiration, the lack of oxygen inhibition, and the greater infinity of their initial carboxylating enzyme for CO₂. Some of the consequences of these features are that C₄ plants have a higher temperature optimum of photosynthesis, a high light saturation value, and higher absolute rates. Further, they expend less water per unit of carbon fixed (11, 23). As an example of the differential water use efficiency of different plants with different photosynthetic pathways, Shantz & Piemeisel (114) found in a study of herbaceous and weedy crop species that C₃ species expended between 380 and 900 g of water to produce a single gram of dry matter, whereas C₄ species utilized 250 to 350 g of water per gram of dry matter. McGinnies & Arnold (83) found similar differences between winter (C₃) and summer (presumably C₄) desert annuals in Arizona. Plants with CAM have even greater water-use efficiencies, with values in the realm of 50 g of water per gram dry matter (63, 93).

Slatyer (115), in a study of C₃ and C₄ species of the genus *Atriplex*, attributes the greater water-use efficiency of plants of the latter species to their relatively lower mesophyll and higher stomatal resistance. C₃ and C₄ plants with equal transpiration rates (equal stomatal resistances) will have dissimilar water-use efficiencies, which favor the C₄ type because of the normally higher photosynthetic rate of the former (23).

Plants with crassulacean acid metabolism are restricted to succulent species. However, they represent such diverse families as the monocotyledonous bromeliads and the dicotyledonous euphorbs. This type of metabolism has evidently evolved polyphyletically, as has the C_4 pathway. Both evidently have arisen from the more primitive Calvin cycle (32).

CAM is similar to C_4 photosynthesis in that both pathways utilize the same initial carboxylating enzyme and have organic acids as their initial photosynthetic products. The important difference is that CAM is not light dependent. It can use stored carbohydrate as the initial carboxylation substrate, rather than substrates directly generated in the light through photosynthesis (120). This metabolic feature has great ecological implications. CAM plants can open their stomata at night as well as fix carbon in the dark. Further, even at their widest aperture the stomata have a greater resistance to water loss than other types of plants (93, 121).

CAM plants may also fix carbon in the light through the Calvin pathway. Only in environments where there is a large diurnal temperature fluctuation with low night temperatures will CAM predominate (120).

The physiological differences in the mechanism of carbon gaining of the three types of photosynthesis have obvious implications in the distribution and competitive capacity of these plants.

C_3 plants have a large range of temperature optima of photosynthesis—extending from 10°C in the case of an alpine psychrophile (100) to 35°C for an evergreen arid-land tree (54). The great bulk of C_3 plants evidently have their thermal optimum in the range of 15–25°C (75). In contrast, C_4 species generally attain temperatures of their thermal-optimum photosynthesis between 30 and 45°C (55). The highest thermal optimum measured so far on a C_4 plant was 48°C (13).

There is some question whether the difference in photosynthetic temperature response between plants with the different pathways is due to dissimilarities in their carboxylating enzymes (100) or to quantitative dissimilarities in the component steps of photosynthesis (12).

One possible reason why C_4 plants evidently do poorly in low temperatures is that photosynthates will accumulate in the leaves rather than being translocated, as normally occurs under warmer night temperatures (56). Changes in the chlorophyll membrane structures may also be involved in these rate reductions (100).

The enzyme systems of C_4 plants are more heat-stable than those of the C_3 plants which have been studied. In contrast, the C_3 enzymes of cold-adapted plants are thermostable at low temperatures (100). These results indicate that enzyme systems can only operate within a given thermal range for maximum efficiency.

Both C_3 and C_4 plants have the capacity to modify their photosynthetic response to temperature within certain limits (91, 100), dependent on growth environment. Such shifts in the temperature of optimum photosynthesis do not normally exceed 5 or 10°C.

The consideration of the above physiological attributes of plants possessing the different photosynthetic systems would lead one to predict that C_4 plants would be found in hot, bright environments where water may be limiting. This is, indeed, where the natural distributions of these plants are centered. In the United States they are well represented in the desert regions as well as on the short-grass prairie. Where they occur together with C_3 plants their activities are normally displaced seasonally. For example, in the Mohave Desert the winter annuals are C_3 plants, whereas most of the summer annuals are C_4 plants (Harrison, personal communication).

Many of our crop plants have the C_4 pathway (corn, sorghum, and sugarcane), as do a large percentage of the world's most serious weeds (14). According to Black et al (14), it is the capacity of C_4 plants to fix carbon at such high rates which makes them such high-yielding crops or successful weeds.

CAM plants are found predominantly, as also would be predicted, in open, water-limited habitats. Their capacity to keep their stomata closed during the day, when there are high evaporative demands in desert regions, and to fix carbon at night are key adaptive features. However, their very low carbon-gaining capacity puts them at a competitive disadvantage in closed communities, from which they are generally excluded (90). Further, they may be excluded from areas of very high nighttime temperature. For example, Percy et al (97) suggest that they are absent from the floor of Death Valley, California, for this reason.

The physiological and biochemical features described above indicate the basis for the differences in photosynthetic rate between most of the various types of herbaceous plants given in Table 1. The difference in rate between the shade and sun herbs is an example of how plants with a single photosynthetic pathway (C_3) can be genetically and physiologically modified to adapt to dissimilar environments.

Shade plants have a lower carboxylating enzyme content than do sun plants, which could explain why their photosynthetic rate is lower than that of sun plants under similar conditions (8). Races of a single species originating from exposed habitats have a genetically determined higher capacity to produce this enzyme than do shade races (9). Since a major portion of the leaf protein is carboxydismutase (8), there can be a considerable conservation of carbon by making less of this enzyme in light-limited habitats, where it would be of little advantage.

Data are presently lacking to explain the large differences in photosynthetic capacities found between the various life forms of woody plants (Table 1). It appears, however, that evergreen plants have higher minimum resistances to gas exchange than do herbaceous plants. For example, the minimum resistance to water exchange of a sun herb is less than 0.5 sec cm^{-1} (57); and that of a pine, about 9 sec cm^{-1} (129). Broad-leaf evergreens have been measured with minimum stomatal resistances in the region of 2 to 5 sec cm^{-1} (27, 92).

Few comparative studies on photosynthetic enzymes have been made on evergreen species. One of the reasons for this is that it is often difficult to isolate enzymes in such material because of the presence of large amounts of polyphenols.

Morphological strategies.—The considerations discussed so far have been mainly concerned with the physiological variability which can influence the carbon-gaining capacity of plants. What will be discussed subsequently is how plants can influence their photosynthetic gain by morphological and behavioral modifications.

Morrow (92) has provided an example of how two evergreen plants with almost identical physiological attributes utilize dissimilar morphological strategies to adapt to their somewhat different native environments. (The magnitude of the photosynthetic rates attained and their temperature responses are similar, and both are able to tolerate low levels of water potential.) One species occurs in more northerly, and consequently cooler, habitats with shorter-duration droughts. This species has larger, generally horizontally inclined leaves which tend to remain above ambient temperature because of high radiant flux and low convective heat transfer. The larger leaves thus extend the period of potential carbon gain to an extent which outweighs the resultant potential water loss. The second species occurs in habitats with longer periods of drought where temperatures are warmer and often near the optimal for photosynthesis. Their smaller and more vertically oriented leaves maximize the periods when temperatures are optimum for photosynthesis while creating a more favorable leaf moisture balance. Further, these plants have a deeper root system which also reduces the period of drought and hence extends the carbon gain.

Mooney & Dunn (90) have viewed the morphological variability of woody plants along aridity gradients in terms of optimization of carbon-gaining capacity. They found that, progressing along a gradient of increasing drought duration in mediterranean climatic regions, the predominant plant form shifts from a deep-rooted evergreen shrub or tree to a shallow-rooted drought-deciduous shrub. The evergreens have a low inherent photosynthetic capacity, probably related to features which enable them to maintain leaves during the drought period, but a long period of potential carbon gain. The drought-deciduous shrubs, on the other hand, have no mechanisms for restricting water loss, and thus have a high capacity to fix carbon during the limited nondrought period.

The physiological potential of the leaf only accounts for a portion of the total carbon-gaining capacity of a plant. The leaf surface of the plant per unit of ground surface (leaf area index, or LAI) is also an important variable. Theoretically, in order to attain maximum production, a plant would display as many leaves as possible within a unit ground area to the rays of the incoming radiation. Of course, the uppermost leaves intercept the greatest amount of light and the lower ones proportionally less. The optimum leaf area index of a plant is the maximum LAI possible where all leaves can still make a

positive contribution to the carbon gain of the plant (22). As a plant grows, new leaves are produced which reduce the light reaching the lower leaves. The photosynthetic gain of these lower leaves may fall below their maintenance costs and they are usually lost. There is, however, a compensation for the lower light environment in that the maintenance costs of the shade leaves are lower (78, 122).

The leaf area indices of natural communities vary from 4 to 7 for herbaceous communities (85), 4 to 6 for deciduous forests (132), 7 to 8 in temperate evergreen forests, to over 12 in tropical forests (67). In natural communities high LAI's correlate with high annual productivity (67). In crop plants, LAI can be increased by dense planting. Production will increase with an increased LAI up to the optimum leaf area, which usually averages about 5, and will decline with further increases (22).

Thus, it is apparent that the annual productivity of a plant is set in part by the LAI it can maintain, which in turn is set by the growth strategy of the plant (deciduous or evergreen herb, shrub, or tree). The leaf productivity must not only balance the maintenance and construction costs of the photosynthetic system, but also the entire shoot and root system.

As structural respiratory tissue accumulates in plants, the same leaf area will result in less and less annual production and proportionally more of the carbon being channeled into maintenance (22).

It takes a certain length of time for a plant to attain its optimal leaf area during establishment or during the annual regrowth cycle of herbs or deciduous plants. The rapidity of the development of the optimal system is of course an important competitive feature of plants and may explain the large commitment of carbon to seed reserves or to storage reserves utilized in regrowth.

The leaves of most plants are not all horizontal and, in some plants, none are. With varying leaf angles the incoming radiation can penetrate deeper into the canopy and a higher LAI can be maintained since the lower leaves can be kept above the light compensation point. The relationship between the light environment and the optimal leaf arrangement is complex. Duncan (26) has stated, "For any particular position of the sun there is one optimal arrangement of leaves. For a whole day, when we assume leaves in a fixed position, the optimal arrangement is a compromise that takes into account all of the differences in solar position and brightness and of skylight brightness. For any change of the solar angle, such as that which resulted from the change in latitude, there is a change in the optimal leaf arrangement. A climate where a sunny morning and a cloudy afternoon were usual would call for different leaf arrangements."

Models have been developed to predict the influence of leaf arrangement on canopy photosynthesis (25, 26, 74). These models have utilized many simplifying assumptions, such as that the leaves of the canopy are random within a plane. However, they have provided useful insights into the influence of varying morphological strategies of plants and production. The model of Duncan (26) predicts that the more vertical the leaves, the higher the LAI

required for maximum photosynthesis. Models accounting for the influence of clustering in the leaf canopy are now being developed (67).

Stem photosynthesis.—The stem surfaces of woody plants may be equivalent to one half or more of the leaf surface (132). Thus, in deciduous species there is the possibility of utilizing these surfaces for a photosynthetic apparatus which would operate under somewhat more severe conditions than the leaves can tolerate, but at a reduced efficiency of gas exchange. In order for such a system to operate, the species must have a minimal corky or other protective tissue that would mask the chlorophyllous cells. Young leafless twigs with little corky tissue, which constitute a sizable fraction of the stem surface of the Sonoran Desert tree *Cercidium floridum*, were found by Adams & Strain (1) to be photosynthetically highly active. They calculated that on an annual basis stem photosynthesis contributed more than 40% of the total photosynthate gained by the plant. These highly branched trees have total stem surface areas which somewhat exceed the leaf surface area.

Bark photosynthesis also has been found in *Populus tremuloides*, a deciduous tree of the cold-temperate region (116).

Massive bark peeling is characteristic of many green trunk drought-deciduous trees of the arid and tropical and subtropical regions (e.g., *Bursera* spp.). The significance of this feature in relation to maintaining a photosynthetically active bark surface has not been investigated. As Adams and Strain point out, however, it is in areas where temperatures are not low during the leafless period that bark photosynthesis can contribute most significantly.

In summary, it would appear that bark photosynthesis would be effective only in deciduous species growing in certain types of climates. The carbon gained in this manner must offset the loss in protection given to the cambial region by not developing protective corky coverings.

MOVEMENT OF CARBON

Porter (101) has recently reviewed the information on the fate of carbon which is fixed in leaves. Developing leaves import carbon from older leaves of the plant, as well as fixing carbon in place. During the developmental period the carbon is utilized primarily for the synthesis of proteins and polysaccharides.

When the leaf attains about half size, it will for a short time simultaneously import and export carbon. Subsequently, the leaf will supply all of its own carbon requirements, as well as exporting a portion to other parts of the plant. Carbon is translocated almost entirely in the form of sucrose. The pathway of export is from the chlorophyllous cells to the leaf vein endings and then to the phloem and to various points of deposition. A portion of the carbon that is fixed in the leaf may be exported directly and rapidly as sucrose without a temporary conversion to starch. Leaves which are near the apex of the plant export primarily upwards, and those lower down, to the root.

Porter (101) gives a generalized carbon balance for a plant based on information from radioactive tracer studies. He estimates that 40% of the total carbon that is fixed remains in the fixation leaves; 10% is exported from mature to developing leaves; 25% goes to the stem, and the remainder to the root. Older leaves apparently cannot import carbon from younger leaves and thus are prevented from becoming parasitic when they are below the compensation point (78).

The above patterns, of course, would vary, depending upon the life form of the plant and the stage of development. For example, in annual grasses proportionally more carbon goes into the stem than in perennial grasses, where larger portions go to the roots and tillers (109). In evergreen trees proportionally greater amounts of carbon may remain in the mature leaf, since they serve as important reserve centers for supply during shoot growth periods (21).

The carbon that is supplied to fruits may be generated in small part by photosynthesis of the reproductive parts themselves. For example, outer cell layers of the apple fruit photosynthesize, but only at one tenth the rate of leaves. In citrus fruits photosynthesis can balance respiration losses (15).

The largest part of the carbon utilized in the development of flowers and fruit comes from the leaves nearest to them. In apple leaves, the photosynthesis of leaves close to the fruit is higher than that of other leaves. This has been attributed to the rapid shipment of photosynthetic products to the fruit, thus preventing product accumulation which can depress photosynthesis (64).

Studies on wheat (18) have shown that the carbon in the grain is derived mostly from the leaflike fruit covering (glumes) and the uppermost leaf (flag leaf). In these studies it was found that 80% of the carbon fixed by the glumes went to the grain, as did 50% of the carbon fixed by the flag leaf. In situations where carbon gain was limited (low-light environment) there was division of assimilates between stem and grain.

These studies have important implications regarding the total structure of the plant. One would deduce that in a noncompetitive evolutionary environment plants would need substantially fewer leaves to attain reproductive success. The implication is that plants devote large quantities of carbon to attaining or maintaining competitive advantage.

To this point the fixation of carbon and immediate transport as sucrose has been considered. Even this short-term transport pattern will vary considerably, depending upon the seasonal demands of the plant. For example, in certain evergreen pines, leaves principally supply the growing roots during the fall, and the growing shoots during the spring (112).

METABOLISM OF CARBON AND FUNCTION OF SELECTED PRODUCTS

The general path of carbon through fixation and hence to the metabolism of building blocks and various products will now be considered (Figure 1). For simplicity, only the central pathways and products are indicated. The

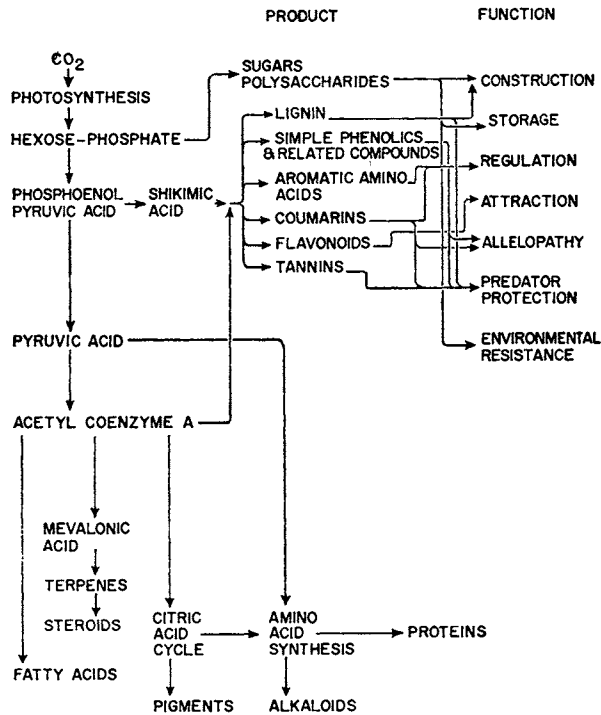


FIGURE 1. Selected metabolic pathways of carbon. The shikimic acid pathway illustrates the diverse functional uses of carbon products which arise from a single major metabolic pathway.

functional uses of carbon are also shown for the carbohydrates, as well as the products of the shikimic acid pathway.

Carbon dioxide is reduced through photosynthesis and hence elaborated into sugar phosphates. These simple sugars form the basic building blocks for all carbohydrates and carbohydrate derivatives. Most of these products are used either for storage (starch and such oligosaccharides as sucrose) or for the construction of cell walls (various polysaccharides, especially cellulose, as well as cellulose and peptic substances). Carbohydrates apparently may also be used directly for environmental protection. For example, an increase in sugar concentration usually accompanies the induction of cold hardiness in herbaceous plants as well as trees (73).

Through glycolysis, phosphoenol-pyruvic acid (PEP) is formed from sugar phosphates, which subsequently is transformed to pyruvic acid and hence to a myriad of organic compounds, including proteins and lipids. Instead, PEP may become directly involved in the shikimic acid pathway, which leads to a variety of phenolic (secondary) compounds.

An indication of the rather recent development of much of our knowl-

edge of secondary plant chemistry is that until about 1950 shikimic acid was only known from a single Asian plant (41). The explosive development of our knowledge of the chemistry of these products (41) has been accompanied by an equally impressive development of our knowledge about the biological significance of these products (30, 61, 76, 131, 133).

The phenolics will be utilized as an illustration of the partitioning of carbon into the various products for diverse functions of the plant. A brief summary of the functions of some of these compounds follows with, wherever possible, an indication of the quantities of these compounds which are involved.

Levins (76) has provided a comprehensive review of the role of phenolics in predator protection, but with a focus on host-fungal parasite relationships. Levins' major thesis is that these compounds are primarily a defense against predation by microorganisms and animals. He cites numerous examples of the protective nature of various phenolics, including simple phenols, tannins, phenylpropane derivatives, phenolic quinones, etc. An important difference in the protective operation of these compounds is that in some plants pools of phenolics are maintained in sufficient quantities to inhibit predators. Levin terms this mode of protection *constitutive resistance* and notes that this operates primarily against animal predators.

In the second case, which apparently is utilized primarily as a defense against microorganisms, the defense products are present at low levels prior to infection but increase greatly in amount after infection. In some cases, the defense products are not synthesized at all until after infection. These are termed *phytoalexins* (107).

In terms of carbon allocation for protection, the latter strategy is considerably more efficient; however, it probably can only be used against organisms in which there is a sufficient time lag between first infection and the build-up of lethal levels, during which the host can respond biochemically to the infection. No such lag time exists, of course, in the attack of many animal predators; thus, constant pools must be maintained for this function.

Data on the quantities of these pools and on their exact mode of action are rare. Several examples from the various types of phenolics are given in order to give a basis for assessing the carbon demands of these various functions.

Not all phenolics are involved in predator protection alone, but may also be related to regulatory or construction functions. For example, indole-acetic acid (IAA), an important growth regulator, is formed via the shikimic pathway from the aromatic amino acid, tryptophan. IAA, as is characteristic of all hormones, is present in minute amounts in plant tissue. In pineapple, for example, its concentration may be only 6 ppb (128). Thus, the carbon cost for regulation, in this case, may be considered quite low.

About 50 coumarins are known which have been implicated in a variety of functions, including regulation of germination inhibition and antibiosis to animals (110) as well as to plants (131). Koeppel et al (68) have quantified

the amounts of the coumarin, scolopin, in tobacco plants. They found that these plants had scolopin concentrations in the range of 6 ppm (fresh weight) in leaves, 20 ppm in stems, and 130 ppm in roots. These concentrations were increased somewhat under low nitrogen, high uv, or cold treatments.

Certain coumarin derivatives, such as isocoumarin in carrot roots and pisinatin in peas, are phytoalexins.

The studies of Feeny (34, 35, 36) have provided a comprehensive picture of the interrelationships of the production of tannins (polymers of phenolic acids) by plants and levels of predation by oak-moth larvae. Apparently, the action of the tannins is through the complexing of proteins, which makes them unavailable to the larvae in a food source which is already nitrogen-poor. Feeny cites additional protective functions of tannins against microorganisms which make their effects very "broad-spectrum." The quantities of tannins found in the oak leaves he studied were in the range of .5% by dry weight early in the season to over 5% in the late season.

The bitter-tasting tannins apparently reduce the digestibility of silage by cattle. This effect has stimulated studies on their occurrence and mode of action (20). In certain varieties of sorghum the tannin content by dry weight will be approximately 10% in the seeds and about 7% in the leaves and stalks. These high-tannin-yielding varieties have "bird-resistant grains." Non-bird-resistant varieties have only 4% tannin content in their grains (20).

Tannins are compartmentalized in plant cells within the vacuole (131).

Lignin, a phenolic polymer derived from the shikimic acid pathway, is a major constituent of plants; it occurs in virtually all cells and, in certain ones, in high amounts. Xylem may contain from 20 to 30% by dry weight of this substance. Apparently, the prime function of lignin is to provide support for the plant through a close interrelationship with the cellulose framework. However, lignin may also provide resistance for the cellulose, which would otherwise be attacked by microorganisms. Evidently only a few types of fungi are directly able to metabolize lignin (99).

The flavonoids, whose basic unit consists of two benzene rings connected by a 3-carbon chain, are nontoxic to man and animals. These compounds are mainly pigments of flowers and fruit (46) and, as such, they operate primarily as the visual signals for pollinators and fruit dispersers.

The flavonoids generally do not constitute a large fraction by weight of a plant; however, in certain tissues such as flower petals, anthocyanin, a flavonoid pigment, has concentrations as high as 30% (105).

Thus, it can be seen that from a single general metabolic pathway, the shikimic acid pathway, a large variety of compounds are produced which can be utilized for such diverse functions of the plant as construction of the basic framework (lignins), regulation of syntheses (IAA), predator protection (tannins), and attraction of vectors for reproduction and dispersal (flavonoids).

Construction costs (competitive cost?) are high in terms of carbon since

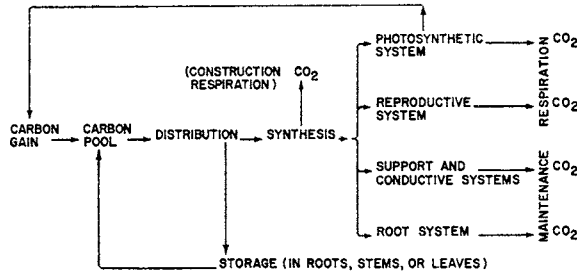


FIGURE 2. The use of carbon in construction.

large fractions are utilized for lignin synthesis by this pathway alone, and even higher amounts for cellulose formation via polymerization of sugars. Regulation involves compounds which are present only in minute amounts, and it thus is an "inexpensive" function.

The phenolic compounds which have been identified in predator protection may be present in differing quantities dependent on their mode of storage and action. Of this class, tannins are noteworthy for the high concentrations produced.

Like regulation, attraction of vectors, via phenolic-derived pigments, is relatively inexpensive in terms of carbon cost. Attraction generally represents one of the smaller fractions of the total cost of reproduction.

The allocation of carbon to various metabolites also varies with season. As an example, Mooney and Chu (unpublished data) have shown that during the nongrowing season the evergreen sclerophyll shrub, *Heteromeles arbutifolia*, will devote almost 15% of the carbon it fixes into the elaboration of phenolic compounds, while during the growing season, when there is a high demand for carbon for the construction of new tissues, relatively little carbon is channeled into these compounds.

USE OF CARBON FOR STRUCTURE AND REPRODUCTION

Structure.—The general aspects of the distribution of carbon for the synthesis of structural materials in plants is outlined in Figure 2. The distribution between the various systems varies greatly with the life form of the plant, and to a certain degree it is dependent on the plant's environment. As examples of the broad geographic trends that are found—in arctic, desert, and grassland communities well over 50% of the plant biomass may be in the roots, whereas in temperate forests only a quarter of the total biomass may be below ground. Evergreen forests have as much as 8% of their total weight in the photosynthetic system, and deciduous forests, only 1% (106).

There is no absolute trend between different classes of plants and their root-shoot ratios (117, 130). For example, Struik & Bray (117) found that annual and perennial herbs growing together in their native habitat overlapped considerably in their root-shoot ratio production. Shrubs, however, gen-

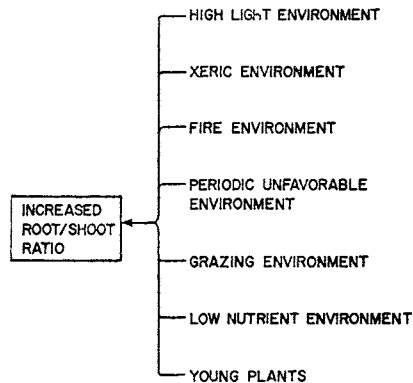


FIGURE 3. Factors influencing the distribution of carbon to roots and shoots.

erally have higher root-shoot ratios than trees (132), and deciduous trees greater ratios than evergreen trees (72, 79).

In perennials a number of environmental features will affect the distribution of dry matter between roots and shoots for any given species (Figure 3). In habitats where light is limiting, root-shoot ratios will decrease (72, 79). Where either water (117) or minerals (7) are limiting root-shoot ratios will increase. In habitats where the shoots are subject to loss by fire (132) or by grazing, species will have a proportionally larger root biomass. Further, in environments where part or all of the shoot must be reconstructed after a long unfavorable season, there will be a higher relative apportionment of carbon to the roots.

The root-shoot ratio will tend to decrease with the age of the plant, as there is a shift from activities which increase the plant structure to those which promote reproduction (17, 130).

There have been a number of theoretical approaches to analyzing the consequences of different structural allocations. For example, Monsi & Murata (87) have recently analyzed the distribution of dry matter between the photosynthetic, support, root, and storage portions of a plant, and how the allotment of new carbon gain to these components influences its subsequent structure. They give a hypothetical example of how lianas can outcompete trees, since a liana need not devote dry matter to support. Thus, they can put most of their carbon gain (three quarters in their example) directly into enlarging their photosynthetic system and thus outcompete the tree for light. Trees with support systems would generally put half of their carbon directly into the vertical development of their canopy.

In an earlier paper Monsi (86) presented growth equations which accounted for photosynthetic gain, maintenance and construction respiration loss, and distribution ratios. He showed how two plants with equal photosynthetic rates but dissimilar distribution ratios would have vastly different

productions. Two plants, one with a distribution ratio of nonphotosynthetic system (support and root systems) to photosynthetic system of 0.7–0.3 and another with a ratio of 0.3–0.7, would accumulate after three growth cycles, 7.5 and 115 g of dry matter, respectively. In another example, he showed how two plants with equal distribution ratios of 0.7–0.3, nonphotosynthetic to photosynthetic, but with dissimilar photosynthetic rates (20 versus 50 g of dry matter per gram dry weight of photosynthetic tissue) would accumulate after 3 years 7.5 and 400 g of dry matter, respectively. Clearly, then, with all things equal, the most productive systems are those with the highest carbon gain capacity, as well as those with the highest redistribution of carbon gain into construction of more photosynthetic system.

Monsi (86) also discusses how deciduous plants lose considerable growth "interest" in the cost of annual replacement of their photosynthetic systems. Thus, evergreenness can be added to the above attributes of the most productive system. Sawada (111), utilizing the approaches of Monsi, has recently analyzed the carbon cost for the construction of wheat seedlings at various seasons. He found that during the cool autumn season the seedlings allocated 50% of their carbon to the photosynthetic system, 30% to the roots, and 20% to the support system. In the hot season, proportionally more went to the roots at 40%. The photosynthetic system under these conditions was just over 40%, and the support system, 17%. Sawada also calculated the percentage of the total carbon gained (considered as net photosynthesis plus dark respiration) that it cost to construct and maintain these systems. During the summer, 16.3% of the total carbon gain went into the photosynthetic system, and 34.9% into the support and root systems. It cost 20.5% of the total carbon gain to build the plant and 28.4% to maintain it (dark respiration). Thus, almost half of the carbon gain was lost in respiration. Comparable values for the colder autumn period were 27.1%, 38.0%, 26.0%, and 8.9%. Considerably less carbon was needed to maintain the system at colder temperatures.

Additional studies have indicated the carbon costs of construction, including respiration losses (Figure 4). For example, 1 g of carbon dioxide will yield 0.62 g of carbohydrate through photosynthetic reduction (113). Assuming this is fixed in a mature leaf and is supplied directly to a pool utilized to build a new leaf, a little over a quarter of a gram of dry matter will result. Almost half of the original carbon gain will be lost in constructive respiration. No account of maintenance respiration, which has been estimated to be about 8% of the gross photosynthesis (134), is given in Figure 4.

Reproduction.—There has been considerable interest in recent years in quantifying the fraction of the plant's resources which are allocated toward reproduction and in determining how this varies with life strategy (38, 51, 52). Certain generalities have resulted from these studies. Annuals allocate a greater proportion of their total resources to reproduction than do herbaceous perennials, which in turn allocate more than woody perennials. For

CARBON COSTS OF LEAF CONSTRUCTION

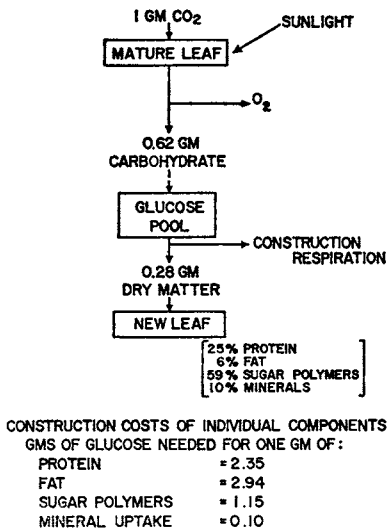


FIGURE 4. The carbon costs of leaf construction.

example, wild annuals may devote between 15 and 30% of their annual net carbon gain to reproduction, whereas herbaceous perennials devote roughly about half this amount to sexual reproduction.

Vegetative reproduction, when present, must also be considered as a fraction of the total reproductive output. However, the analysis is complex in many cases because the asexual reproductive tissue may be also partially photosynthetic and supportive.

An example of the relationship between environment and reproductive expenditure is that different races of the same perennial species may shift their balance from sexual to vegetative reproduction, dependent on the severity of the environment of origin. Populations of *Oxyria digyna*, an herbaceous perennial, have decreasing amounts of seed production the further north their origin, and vegetative reproduction becomes predominant (89). Another example is that plants in disturbed habitats generally allocate more resources to reproduction than do plants in more "mature" sites (38).

The costs of reproduction of course constitute a greater fraction of the plant's energy than would be accounted for by simply assessing the ratio of propagule weight to total plant biomass. That is, not only are there respiratory costs of producing and maintaining these structures, but there are also costs of manufacturing numerous compounds and structures (attractants, nectar, and pollen) which are utilized in the mechanics of reproduction but which are lost during the life of the plant.

Nectar is one such compound. It is a sugar solution which varies in concentration from 25 to 75% (33) and in composition (generally a balance

between sucrose, fructose, and glucose), dependent upon species, although there may in some cases be intraspecific variation (98).

The quantity of nectar produced per flower per day varies between plants and with environment. The bee-pollinated milkweed, *Asclepias cornuti*, may produce as much as 5.3 mg of nectar (60% sugar) per flower per day (84). Another bee-pollinated plant, the fireweed, *Epilobium angustifolium*, produces an average of 1.85 mg of sugar per day (53). Bird-pollinated flowers generally have larger amounts of nectar which is more dilute (84).

Not all nectar produced by flowers is utilized as an attractant for pollination. It may instead maintain ants, which in turn repel predators. Extrafloral nectar production, which can be significant in certain plant groups, may have this same role (62). Similarly, certain plants may produce "mullerian bodies" at petiole bases which are rich in lipids, proteins, and carbohydrates. These sustain ant colonies, which can keep damaging vines away from the tropical *Cecropia* trees (60).

It appears that plants are conservative with the considerable amounts of readily usable carbon that are tied up in nectar. Following successful utilization, the nectar can be resorbed by the plant and directed toward the developing ovules (65). Also, the closing of flowers during bad weather may be a mechanism of protecting the plant's investment in both nectar and pollen (33).

Pollen, itself, may provide the energy reward for flower visitation and it can be the prime food supply of certain insects since it has a high protein content (16 to 30%) in addition to the presence of sugars, starch, and fat (33).

There is a great variation in the species-specific size, as well as the quantities, of pollen produced, both of which depend primarily on the mode of transport. Pollen may vary from a maximum diameter of 250 μ in pumpkin to only 2 to 5 μ in *Myostis*. The size of most wind-dispersed pollen is in the range of 20 to 50 μ (29).

Wind-pollinated species produce large quantities of pollen. For example, the hazel tree (*Corylus*) produces on the average of 2.5 million grains per ovule. In contrast, a flax plant (*Linum*), which is insect-pollinated, may produce only 20,000 pollen grains (29). There are large overlaps between these types, but the trend is marked.

The weight of a pollen grain varies considerably with moisture conditions. A pine pollen grain can vary in weight between 30 and 300×10^{-6} mg.

The economic trade-offs involved in reproductive effort are obvious when comparing wind and insect-pollinated flowers. The latter devote a considerable portion of their effort to devices to attract pollinators, for example, colored petals, nectaries, odors, etc. They generally have small amounts of large pollen. Economies can be realized in this scheme when, as in certain composites, a few large petals serve as the attractant for a whole cluster of ovules. Wind-pollinated flowers generally do not have the costs of petal and nectar production, but this is balanced by their vast production of pollen (33).

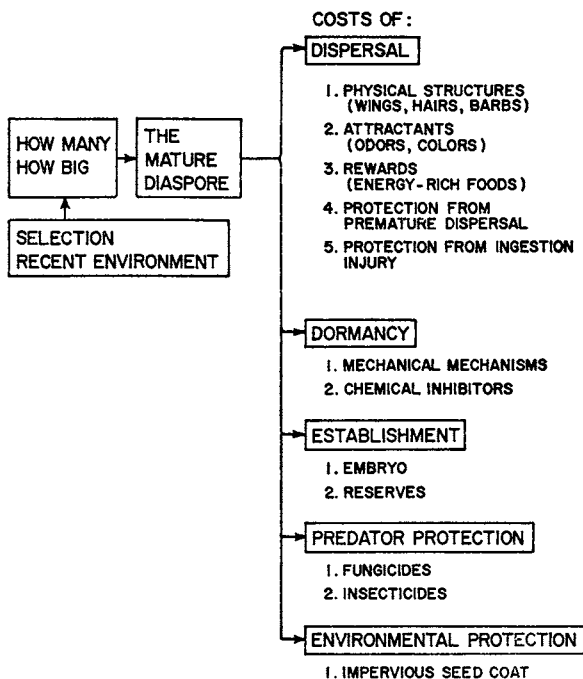


FIGURE 5. The diverse requirements of plant dispersal units.

Recent reviews by Harper, Lovell & Moore (51) and Janzen (59, 61) have focused heavily on ecological aspects of the seeds of plants; thus, a detailed consideration need not be given here. Janzen in particular has emphasized the selective influence of predators as determinants of seed size and chemistry. Harper et al, on the other hand, relate seed size and shape variability to the adaptive compromise which results from their multiple functions.

Seeds (considered here as the dispersal unit of a plant), unlike most plant structures, perform several disparate functions, all of which have energy demands (Figure 5). The seeds are not only the units of dispersal and establishment, but through dormancy they endure environmental conditions which the parent plant cannot tolerate.

Seeds normally contain large amounts of reserve materials in the form of carbohydrates, fats, or proteins. As a group, seeds differ from other plant parts in having a high concentration of energy-rich lipids (82). The high investment in reserve materials in tree seeds shown in Table 2 (71) is typical of most classes of plants (82), although data are generally restricted to economic plants.

Since most of the contents of seeds are in the form of reserve materials which can only be devoted to growth, it would appear that the priority of

TABLE 2. Relative carbohydrate, fat, and protein contents of tree seeds*

Species	Percentage of air-dried seeds		
	Carbohydrates	Fats	Proteins
<i>Acer saccharinum</i>	62.0	4.0	27.5
<i>Aesculus hippocastanum</i>	68.0	5.0	7.0
<i>Castanea vesca</i>	42.0	3.0	4.0
<i>Quercus pedunculata</i>	47.0	3.0	3.0
<i>Quercus alba</i>	58.4	6.8	7.4
<i>Aleurites molucanna</i>	5.0	21.0	62.0
<i>Pinus strobus</i>	4.8	35.4	30.2
<i>Pinus palustris</i>	4.5	31.7	35.2

* From Kozlowski (71).

investment is generally toward establishment. The other adaptive functions of seeds are probably less costly in terms of carbon.

For example, dispersal may be effected by relatively simple structural features like barbs, wings, or hairs. In these cases the seed is carried by the wind or passively by animals. Active dispersal by mammals or birds usually involves more complex systems having signals or attractants, such as colors or odors which indicate that the fruit is ripe. (There may also be elaborate biochemical systems to prevent premature harvesting.) Furthermore, there must be sufficient energy content in the fruit (the reward) to make it worth the energy expended by the animal harvester. To be effective, the aromatic signals of fruits only need be present in virtually trace amounts (94). Apparent attractant colors, such as various carotenoids, are also present in relatively small quantities (42).

Certain fruits may devote a considerable carbon allotment to predator protection, be it the woody scales of cones or such highly toxic compounds as the amino L-Dopa, which is present in the seeds of *Mucuna* in amounts of from 6 to 9% (excluding seed coats) (6).

STORAGE OF CARBON

There are a number of sources detailing and synthesizing our knowledge of the carbohydrate reserves of plants (19, 70, 73, 102, 103, 135).

In perennial plants, surplus carbon may be stored and then utilized during periods when there are high construction demands. In most climates, these demands come when conditions are favorable for regrowth and the race to build a productive and competitive system begins. However, demands may also come at unpredictable times when the productive system is entirely or partially destroyed through defoliation by insects, grazers, or fire. In some cases, the seasonal construction of reproductive parts also is built from reserves rather than from current photosynthate. Further, some plants may

store reserves for many years before committing them to a costly reproductive apparatus (e.g., *Agave*).

Starch and various mono- and disaccharides are the primary storage products of plants. However, fructosans (polysaccharides with fructose-repeating units) are a common storage product of cool temperate grasses (19). Inulin, a type of fructosan, is found as a storage product in members of the Compositae (105). Further, fats and oils may also be storage products in certain plants.

The quantities of carbohydrate involved in storage can be considerable. For example, in such perennial alpine herbs as *Polygonum bistortoides* and *Geum rossii*, the underground rhizomes may contain as much as 60 and 35% carbohydrate, respectively, at the end of the growing season (88). Even in more temperate climates certain deciduous trees store considerable amounts of carbohydrate. For example, the drought-deciduous tree of the California mediterranean climate region, *Aesculus californica*, may contain up to 40% available carbohydrate in the new bark and wood. In this tree carbohydrates are stored in virtually all parts of the plant to provide reservoirs for new leaf growth in the spring, as well as for a large commitment to fruit development subsequent to leaf fall (Mooney & Hays, unpublished data).

Kimura (66) has calculated the use of stored carbohydrate in the initial growth phase of an evergreen conifer in relation to the total dry matter accumulation during the annual season. He found that a carbohydrate quantity equal to 40% of the yearly production was depleted during early growth. Most of this carbohydrate was stored in the over-wintering needles. Kimura compares his results with similar published values for a deciduous tree (105 year-old beech tree) where 26 kg of carbohydrate were depleted during growth initiation, whereas only 87 kg of dry matter were produced during the entire year.

Plants which heavily deplete reserves in their annual regrowth cycle have a considerable amount of capital to repay during the growing season. If the season is short, poor weather can significantly reduce the pool of available carbohydrate for the subsequent year (37). Depletion of reserves in palatable perennials by grazing can shift the competitive balance toward nonpalatable species and result in a change in community composition (19).

Timing of growth initiation.—Plants which are equal in all regards in relation to their growth forms, efficiency of carbon gain, and in the amounts of reserves they store for subsequent regrowth, could have dissimilar competitive capacities dependent upon the time at which a commitment is made for regrowth. In a simple case, in temperate or colder climates plants which commence growth at a very early date during the season may lose what would be an obvious competitive advantage by subsequent damaging weather. In this event, the later-initiating plant would win. The results of this race could vary

from year to year. The time of commitment of reserves is certainly as important as the innate carbon-gaining capacity of the plant in competition.

Even in wet tropical climates there can be a differential periodicity of growth activity of the various tree species (69). This may be a mechanism to desynchronize predators, although there is a lack of evidence to substantiate this.

Of course, there are many components to growth of a plant and they can be initiated at different times. For example, cambial growth may be initiated prior to leaf-out in ring-porous deciduous trees (135). Also, root elongation on trees in temperate climates may precede the annual elongation of shoots. Further, the growing period of roots may be longer than it is for the shoot (72). Detailed information on the timing of growth initiation of various plant components and trees is given by Kozłowski (71, 72).

SYNTHESIS, STORAGE, AND TRANSPORT OF ORGANIC NITROGEN

Since nitrogen is often the limiting element in plant growth and since carbon is utilized in its transport and metabolism, it will be considered briefly here. Mineral nitrogen is assimilated into organic nitrogen in the roots (carbohydrates from the shoot provide the energy for the reduction of the inorganic nitrates), and hence it is transported through the xylem to the shoot. The nitrogen is transported primarily in the form of the amino acids, asparagine or glutamine (135).

A review by Taylor (118) provides a broad view of nitrogen utilization in plants. There is ample evidence that nitrogen is stored in various tissues and then mobilized to growing points during periods of high demands. Further, it appears that during periods of synthesis nitrogen may be shipped as amino acids to a given tissue, built into protein, and then hydrolyzed and retransported back to storage regions prior to the loss of the tissue.

In deciduous trees, nitrogen is taken up by the roots during autumn and winter (providing the soil is above freezing), and it accumulates in the larger roots as well as in the shoot, particularly in the bark tissue. During the autumn, nitrogen is also transported to the shoot from the leaves prior to their abscission. This conservation of nitrogen is particularly important in deciduous trees since the foliage of the mature tree may contain half of the total nitrogen of the plant.

Arginine is the main storage nitrogen, along with glutamine and asparagine, in many plants. During the period of regrowth of trees during the spring there is a drop in the level of these compounds in the storage regions (123).

Flowers are high in nitrogen content and nitrogen is transported to them from the shoot. If the flowers abort, the nitrogen will return to the shoot prior to abscission, presumably as amino acids (118).

Evergreen trees show similar cycles of nitrogen storage and utilization as those of deciduous trees described above (118).

LOSS OF CARBON

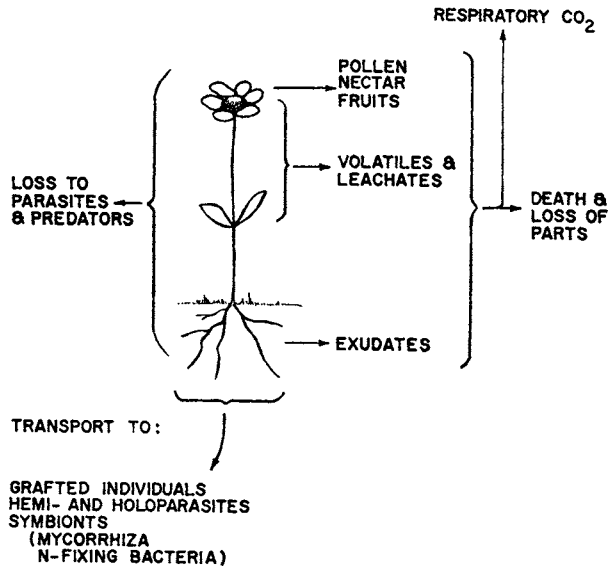


FIGURE 6. The various pathways of the loss of carbon by plants.

LOSS OF CARBON

Plants lose carbon through a variety of pathways, which are indicated in Figure 6.

Root grafting.—In trees, root grafting is common between roots of the same tree, as well as between trees of the same, and even different, species, although the latter case is somewhat rare. Root grafting has been reported in over 150 woody species, including more than 60 genera of angiosperms and gymnosperms (44).

Kozlowski (72) is of the opinion that there may be considerable transfer of materials between grafted individuals, including carbohydrates, hormones, water, minerals, and pathogens.

In one detailed study of root grafting, Bormann (16) estimated the exchange of organic substances between grafted trees. In trees which are equally codominant, there is more or less balanced exchange. If, however, one of the trees is suppressed, it will function as a hemiparasite and will utilize organic substances from a dominant partner to completely support its own root system and lower stem. In this case there apparently is little compensation to the dominant tree in either minerals or water. Bormann indi-

cates, though, that the drain on the dominant tree is minor and will account for less than 2% of its downward translocates.

When the crown of the suppressed tree eventually dies, the translocates from the dominant tree will continue to keep portions of its root system alive. With its crown gone, the water and minerals obtained by the root system of the suppressed tree will now be transported to the dominant tree through the graft.

Hemi- and holoparasites.—Certain types of plants may gain their carbon by wholly (holoparasites) or partially (hemiparasites) parasitizing other plants through the use of haustorial connections.

There have been a number of recent studies of the ecology and physiology of hemiparasites (2-5, 43, 95).

More than 2000 hemiparasites that have been described, and they include all of the major growth forms of plants. They are found in climates from tropical to subarctic (2). They occur in eight separate families but are particularly prevalent in the Scrophulariaceae and Santalaceae (80).

Carbon moves freely from the host plant through the haustoria and then to all parts of the hemiparasite. In contrast, very little carbon moves from the parasite to the host (43).

Hemiparasites differ from holoparasites in their capacity to utilize many different host species and to adjust to the kinds of compounds that they receive from their particular hosts. For example, in a study of *Odontites verna*, it was found that when attached to barley they received primarily monosaccharides, and when associated with clover, mainly amides. Interestingly enough, although the carbon fixed in the host plant is translocated to its roots as sucrose, it evidently is converted in the haustorial tissue to other compounds (43).

Certain hemiparasites can survive without a host, but their productivity is greatly enhanced when they are grown in monospecific clusters or when they are attached to hosts. Any plant may be simultaneously attached to a number of host plants which may belong to a diversity of families (2).

Little attention has been given to the effect of hemiparasites on the production of the host. Malcolm (80), however, described an experiment in which, as would be anticipated, host production (*Kalanchoë*) is significantly lower when associated with a hemiparasite (*Castilleja*).

Further studies should be made to determine what mechanisms plants utilize to avoid being so parasitized. Apparently not all species are equally good hosts for hemiparasites (5). Have the resistant species evolved escape mechanisms? If so, what are they?

Leaching and volatilization.—Tukey, in a series of recent reviews (124-126), has summarized our knowledge about the loss of substances from the leaves of plants through leaching by the action of such aqueous solutions as

rain, dew, mist, or fog. The list of such substances is impressive for its length and includes all of the essential minerals, as well as numerous organic compounds such as carbohydrates, amino acids, organic acids, vitamins, gibberellins, alkaloids, and phenolic substances.

The quantities of material lost by leaching can be considerable. Tukey cites figures that indicate as much as 800 kg of carbohydrate may be lost in a year from a hectare of apple trees. Apparently, up to 6% of the dry weight equivalent in carbohydrates can be lost from bean leaves during 24 hours of leaching. Quantitative data for different species and for other organic compounds are lacking.

The younger leaves of plants, which are often nonwetable, are not as susceptible to leaching as are older leaves. There is also a difference between plant types in their susceptibility to leaching. Conifers are less susceptible than deciduous trees. Tropical rain-forest plants are not easily leached.

It appears that the loss of substances from leaves is a passive process. The substances are not lost through the stomata or directly from cells. Rather, the cations may be lost from "free space" (cell walls and intercellular spaces). Organic compounds are leached from materials as they are being translocated. Tukey & Tukey (127) think that pectinaceous layers and plasmodesmata may form continuous avenues for transport from the vascular tissue through to the epidermis.

These manifold compounds which rain down onto the lower layers of the vegetation may have great significance in the functioning of the ecosystem. Tukey (124, 125) has discussed many of the possible system interactions, as have Whittaker (131) and Whittaker & Feeny (133).

The possible significance and selective value of many of the secondary plant compounds in predator protection and competitive interactions has been discussed. It is certainly not clear, however, how the loss of energy by the plant in the form of such organic building blocks as carbohydrates and amino acids can be adaptive. For example the loss through the leaf surface of glucose may not only be a carbon drain on the plant, but it may also be detrimental by providing an energy source for the germination of pathogenic fungal spores (28).

Whittaker (131) proposes that these losses are consequences of the plant being a rather open system which is adaptive, since this provides pathways for the loss of toxic metabolic "waste products." There is by no means accord on this idea (125). Obviously, considerably more work is needed in this area. It seems rather paradoxical that such considerable quantities of organic material can be lost by plants in any environment, much less one in which they may be in short supply. Why haven't plants which have evolved such elaborate systems of biochemical and physical compartmentation (e.g., resin canals, glandular hairs, Kranz anatomy, etc) been able to evolve systems for the efficient disposal of toxic by-products, if such things do indeed exist, without the loss of innocuous and invaluable organic building blocks?

Very little information is available on the quantitative losses of volatile

substances by plants, although there have been some recent attempts to obtain such values (119). It has become clear, however, that such volatiles as monoterpenes are metabolically active and are not irreversibly formed, as was once thought. Thus, they are not secondary or "waste" products in the traditional sense (77).

Root exudation.—The roots of plants are evidently as leaky as leaves. Exudation by intact roots of a large number of compounds has been noted; these include sugars, amino acids, organic acids, enzymes, and vitamins (108). The quantities of these exudates is, however, generally rather small. Rovira (108) cites values for vetch that indicate that exudation of carbon compounds amounts to only 1.5 to 3% of the total carbon content of the roots during a 2-month period. Root exudation values for corn amounted to 0.4% of the total plant's dry weight during a 20-day experimental period.

Microorganisms apparently can greatly stimulate root exudation (108). There is further evidence that rhizosphere microorganisms are dependent on these exudations, not only as organic substrates, but also for such growth factors as thiamine and biotin (45).

The role of exudates in influencing microbial populations needs much further study. Of considerable interest is the possibility that rhizosphere microorganisms may be of importance in influencing nutrient availability. For example, there are rhizosphere microorganisms which break down organic phosphates. These phosphates are subsequently available for plant uptake. Further, root exudates may operate directly in releasing organically bound minerals (45).

Maintenance of symbionts.—Plants may divert a portion of their carbon to the maintenance of symbionts. In return for this investment they gain certain raw materials which are utilized in photosynthesis, which compensates for the loss. Unfortunately, our knowledge is rather obscure on the quantitative aspects of these exchanges. Such information is vital for any assessment of the dynamics of the evolution of the symbiotic systems.

Harley (47-49) has provided recent comprehensive reviews of the biology of mycorrhizal fungi (soil fungi associated with plant roots). These associations are extremely prevalent in nature. However, apparently, mycorrhizal infections are not necessary for the survival of the host in most cases.

Mycorrhizas (only ectotrophic types are discussed here) absorb sucrose, glucose, and fructose from the host and then convert this to carbohydrate forms (mannitol, trehalose, and glycogen) which cannot be reabsorbed by the host (47).

The flow from the host to the fungi must be considerable. Fungi are evidently completely dependent on the host for its carbon. Further, the quantities of these fungi may be quite high. It has been estimated that in the upper 6 inches of the soil in Monterey pine plantations there are nearly 1400 kg of mycorrhiza per hectare (81). Harley (49) cites values for fruiting bodies of

mycorrhizal fungi in spruce forests which alone amount to 80 kg per hectare. He also gives values which indicate that as much as 4% of the total root biomass in a forest may be mycorrhizal fungi and as much as 40% of the dry weight of the absorbing rootlets is composed of these fungi.

The cost to support these fungi must be quite high. Harley (49) indicates that as much as one tenth of the annual potential wood production in a spruce forest is diverted to the production of fruiting bodies of mycorrhizal fungi alone. He further cites studies of Tranquillini which indicate that *Pinus cembra* at timberline may lose as much as two thirds of its net photosynthetate to mycorrhiza.

The benefit that plants derive from these fungi may also be high. The prime gain of this association for the host is a greatly enhanced nutrient uptake mediated through the fungi. These fungi may act as storage reservoirs for minerals and supply them to the host during periods of low habitat availability or during periods of rapid growth and high demand (48). In low nutrient soil, plants may simply not survive without mycorrhizal infection. Conversely, in high nutrient soils plants often will not become infected, even if they are inoculated with these fungi (48).

Certain types of plants maintain a variety of microorganisms which are capable of fixing atmospheric nitrogen and thus contribute to the nitrogen economy of the host. These N-fixing organisms are quite diverse and include the root nodule bacteria of the legumes (*Rhizobium*) as well as root nodulating organisms, like blue-green algae, which are found in nonleguminous plants. There are also N-fixing nodulating bacteria and blue-green algae found on leaves. Further, there may be a variety of nitrogen fixers which live on moist leaf surfaces, particularly in the tropics, which are not associated with nodules (31). Thus, the possibility exists that the leachates from leaves may actually sustain symbiotic organisms.

Studies on nodulating bacterial symbionts show that they derive carbohydrate substrates from the plant host. The carbohydrate costs of maintenance of these symbionts has been investigated, but the results have been quite variable (40).

Death and predation.—The annual loss of carbon from plants through litter fall (leaves, stems, bud scales, flowers, etc) can be considerable. In a deciduous woodland, for example, this loss can amount to 40% of the annual production (58). As noted earlier, often prior to the dehiscence of these plant parts, certain limiting nutrients may be withdrawn and returned to the living plant body. Oland (96) has found that, prior to abscission of apple leaves, half of the nitrogen present during maximum development migrates back to the tree, as does over 15% of the total leaf dry weight, which includes the nitrogen.

There can be no such withdrawals, however, prior to most types of predation. Predation losses, though, generally are not high on a *community* basis, except in insect outbreaks (104).

In a deciduous woodland it was found that a little over one half of 1% of the above-ground energy that was fixed was lost to herbivores (58). However, this may represent a considerable genetic loss from a population since there probably is a preferential loss of seeds and seedlings through herbivory.

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