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THE ECOLOGY AND ECONOMICS OF STORAGE IN PLANTS

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INTRODUCTION

Storage is a characteristic feature of most plants, particularly perennials, and the subject has been thoroughly reviewed according to its chemistry and physiology (9, 40, 59, 80, 133, 139). However, in ecology much of the information on storage is based on observation rather than experimentation, and experiments often fail to confirm common perceptions of the nature and dynamics of stored reserves. For example, clipping studies show that not all carbohydrates are available to the plant, even though they are considered to be stored reserves. In this review we suggest criteria for defining storage in ecological and economic contexts in order to examine the costs and benefits of storage. We then evaluate the evidence for, and ecological importance of, different types of storage. We discuss storage in relation to vegetative growth

and reproduction, but we ignore storage in seeds and fruits in this review (41,85) because the purposes and constraints on storage differ somewhat between vegetative and reproductive tissues.

WHAT IS STORAGE?

Storage is a major plant function, along with acquisition, transport, growth, defense, and reproduction. The term storage is confusing, however, because it is seldom defined explicitly and has been used differently in various disciplines. We define storage broadly as *resources that build up in the plant and can be mobilized in the future to support biosynthesis for growth or other plant functions*. We recognize three general classes of storage: accumulation, reserve formation, and recycling (Figure 1).

1. *Accumulation* is the increase in compounds that do not directly promote growth. It occurs because resource supply exceeds demands for growth and maintenance (96).

2. *Reserve formation* involves the metabolically regulated compartmentation or synthesis of storage compounds from resources that might otherwise directly promote growth. Reserve formation directly competes for resources with growth and defense.

3. *Recycling* is the reutilization of compounds whose immediate physiological function contributes to growth or defense but which can subsequently be broken down to support future growth. In the absence of recycling, these compounds would be lost as litter.

Biochemists generally define storage more restrictively as specific compounds that do not directly promote growth but which may be mobilized in the future to support structural biosynthesis (e.g. daily starch storage in leaves). This includes accumulation and reserve formation (Figure 1). By contrast, whole-plant physiologists and ecologists may include reserves and recycling

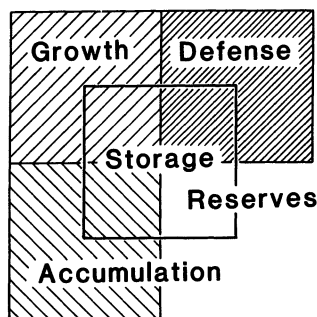


Figure 1 Storage includes reserves and components of defense, growth, and accumulation.

as storage but exclude accumulation (96). Some defensive compounds turn over and have the potential to support future structural biosynthesis (36, 62). Our definition of storage encompasses both the biochemical and the ecological definitions of storage but emphasizes the potential of stores to contribute to future growth.

Accumulation occurs when acquisition exceeds inputs to growth (and associated defense and reserve storage; flux 1 > flux 2 in Figure 2). Accumulated compounds can be lost from the plant or can contribute to future growth (flux 6). Reserves are formed when acquisition is partitioned among growth, defense, and stored reserves (flux 2 = fluxes 3, 4, and 5 in Figure 2). The partitioning to reserves (flux 5) therefore competes with growth (flux 3) and defense (flux 4). Accumulation, reserves, and defense can subsequently support growth (fluxes 6, 7, and 8, respectively). Recycling involves breakdown of components of growth to form a pool of recycled materials that supports additional growth (flux 9). Storage is mobilized through the sum of fluxes 6, 7, 8, and 9 (Figure 2). Those resources that are not mobilized from growth, reserves, accumulation, and defense are lost as litter.

The role of storage must be evaluated in the whole-plant context and in light of alternative patterns of allocation (34, 100). In particular, we must clearly define growth and its controls. We define *growth* in a restricted sense as the buildup of those components of biomass that directly promote further acquisition and transport of resources. Growth includes structure (e.g. cellu-

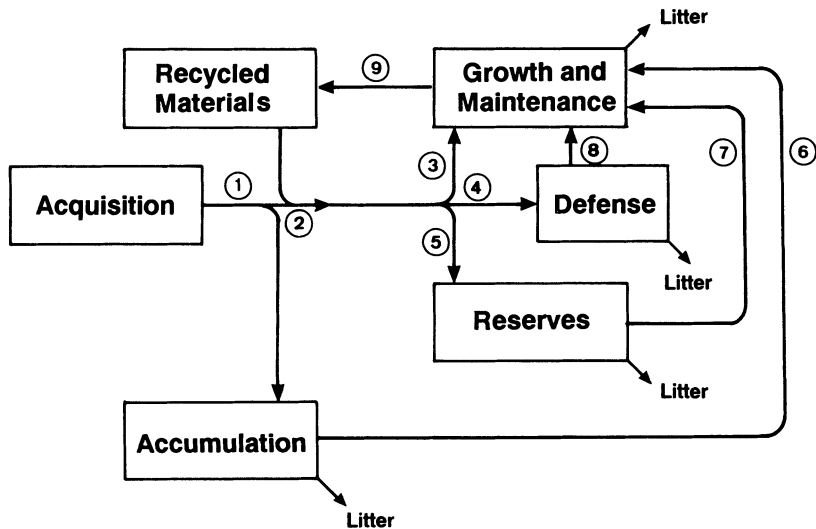


Figure 2 Interrelationships among pools (boxes) and fluxes (numbered arrows) associated with storage. See text for explanation.

lose), biochemical machinery (e.g. functional enzymes), and small pools of metabolic intermediates (e.g. cytosolic sucrose). It excludes compounds whose major function is storage (e.g. starch, vacuolar sucrose) or defense (e.g. tannins and phenolics), because allocation to these pools competes with growth at the time of allocation. Growth by our definition also excludes compounds that have accumulated due to an excess of supply over demand and which, therefore, do not promote growth at the time they are produced or accumulated (e.g. nitrate), or compounds which have no growth-promoting function (e.g. heavy metals). We prefer to talk about growth in a restricted sense rather than total growth (e.g. biomass accumulation), because the latter includes storage and defense and would lead to circular reasoning when we define reserves and defense as being formed in competition with growth.

Growth and allocation can be considered at several levels: whole-plant allocation to organs, functional allocation to sources and sinks, and biochemical allocation to specific compounds (34, 100). In the context of storage we prefer the biochemical rather than the anatomical allocation scheme, because storage is generally distributed throughout the plant. There are four potential sources of confusion in our concept of storage that must be addressed:

1. A given compound may be formed by one or more types of storage processes. For instance, starch may be synthesized when carbon gain exceeds the carbon demands for growth (accumulation) or when the plant partitions carbon between growth and reserves. Amino acids, especially proline, may accumulate as osmoticants during drought, but amino acids can also act as overwinter nitrogen reserves (31, 64, 111).

2. A given compound may serve both a storage and a nonstorage role. For example, RUBISCO (ribulose bis-phosphate carboxylase) is an essential photosynthetic protein but is also one of the major nitrogen stores in leaves (96). The opportunity cost of storage (e.g. the benefit of the next best alternative allocation) is decreased if a compound serves other physiological functions during the storage period. Because of the multiple physiological roles played by many compounds, the classification of broad classes of compounds is difficult. For example, tannins serve both a defensive and a metabolic role (160). Moreover, the extent to which a given compound serves a storage role depends on environment. For example, RUBISCO can perform a more important storage role in a low-nitrogen environment than on fertile soils (97).

3. The time scale of the costs and benefits of storage must be explicitly stated. Reserves differ from accumulation in that they compete with growth *at the time the stores are produced*. We assume that all stores have the potential to promote growth in the long term. Stores produced and used on different time scales are interdependent (Figure 3). Starch content of leaves increases during the day and decreases at night to support growth. Any daily cycle of

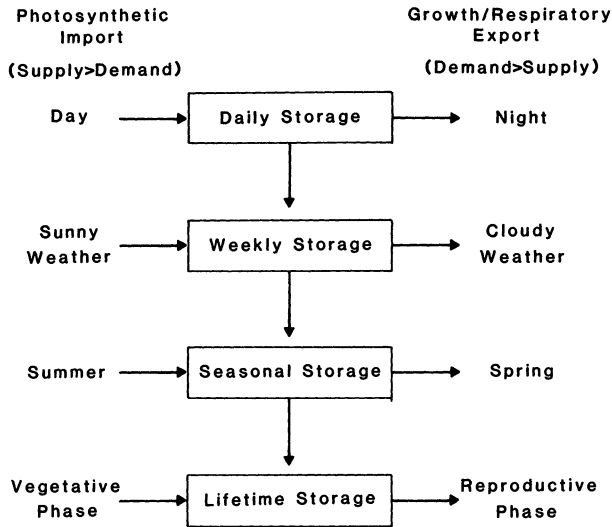


Figure 3 Causes of changes in storage occurring over different time scales.

storage components contributes to storage pools that may be drawn down over various time scales (e.g. daily, weekly, seasonally) to support future growth or reproduction. The ultimate benefit of stores in supporting reproduction depends on net balances of reserve production and use occurring at several shorter time scales.

4. Two distinct measures are useful in describing the production and use of stores. Allocation in a storage organ can be characterized by concentration, providing allocation ratios remain constant during the period of interest. For example, a constant starch concentration in a growing potato could reflect a constant proportional allocation to starch vs other components of the potato. However, allocation at the whole-plant level is best measured by the pool size of stored reserves as a fraction of total growth. Moreover, the pool size of stored reserves is probably the best measure of the potential of stores to contribute to future growth. Thus, both concentration and pool size are useful in describing the processes that control formation and use of stores.

AN ECONOMIC ANALOGY OF STORAGE

Microeconomic theory predicts how a business firm or plant should allocate resources to maximize profit (the excess of revenues over cost; 15, 16). Here we discuss those aspects of the economic analogy that relate to storage by

plants. Although the analogy between plants and business firms has limitations, it provides a framework to evaluate the costs and benefits of storage.

A business firm earns profits when its revenues exceed costs. The firm can grow by investing profits and savings in additional inputs. If the economy is perfectly stable and predictable, and the output of the firm is small relative to market demand, a profitable firm can grow exponentially by reinvesting all profits in additional inputs, thereby saving nothing. Any savings detract from the exponential growth rate that the firm can realize. Similarly, investment by a plant in growth results in a compounding of the investment in terms of new resources gained, and any stored reserves detract from the potential exponential growth rate of the plant.

Reserve Storage

Although reserve storage (savings) detracts from growth, all successful firms and plants invest in some savings (i.e. have some resources that are not used in a productive function). Three main reasons exist for saving:

1. *Asynchrony of supply and demand.* Some firms, such as those that process tomatoes, experience large asynchronies in anticipated supply and demand. Such firms must save to purchase and process large quantities of tomatoes when they are cheap. Asynchrony of supply and demand is the rule rather than the exception for plants, and the growth demand may be supported largely by stored reserves. The greater the asynchrony of supply and demand, the greater should be the expected storage reserve.

2. *Risk aversion.* Firms save primarily to minimize risk of a large catastrophic loss such as from a fire. In the economic realm this risk is averted by purchasing insurance from another company, in which case the business firm invests less in insurance than it expects to regain in the event of catastrophic loss. By contrast, plants can only use internally stored compounds to recover from catastrophic events like fire or grazing. In this case the plant must store internally more resources than are to be used in recovery from catastrophe because of respiratory losses. There is a continuum from risk aversion to asynchrony of supply and demand. This continuum depends on the predictability of the timing and magnitude of demand. The greater the risk (high probability of a large or frequent loss), the more a firm or plant should save. The alternative to storage is to shorten the life cycle to minimize the risk of catastrophe.

3. *Change in type of product.* Firms occasionally undergo large changes in patterns of production (e.g. change from producing guns to producing butter). These expensive one-time investments can be accomplished only if the firm has substantial savings or can borrow money. If plants change patterns of production from a vegetative to a reproductive state, such large bursts of biosynthesis may be supported largely by internally stored reserves (savings).

The best way to evaluate the costs and benefits of savings is through estimation of opportunity costs of storage—i.e. the benefit achieved from the most favorable alternative pattern of allocation. Plants should store if the opportunity cost is less than the benefit achieved by storing now and using resources to support growth at a future date. For example, a plant may store carbohydrates during mild water stress and initiate growth again after the rain rather than allocate carbohydrates to additional root growth with the danger of exhausting the water resource. Obviously, the opportunity cost of storage depends critically on the time scale over which the calculation is made. In the context of fitness, it should be evaluated over the lifetime of the individual in the environment of interest. Short-term analysis might produce quite different conclusions, because catastrophic losses are less likely to occur over a short than over a long time interval. Opportunity costs depend on environment because the relative benefit of different allocations is environmentally determined.

Accumulation

The economics of accumulation are quite different from those of storing reserves, because accumulation does not directly compete with growth and therefore has a lower opportunity cost. There are two economic analogs of accumulation: by-products and inventory. By-products are materials that accumulate as an inevitable consequence of the productive process; they may be either useless, in which case they are expensive wastes, or they may be useful, in which case they can be sold and contribute to profit. Useful by-products are components of inventory, i.e. the materials and products held in stock by a firm for future production and sale. Inventories that result from a decline in demand (sales or growth) are disadvantageous, whereas those resulting from abundant (cheap) supply are beneficial to plants and firms. Plants differ from business firms in that they can control demand more tightly than supply, whereas firms have tighter control over supply. Consequently, within certain limits, inventories are generally good for plants but bad for firms.

Wastes are by-products of production and are costly to store and dispose of. For instance, plants accumulate heavy metals and salt as a result of cumulative transpiration in metal-contaminated or saline environments. These leaves become inefficient due to waste accumulation and must therefore be replaced. Such plants typically have low transpiration rates (and therefore low photosynthetic rates) which minimize waste accumulation (4, 18).

Recycling

When firms undergo major changes in patterns of production, they convert as much of the equipment and buildings as is profitable to the new function. Plants undergo a dramatic change from vegetative to reproductive growth,

requiring large resource inputs into new structures and biosynthetic equipment. This is supported in large part by recycling materials from ageing tissues. The opportunity cost of recycling a structure is the additional growth that could be achieved by retaining and continuing to use that structure. We expect the plant to recycle as much resource as possible, because any remaining resources are lost in litter.

STORAGE COMPOUNDS

Accumulation and reserve storage occurs primarily in vacuoles and plastids, because this prevents degradation of stores by isolating them from other metabolic pathways. Vacuoles also protect cellular machinery from potentially toxic metabolites (1, 17, 89). Accumulation is the least expensive and probably most common mode of storage in plants.

Carbon accumulates primarily as starch, fructosans, and sucrose, depending on species and plant part (Table 1: 9, 66, 115, 133, 155, 159). Carbon accumulation occurs under conditions of high light, low nutrients, or mild water or salt stress (25, 63). These carbon stores subsequently support growth after the stress is alleviated (93). Starch storage occurs in plastids, so its synthesis and breakdown are tightly coupled to photosynthesis (9, 139).

Other carbon compounds are generally less important storage products: In response to high carbon supply, organic acids increase in some species and decline in others (39). Soluble phenolics and hydrolyzable tannins can increase in response to carbon surplus and exhibit turnover (20, 21, 83), but it is unclear whether their breakdown products can be mobilized to support growth. Lipids, which were once thought to play a major storage role in vegetative tissues of shrubs, are primarily cutins, waxes, and antiherbivore resins that cannot be broken down to support biosynthesis (30, 31, 67, 145). However, many trees build up lipids (fat trees; 80, 158, 159), which can be storage (10) or nonstorage lipids (105). Lipids are usually quantitatively less important than carbohydrates as an energy store (105). The possible use of hemicellulose as stores is equivocal (31, 155, 159). Of the other classes of compounds that could conceivably build up under conditions of carbon surplus, some are insensitive to carbon supply (cellulose), and others increase but are not broken down (lignin, condensed tannins, terpene resins, calcium oxalate; 19, 20, 21, 81, 151). These compounds therefore cannot serve a storage function.

Nitrogen builds up in concentration and pool size under conditions of high nitrogen or low light, primarily as specialized storage proteins, amino acids (especially arginine, glutamine, and asparagine), and nitrate, depending on the species (Table 1; 28, 30, 40, 89, 111, 141, 143, 146, 149). Some of the RUBISCO which builds up under high-nitrogen conditions is inactive and

Table 1 The role that major chemical fractions in plants play in storage and in nonstorage aspects of growth and accumulation.

	Components of Storage				
	Accumulation		Stored Reserve	Growth	
	Nonstorage	Storage		Recycled	Nonrecycled
Carbon fractions					
Polysaccharide	-	+	+	-	-
Sugar	-	+	+	-	-
Organic acid	-	+	?	+	-
Phenolics	+	?	?	?	-
Tannins	+	?	?	?	+
Hemicellulose	-	?	-	?	+
Lipids	+	?	-	-	-
Cellulose	-	-	-	-	+
Lignin	+	-	-	-	+
Nitrogen fractions					
Protein	-	+	+	+	-
Amino acid	-	+	+	+	-
Alkaloid	-	+	-	+	-
Nitrate	-	+	-	+	-
Nucleic acid	-	+	?	+	-
Phosphorus fractions					
Phosphate	-	+	-	+	-
Polyphosphate	-	+	+	-	-
Phospholipid	-	+	+	+	-
Nucleic acid	-	+	?	+	-
Sugar phosphate	-	+	+	+	-
Ions					
Potassium	-	+	-	+	-
Calcium	+	-	-	-	+
Magnesium	+	+	-	+	+
Salt	+	-	-	-	+
Heavy metals	+	-	-	-	+

therefore should be considered accumulation (96). Some alkaloid-producing plants increase alkaloid content under conditions of nitrogen surplus, but others do not (147). Under conditions of nitrogen stress, these alkaloids are broken down to support growth. Proline often increases in response to drought or salinity, because it serves as an osmotically active, nontoxic nitrogen store (96).

Phosphorus is stored as inorganic phosphate or polyphosphate, and to a lesser extent as ribonucleic acids and phospholipids, depending on the species (13, 14, 26, 28, 30, 74, 104). Some compounds (e.g. ribonucleic acids) contain carbon, nitrogen, and phosphorus and consequently can serve a storage role for all three of these elements. However, ribonucleic acid con-

stitutes a larger proportion of the plant's total phosphorus than of its nitrogen or carbon store, and amino acids constitute a larger proportion of the plant's total nitrogen than of its carbon store. Thus, the potential importance of different classes of compounds in storage is largely as described in Table 1.

Mineral ions other than phosphorus can increase in plants either when supply exceeds demand (luxury uptake) or because the plant fails to exclude them (46, 57), as in the case of potassium in xylem-tapping mistletoes (43, 125, 130). Some are essential nutrients required by plants (e.g. potassium, calcium, and magnesium). Others serve as osmoticants in halophytes (sodium chloride). Some ions are stored and support future growth (e.g. potassium, and magnesium). Others are shed in litter when the tissue senesces (e.g. toxic heavy metals, calcium, and sodium chloride). Inorganic ions never form a reserve in the sense that they are not sequestered in competition with growth (14, 46, 57).

STORAGE AT DIFFERENT TIME SCALES

The costs and benefits of storage must ultimately be evaluated in terms of contributions to fitness over the lifetime of the organism. However, individuals seldom differ only in storage, making it difficult to estimate the contribution of storage to fitness. It is, therefore, useful to estimate costs and benefits of storage over shorter time scales, particularly for long-lived plants.

Daily Storage

Leaves of most plants store starch and/or vacuolar sucrose during the day and break starch down for export at night. The demand by the plant for carbohydrate determines export rate from a well-lighted leaf. Partitioning between starch and sugar is enzymatically regulated and feeds back to control photosynthesis (137). Manipulations of photoperiod, nutrition, and source/sink activities demonstrate that regulation of this storage reserve results in a nearly constant export rate throughout the 24-hr cycle (6, 33, 52, 53, 72, 116, 140). However, under natural conditions, hourly and daily fluctuations in carbon supply or growth demand cause variations in leaf starch content. In this short-term sense, starch acts as an overflow (131, 138, 159). Plants export recent photosynthate before mobilizing starch stores, suggesting an opportunity cost to starch storage (131).

Mutants that cannot produce starch accumulate sugars in the leaves during the day. The higher sugar concentration in turn leads to a higher leaf respiration rate, causing overall plant growth to decline (140). This demonstrates that, over a 24 hr cycle, starch storage has a low opportunity cost, e.g. the plant gains more by storing starch than by leaving soluble sugars in the cytoplasm. Consequently, plants should store starch during the day for use at

night rather than using some alternative allocation. Mutants that cannot store starch provide a system in which the fitness consequences of starch storage could be directly measured.

Nitrate concentration in leaves also shows a diurnal pattern in many species, increasing at night and decreasing during the day (58, 94, 127), because nitrate reduction is closely coupled to photosynthesis. During the day leaves often have excess reducing power and can reduce nitrate with little or no decline in carbon reduction (16). Thus, the daily cycle of nitrate storage appears to have a low opportunity cost. The alternative of nitrate reduction in roots would be energetically more expensive (16). Avoiding uptake of nitrate under conditions where it cannot be immediately assimilated is another alternative to nitrate storage. However, this might well have a negative effect on total plant nitrogen gain and therefore on fitness in a competitive environment.

Daily water storage is generally of little ecological importance, because the daily turnover of water by a leaf may be ten times its water content. There is no tissue in which water can be sequestered from the main transport path in amounts large enough to cope with this turnover, except in large trees. In *Picea abies*, water storage causes water flow to begin in the crown two hours before it begins in the base of the tree (122). Even this water storage is small compared to total daily water turnover. It would be expensive for a plant to produce a structure large enough to store enough water for more than a few hours' use. In other words, the opportunity cost of water storage is high, and most plants invest little or nothing in a water-storing structure.

Short-Term Fluctuations

Manipulation of light, nutrients, and water clearly indicates that storage levels are sensitive to short-term changes in environment. Under natural conditions the level of carbohydrates declines during cloudy weather when respiratory and growth demands exceed net carbon gain (51). These reserves build up again under conditions favoring photosynthesis. The opportunity cost of this short-term storage might be either a larger leaf biomass to supply carbon dependably even during periods of cloudy weather, or pronounced reductions in growth rate during cloudy weather. In both cases the expected benefit is probably less than observed patterns of fluctuation with weather.

Nutrient availability is highly pulsed. Plants accumulate nitrate in response to pulses of nutrient availability (78, 127) and use these accumulated stores to support continued growth when nutrient availability declines (25, 32, 78, 94). The opportunity cost of this short-term nitrate storage is probably small because it reflects accumulation in excess of immediate demand rather than competition with growth (96). This opportunity cost is further reduced because nitrate may be essential as a counter-ion during uptake of cations.

Short-term water storage can occur in trunks of trees (128, 150). However, in succulents where short-term changes in water content are most pronounced, this storage is either a consequence of salt accumulation, or it is related to acid metabolism. It thus serves other functions than just storage and is not readily available for transpiration.

Seasonal Storage

ACCUMULATION AND RESERVES In perennial plants growing in a seasonal environment, stores of carbon, nitrogen, and phosphorus decline when growth is most rapid and recover when growth stops and/or when senescence recycles leaf nutrients back to storage organs (27, 29, 31, 40, 70, 76, 102, 122, 124, 133, 141, 146, 155, 159). Current acquisition is used before stores when plants have access to both (60, 141, 146), which suggests an opportunity cost to storage. Although seasonal storage is generally viewed as a carefully regulated reserve storage, the pattern could also be interpreted as accumulation in response to supply and demand (105, 146, 159). Only a few studies distinguish between these possibilities.

Sugar beet is one species that clearly builds storage reserves in competition with growth. This species maintains a nearly constant partitioning of carbon between sucrose storage and root growth over a spectrum of light and nutrient conditions ranging from optimal to moderately growth-limiting (95, 152). However, outside the "normal" range of light and nutrient supply, sugar beet stores little sugar at low light or high nitrogen (86, 148). Grafting experiments also demonstrate that reserve storage competes with growth. Sugar beet, which allocates strongly to storage, decreases shoot growth when grafted to shoots of a leafy variety of the same species (chard), whereas chard roots, which have a small capacity for storage, cause grafted sugar beet shoots to grow larger than normal (117). Thus, in crops that have been bred for storage, allocation to storage is maintained under growth-limiting conditions, and this competition causes a decline in growth. However, under conditions of extreme carbon limitation, carbon storage declines even more than does growth. Much less is known about controls over carbon storage in wild species.

Nutrient reserves are also stored in competition with growth. In the biennial *Arctium tomentosum*, the proportional allocation of nitrogen to storage and growth and the final concentration of nitrogen in storage organs were the same for shaded and fertilized plants, plants with reduced leaf area, and control plants (64, 136). This indicates that the increase in asparagine, arginine, and proline in the hypocotyl competed with growth, according to a preset genetic program. In this species, growth rate and carbon balance determine the size of the store (i.e. hypocotyl size), and nitrogen status determines the extent to which this storage organ is filled with nitrogen. Because both carbon and

nitrogen are allocated to the hypocotyl over a range of conditions in which either carbon or nitrogen become limiting to growth, this is a clear example of carbon and nitrogen reserve storage in competition with growth.

In perennial rhizomatous plants it is more difficult to distinguish between reserve storage and accumulation of stores, because growth of new stores and use of existing stores may occur simultaneously. In the nitrophilous *Urtica dioica* growing in full sun, or in various degrees of shade that were limiting to growth, old rhizomes accumulated starch during the growing season in all treatments, indicating reserve storage in competition with growth (142). These stores were broken down in autumn, when leaves were shed and new rhizomes started to grow. At the same time rhizomes accumulated amino acids that were recycled from senescing leaves or were acquired by nitrate uptake and assimilation. The assimilation process further depleted carbohydrate stores. In this species patterns of nitrogen storage could reflect either accumulation or reserve storage but clearly depended on recycling.

Seasonal patterns of storage pools in relation to growth suggest that an increase of stores in late season may compete with growth. Nutrient-limited individuals of the tundra sedge *Eriophorum vaginatum* greatly diminish their growth rate when reserve accumulation begins in late summer. If provided with added nutrients, both growth and reserve accumulation (in the form of sugars, arginine, and sugar phosphates) continue simultaneously (31). In a tundra environment where spring growth begins before soils thaw, nutrient storage is essential to support spring growth and therefore has a low opportunity cost.

The examples described above indicate that seasonal storage often reflects reserves that are stored in competition with growth (i.e. money in the bank). However, pool sizes and dynamics of stores also reflect accumulation. For instance, nutrient concentrations in storage organs generally increase more in response to fertilization than do concentrations in vegetative tissues (132, 146, 149). Unfavorable conditions for growth (i.e. low demand) at high altitude or latitude also cause accumulation of nitrogen in tundra plants (79). The extent to which seasonal fluctuations in stores reflect accumulation vs reserves formed in competition with growth remains uncertain, particularly in wild plants.

RECYCLING Other than some organic acids, few non-nitrogenous organic compounds are recycled from senescing leaves (143). During senescence, only about 10% of the leaf weight is lost in respired or resorbed material (28, 54), and most of this can be accounted for by recycled nitrogenous compounds (54). This fact supports the idea that non-nutrient-containing compounds are not recycled to any large extent. By contrast, about half the nitrogen, phosphorus, and potassium are recycled from a senescing leaf to

support new growth (28). Thus, recycling constitutes a large store of nutrients but a small store of carbon.

Recycling allows nutrients that have been used to support previous growth to be reused. In *Arctium* the same molecule of reduced nitrogen can be reutilized as many as six times in a single growing season: from hypocotyl to rosette leaves to leaves on the flowering stalk to the flower stalk to the flowers and finally to the seeds (64). Even within the canopy of the same individual, recycling takes place from old leaves to young leaves and from shaded parts of the canopy to more sun-lit leaves, maximizing carbon gain (50, 69, 76). Similarly, carbohydrates from the heartwood can be recycled to support growth of outer tree rings (70).

The widespread forest decline in Europe shows the importance of recycling (123). Here acid rain has caused a dramatic increase in plant nitrogen and a decline in cation availability. The flush of spring growth in Norway spruce depends primarily on stored nitrogen and magnesium (49), because soils are too cold to allow much uptake at this time. In trees stressed by acid rain, new growth depletes the magnesium stored in older leaves, causing them to become chlorotic and die (108). Wood growth occurs after foliage development has depleted magnesium stores and is directly limited by magnesium deficiency. When recycling is prevented by clipping off leaf buds to prevent spring growth, trees remain green and have magnesium concentrations in old foliage that are comparable to those of healthy trees (129, 153).

In other cases recycling of nutrients from old leaves has no major effect on nutrient supply to young leaves. In several evergreen species, ranging from arctic to mediterranean, removal of old leaves prior to senescence had no effect on the nutrient pool size of young leaves (75). However, growth of new leaves was reduced in defoliated plants, suggesting that leaf growth in these species was limited more by carbon supply than by recycling of nutrients. Clearly, more experimental studies are needed to demonstrate the conditions under which recycling constitutes an important storage process.

STORAGE AND RECOVERY FROM CATASTROPHE

In perennial plants there is no clear relationship among species between the amount of stored carbohydrate and capacity for regrowth after grazing (144). Moreover, most plants fail to use a large proportion of their stored carbohydrate in response to clipping, raising questions of whether these reserves are completely accessible to the plant (22, 38, 47, 90, 98, 121, 144, 155). Similarly, even though regrowth after fire depletes carbohydrate reserves, substantial carbohydrate concentrations remain (113). Such studies generally emphasize the magnitude of decline in carbohydrate reserves in response to clipping, but they fail to point out that substantial carbohydrates remain at

levels of clipping that greatly repress regrowth. In fact, if plants are repeatedly clipped and kept in the dark to prevent photosynthesis, they generally cease regrowth well before carbohydrate reserves are exhausted (121).

We suggest four potential causes for the failure of plants to use all carbohydrate reserves following catastrophe. (a) Intense defoliation may deplete nitrogen and phosphorus reserves more strongly than carbon reserves (3, 24), so that nutrients rather than carbon may limit regrowth. However, grazing usually causes tissue nutrient concentrations to increase (73), suggesting that grazing usually depletes carbon more than nutrient stores or that high root-shoot ratio of grazed plants enables the plant to meet nutrient demands more readily than carbon demands. (b) Some carbohydrate stores may become inaccessible to the plant with time because they are in dead cells and cannot be retrieved (158). (c) These clipping experiments may not have provided the appropriate cue to trigger mobilization of the stores. (d) Our chemical measures of stores may include some nonstorage forms such as breakdown products of hemicellulose. Because of the uncertainty in estimating the pool size of stores available to the plant after catastrophe, it is presently impossible to estimate their opportunity cost. A comparison of the clipping response of individuals that differed only in the magnitude of stored reserves (due to differences in carbohydrate or nutrient status) or in genetic potential to store could provide insight into the opportunity costs of storage for recovery from grazing. The observation that plants use concurrent photosynthate rather than stores to support regrowth, when both are available, suggests an opportunity cost to storage in support of recovery from catastrophe (155).

In semi-arid environments, fire has led to quite different strategies for recovery from catastrophe. In California, woody species recover from fire as sprouters, i.e. species which activate dormant buds for growth following fire; sprouters contain specialized tissues in their root (lignotubers) which store large quantities of starch (77). By contrast, seeders, which recolonize from seed following fire, lack such storage tissues. The observation that both strategies are well represented in this ecosystem suggests that the opportunity cost of lignotuber formation (in terms of reduced reproductive output) must be substantial.

STORAGE FOR REPRODUCTION

If stores are important to reproduction, we expect strong depletion of stores when the plant switches to the reproductive mode, particularly in monocarpic plants. Optimality models of allocation predict that reserve storage in annuals will be best developed when the switch to reproduction occurs late in the season, particularly in monocarpic species, because such species have a greater probability of loss of productive potential and recycling stores to herbivores (35). Field data with *Hemizonia* conform to this prediction.

When annuals are grown under optimal conditions, less than 25% (generally less than 5%) of seed carbon comes from stores (11, 12, 48, 112, 118, 157). The remaining carbon comes from concurrent photosynthesis. The reproductive structures themselves contribute as much as 30–65% of their carbon requirement through photosynthesis (7, 8, 48, 119). This may explain the close relation between seed yield and evapotranspiration (126). Thus, under optimal conditions these crops rely primarily on current photosynthate to support seed production. By contrast, 50–90% of the nitrogen and phosphorus in seeds of annual plants is recycled from vegetative tissues rather than taken from concurrent uptake (11). Thus, as with autumn leaf senescence, recycling is a much more important source of nutrients than of carbon to support reproduction. However, under conditions of drought severe enough to restrict photosynthesis, carbon for grain growth comes mainly from stores (12, 56, 110). Similarly, plants under nutrient stress draw proportionally more on stores of nitrogen and phosphorus than do plants growing under optimal nutrition (5, 11, 156). Thus, the opportunity cost of storage may be less under conditions of low-resource supply. There is remarkably little evidence on the extent to which wild plants draw on nutrient stores to support reproduction.

Biennials are an excellent example of the importance of reserves for supporting reproduction at the end of the life cycle. In *Arctium*, reserves accumulated during the first year support rapid vegetative growth at the beginning of the second year. At seed filling, more than 70% of the total N in the plant is recycled into seed production (64). Stored reserves also have an indirect effect on nutrient supply to reproduction. Large stores in *Arctium* support production of large rosettes which exclude competing individuals and provide access to a larger soil pool of mineralized nitrogen than in the first year. For this reason, *Arctium* absorbs two thirds of its nitrogen in the second year, when it has a larger rosette despite a constant or decreasing root biomass (64).

In biennials, rosette size is a good predictor of the quantity of stored reserves, which in turn is a good predictor of seed output (154). Biennials that delay reproduction and remain vegetative to attain a larger size depend more strongly on stores but achieve greater reproductive output (68). This dependence on stores is particularly important in infertile and dry environments (55, 68, but see 120), again supporting our economic prediction that the opportunity cost of storage is reduced in low-resource environments.

In perennials there is clear evidence of the importance of reserves in supporting reproduction. In an extreme case, *Aesculus californicus*, a drought-deciduous tree, produces large fruits which develop after leaves have been shed from the trees. Its fruits must, therefore, draw their carbon entirely from stored reserves (101, 103). Reproductive branches show delayed bud

break and less growth the following year than do nonreproductive branches, indicating that this reserve allocation to reproduction competes with future growth (106). Similarly, mast-cropping conifers (37, 44, 87, 91, 92), biennially bearing fruit trees (23, 65, 122), and some herbaceous species (2, 84, 99, 134, 135) show marked declines in carbon reserves and growth following heavy reproduction. In most of these cases, carbohydrate reserves are drawn down more strongly by reproduction than is nitrogen. The nitrogen and phosphorus that support reproduction come largely from recycling of nutrients from senescing leaves (11, 156). If grazing or browsing depletes storage reserves, this often causes a decline in reproduction (42, 82, 107). This effect is particularly pronounced in females of dioecious species which are more dependent on stored reserves for reproduction than are males (45). This impact of grazing on reproduction is most pronounced in infertile soils (107), again suggesting that the dependence of reproduction on reserve storage is most pronounced (low opportunity cost) in low-resource environments.

In other cases, reproduction shows no clear relationship to reserves. For example, in two arctic sedge species, reserves were drawn down no more strongly to support reproductive development than to support normal spring shoot growth (88). Similarly, in many perennial grasses and herbs, extent of reproduction had little or no influence on vegetative growth (71, 114, 120). Clearly the importance of reserves in supporting reproduction varies among species and deserves further study.

ADAPTIVE PATTERNS IN STORAGE

Drought-deciduous plants show large seasonal variations in carbohydrate stores whereas co-occurring evergreen species do not (103). Similarly, in tundra, deciduous species show more pronounced seasonal fluctuations in carbohydrate and nutrient stores than do co-occurring evergreens (27, 30). The greater dependence on storage probably reflects the lower opportunity cost (benefit of an alternative allocation) in species which experience a large asynchrony in resource supply and demand, as predicted by our economic assumptions.

Species adapted to low resource supply have an inherently low growth rate even under conditions of high resource supply (25, 61, 109). These plants accumulate larger nutrient stores in response to a pulse of nutrients than do plants with a high growth rate, because rapid growth dilutes the nutrient pool over a larger biomass (25). This nutrient storage (luxury consumption) by species adapted to low-resource environments suggests that the opportunity cost of such storage is lower here than in environments which support more rapid growth.

CONCLUSIONS

1. Economics provides a qualitative framework to evaluate the adaptive significance of storage. Concurrent uptake is used before stores during daily and seasonal cycles and to support reproduction or recovery from grazing, presumably because of the greater cost of storage. Carbohydrate and nitrate contents of plants show greater daily fluctuation than does water because they have a lower opportunity cost of daily storage. Seasonal and lifetime storage of carbon and nutrients has a lower opportunity cost (and is therefore better developed) in plants of low- (compared to high-) resource environments. The greater allocation to storage in monocarpic plants (e.g. many biennials) compared to polycarpic plants is consistent with the greater risk associated with the monocarpic strategy. Greater storage by deciduous than by evergreen species reflects the greater asynchrony of supply and demand experienced by deciduous species. Storage for reproduction supports a large change in pattern of production at the end of a plant's life, particularly for monocarpic plants; this storage for reproduction appears to be much more pronounced for nutrients than for carbon. Future experiments will be necessary to test these hypotheses more rigorously and to provide a more quantitative assessment of the adaptive value of storage.

2. Distinguishing among the components of storage (accumulation, reserve, and recycling) allows estimation of the cost of storage in different environments. Accumulation is most pronounced in species with inherently slow growth rates. Reserve storage has been critically demonstrated in only a few studies, making it difficult to detect any broadscale ecological pattern in reserve storage. Recycling stores are unimportant for carbon but critical for nitrogen, phosphorus, and potassium. The dependence of growth on recycling may be greater in infertile environments, suggesting that the opportunity cost of recycling is higher in fertile sites.

3. In order to distinguish among different components of storage and to relate these to controls over growth, defense, and reproduction, field experiments which perturb these processes (e.g. shading and fertilization) will be necessary. Even then, however, it will be difficult to dissect the causes of the coordinated whole-plant response. An alternative is to manipulate the storage properties of plants through comparisons of storage mutants or closely related ecotypes that differ only in storage characteristics. A combination of these approaches may be particularly fruitful.

4. An appreciation of time scale is critical to an understanding of the causes and benefits of storage. The cause of storage (reserves vs accumulation) must be evaluated at the time of allocation. The benefit of storage should be measured in terms of fitness and thus should incorporate probabilities of survival and reproduction over the life of the individual. In long-lived species

where fitness is difficult to measure, the benefits of storage can be approximated over the length of repeatable cycles such as a day, season, or cycle of mast cropping.

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