

The capture and gratuitous disposal of resources by plants

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Summary

1. Every plant will die if light, water or nutrients are withheld for long enough. It is natural to think of plants in general as having evolved a strong drive for resource acquisition as a survival mechanism. All else being equal, an individual that sequesters more material from the environment than its neighbour must be at a competitive advantage.

2. But the resource capture imperative seems at odds with the profligacy of some characteristic developmental and metabolic processes in many plants. Here, using leaf senescence as a vantage point, we consider whether a kind of wilful inefficiency of resource use may not be essential for success as a terrestrial autotroph.

Key-words: abscission, carbon, evolution, leaf, nitrogen, photosynthesis, root, senescence

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Sequential senescence

Although not all botanists would accept the proposal, it can be argued that the default green plant form is the thallus, and that morphology and anatomy are generated by means of body sculpture and body piercing, that is, by the schizogenous and lysigenous elimination of protoplasts, cells, tissues and organs to generate shapes, holes and tubes (Dangl, Dietrich & Thomas 2000). Repetition in space and time, and variation in the arrangement of units thus generated, adds to the structural complexity of plants (Room, Maillette & Hanan 1994; White 1979). Cell death is accepted as a creative as well as a pathological force in development and adaptation, not just in the animal and biomedical fields (Hengartner & Bryant 2000) but across the range of plant species and structures. For example, Raven (1986) discussed the relevance of programmed cell death, lysigenous and schizogenous processes for the evolution of xylem. The contributions of selective cell and tissue death to plant architecture and life-cycle are increasingly understood to be critical (Bleecker & Patterson 1997). And cell death, in the form of the hypersensitive response, is now seen as central to our understanding of plant reactions to biotic and other stressful challenges (Heath 1998). Individual plants behave as competing populations of redundant organs wherein auxin-mediated control of vascular orientation and internal competition between genet-

ically equivalent shoots contribute to the adaptation of the plant to heterogeneous environments (Sachs, Novoplansky & Cohen 1993). The throw-away lifestyles of higher plants are often conducted on a grand scale. For example, most cells of a tree are dead, and the autumnal shedding of foliage in northern temperate regions is clearly visible from space.

A close look at a more modest example of programmed disposability – the progressive or sequential senescence of leaves related to position on the shoot axis – raises questions about the significance of resource capture that suggest counterintuitive answers. There is clearly an association between leaf senescence on the one hand and declining photosynthesis on the other, and some models propose an effect–cause relationship (e.g. Hensel *et al.* 1993). It is reasonable to suppose, therefore, that the shade cast by foliage at the top of the canopy induces sequential senescence of older, lower leaves, and that the critical factor is the photosynthetic compensation point. If a layer of foliage is deep enough to be permanently located beneath the lowest limit to which light at the compensation flux penetrates into the canopy, these leaves would be expected to be discarded, usually following the initiation of senescence and salvage of reduced N and other mobile materials (Aerts & Chapin 2000).

But there are many instances in the literature of plants supporting unexpectedly large numbers of ‘unproductive’ leaves. For example, Fig. 1 presents data from a study of maize by Lemon & Wright (1969). Profiles of CO₂ flux at different heights in the

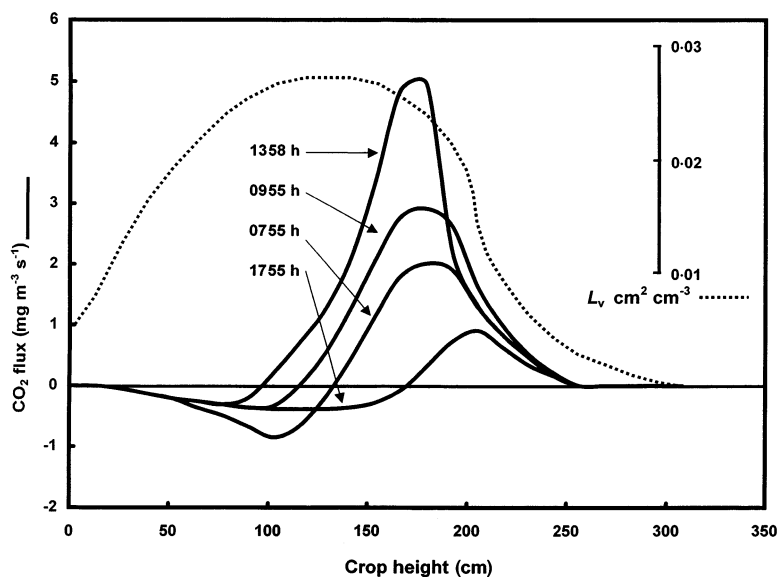


Fig. 1. Profiles of CO₂ fixation and efflux at different heights in a maize crop, measured at four times during a clear September day in Ithaca, NY, USA. Also shown is the distribution of leaf area density, L_v (after Lemon & Wright 1969).

crop are presented for four occasions during a clear September day in Ithaca, NY, USA. Superimposed is the curve for leaf area density (area of foliage per unit volume of space occupied by the canopy). During the day the point at which net CO₂ fixation crosses into net CO₂ efflux (respiration) never penetrates beyond about 100 cm; and yet more than 30% of the foliage in the canopy is located below this level. The authors comment that ‘all leaves were still green and evidently very active photosynthetically despite the late date.’

It is difficult to find non-anecdotal evidence in support of the simplistic proposition that senescence is triggered by shade as leaves move deeper into the canopy. Some studies suggest that light quality (specifically the red : far-red ratio) is better correlated than light flux with foliar gradients of senescence and N remobilization (Rousseaux, Hall & Sánchez 1999). Although lower leaves are often older, chronological (as distinct from physiological) age appears to be less important than position and/or orientation in determining photosynthetic capacity (Ackerly 1999; Murchie *et al.* 1999). Hikosaka, Tersahima & Katoh (1994) elegantly isolated the effect of leaf age and leaf position by growing plants of *Ipomoea tricolor* horizontally to avoid mutual shading of leaves.

Considering that plants are obligately light-driven organisms, they have unexpectedly high tolerances of prolonged darkness. Hutchinson (1967) deprived 14 species of light and found survival times of 23–82 days at 15 °C and up to 227 days at 5–7 °C. Pretreatment with light before transfer to darkness generally shortened survival times, and the author speculated that ‘build-up of dry matter in the light imposes a respiratory burden during long periods of darkness’. Read & Francis (1992) found that several tree species from the southern hemisphere were able to survive

prolonged exposure to darkness simulating polar winter conditions at high latitudes. Fossil and biogeographical evidence suggested that the taxa investigated in this study occurred at such latitudes during the Cretaceous or early Tertiary, and the authors suggest that differential responses to darkness and temperature were significant for species adaptation during tectonic movements.

There is good evidence that leaves at full expansion, and even at incipient senescence, retain the potential to acclimate to low light by reconstructing the photosynthetic apparatus (Mae *et al.* 1993). The picture emerges of a deep zone in many canopies consisting of leaves that, according to criteria of usefulness based on net positive contribution of assimilate, are inefficient consumers of resources the disposal of which would be beneficial to the plant. And yet this ‘overdraft’ layer is retained and, in some cases, represents a rather large fraction of the total above-ground biomass. What function could it have?

Roles of the overdraft layer

If a leaf that exists most of the time beneath the compensation point is preserved, the plant must suffer no survival penalties from expending the energy necessary to retain it. How might such leaves be useful? A plausible function for leaves in carbon overdraft is as sites of temporary storage. Studies with soybean (*Glycine max*) have been instrumental in establishing the physiological basis of senescence processes in annual plants, including early theories on plant ‘self-destruction’ (Sinclair & de Wit 1975). More recent work with sunflower (*Helianthus annuus*) highlights the functional conflict derived from seed depending on leaves for the supply of both reduced nitrogen – which requires degradation of leaf nitrogenous compounds – and reduced C, which requires maintenance of the N-rich photosynthetic apparatus (Sadras, Hall & Connor 1993). The vertical distribution of foliar N in plant canopies, partially driven by differential leaf senescence, closely approaches the theoretical pattern that maximizes canopy photosynthesis (Werger & Hirose 1991). The optimization theory underlying this interpretation of leaf N distribution in canopies has shortcomings, discussed by Chen *et al.* (1993). For instance, there are time constraints related to optimization theory being determined over a definite time integral (e.g. day, season) that implies plants can ‘foresee’ the patterns of relevant variables. Moreover, Rousseaux (1997) recently demonstrated that leaves at the bottom of reproductive sunflower canopies can retain much more N than is required to maximize C assimilation. Sinclair & Sheehy (1999) have pointed out that the high values of L_v , up to 7 or more, for green-revolution rice varieties are obligatory simply to store the N that remobilizes to support the yield of these extremely productive plants. During the second year of growth in the biennial monocarp *Arctium*

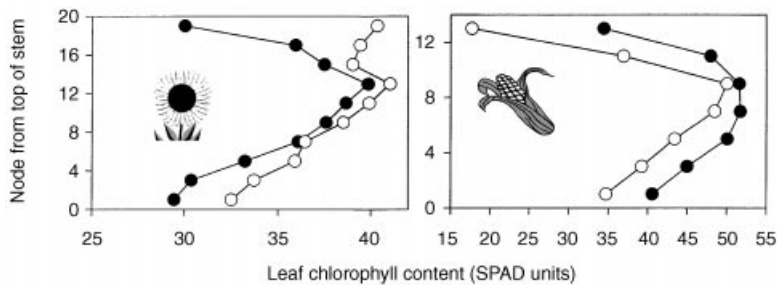


Fig. 2. Lack of seed (○) delayed senescence in sunflower and accelerated senescence in maize in relation to undisturbed controls (●). Measurements of leaf chlorophyll concentration were taken 20 days after flowering in both species. Differences in chlorophyll content between plants with and without seed were significant at $P < 0.0001$ in sunflower and $P < 0.003$ in maize. Adapted from Sadras *et al.* (2000).

tomentosum, N is recycled three times, from tuber to rosette leaves and further to flower stem leaves, and eventually into seeds (Heilmeyer, Schultze & Whale 1986). This species may be regarded as inefficient in terms of dry matter (harvest index, 0.19), but it is comparable to crop species in relocating N, having an N harvest index of about 0.7. The major leaf proteins, notably Rubisco and the chlorophyll-binding polypeptides, have a dual role: in photosynthesis and as N reserves. A deep layer of foliage in negative C balance but retaining colour and photosynthetic capacity is functionally a storage tissue, like a seed or a tuber.

Sub-compensation point leaves can be useful in other ways. They would be valuable for species growing in variable light environments. Some herbaceous species might benefit from retaining a reserve of foliage to replace upper leaves taken by grazing animals. Such a reserve may provide insurance cover against defoliation by insects and other arthropods, as found in cotton (*Gossypium hirsutum*) canopies infested with two-spotted spider mites, *Tetranychus urticae* (Acari: Tetranychidae). In comparison to uninfested controls, leaves at the bottom of infested canopies had greater concentration of chlorophyll and greater photosynthetic rate owing to more light penetration which derived, in turn, from faster senescence of uppermost leaves induced by mite activity (A. A. Reddall, unpublished results). Other possible roles for leaves in negative assimilatory balance are as decoys for predators and pathogens; as cooled surfaces for condensation; and as counterweights reducing top-heaviness and susceptibility to physical damage (Farnsworth & Niklas 1995).

There is an instructive parallel to be drawn between, on the one hand, these population-like interrelations of particular leaves or layers in a canopy and, on the other, the behaviour of foliage in plant populations. Certain environmental and plant factors, including reproductive growth, affect the onset and/or rate of leaf senescence (e.g. Rousseaux, Hall & Sánchez 1993). Experiments in which grain set was prevented demonstrated a consistent delay and/or slowing down of leaf senescence in oilseed

species, including sunflower and soybean (Ho & Below 1989; Lindoo & Noodén 1977). In cereals, on the other hand, ear removal may delay or accelerate leaf senescence, depending on genotype (Thomas & Smart 1993). Figure 2 illustrates the contrasting responses to reproductive growth of sunflower and maize. Little attention has been paid to ecological and evolutionary aspects of this contrast. Competition and herbivory are two major selective forces for plants (Aarssen & Irwin 1991; Burger & Louda 1994; Swank & Oechel 1991). The proportion of barren plants increases with competition for light and soil resources in maize stands (Tollenaar, McCullough & Dwyer 1994). Sterility caused by competition is less frequent in sunflower. In a comparative study, sterility associated with high population density was 28% in maize and 8% in sunflower stands (Vega *et al.* 2000). Sterility in sunflower can also be caused by severe boron deficiency (Connor & Sadras 1992) and insects, including thrips (Thysanoptera; Vega 1997). Irrespective of the cause of sterility, it is obvious that natural selection cannot act on barren annuals. Thus contrasting senescence patterns in sterile plants might result from (i) random processes that maintain genes for accelerated or delayed senescence with no consequence for the fitness of the population; or (ii) selective forces that operate at the population level. The latter would involve gene replacement, that is, an allele frequency change that results from population phenomena (Endler & McLellan 1988). Hence, accelerated senescence of sterile plants might benefit the population by reduced competition. On the other hand, sterile plants that remain green might benefit the population by reducing the pressure from herbivores and pathogens – that is, they have some of the features and functional significance of the non-senescent sub-compensation point layer in a canopy. Accelerated or delayed senescence of sterile plants (and, by analogy, the occurrence and size of a canopy overdraft layer) may thus have been favoured depending on the relative importance of herbivory and competition (Sadras 2000). In this context, a role for jasmonates (Sadras *et al.* 2000) is supported because of their effects on the expression of wound-responsive genes and chemical defences (Sembdner & Parthier 1993).

By reflecting on a single narrow physiological issue – the control and significance of sequential senescence – a picture emerges of benefits to be obtained from what at first sight appears to be physiological inefficiency. But the idea that plants can and do support organs in negative C balance may have more general significance, as a look at the evolution of the terrestrial habit reveals.

Evolutionary origin of the photosynthetic apparatus

Around 500 million years ago, plants took the evolutionary step from aquatic to terrestrial existence.

Some aspects of the physiology of terrestrial plants have been greatly modified in the process, but others are more or less unchanged relics of the preterrestrial era. There may have been very early evolutionary experiments with different ways of utilizing light energy biologically, but it seems certain that the photosynthesis in all known modern photoautotrophs evolved only once. All three main pigment types of O₂-evolvers – chlorophyll *a*/phycobilin; chlorophyll *a*/chlorophyll *b*; and chlorophyll *a*/chlorophyll *c* – were established by the Silurian (Raven 1986). The photosynthetic apparatus evolved under water and was adapted to function optimally in relatively dim light and cool temperature, as discussed by Raven (1986). He pointed out that the high ratio of UV (280–320 nm) to photosynthetically active radiation (PAR, 400–700 nm) at the sea surface 2·10⁹ years ago may have forced phototrophs to live in habitats with a low photon flux density of PAR if they were not to be exposed to intolerable UV levels. The attenuation of radiation could have occurred in planktophytes deep (>10 m) in a stratified water column. On these grounds, Raven concluded that genotypic shade adaptation was likely to be the primitive condition, with sun adaptation being possible only when the UV/PAR ratio had decreased sufficiently because of the accumulation of O₂, and hence UV-absorbing O₃. Chloroplast organization and function were not radically reworked when plants colonized the land. For example, the basic design principles of photosynthetic membranes are remarkably conserved across the whole range of autotrophic organisms. Notwithstanding the vast taxonomic gulf, the photosynthetic reaction centre of the purple bacterium *Rhodospseudomonas* shows virtually complete polypeptide-for-polypeptide (and gene-for-gene) homology with photosystem 2 of higher plants (Cogdell & Lindsay 2000).

Plants emerging onto the land were therefore equipped with a primary metabolic process that was far from optimally organized to meet the challenges of the new environment. As usual, evolution did not take the course of fundamental redesign. Instead, the aquatic photosynthetic apparatus was retrofitted with a range of physiological fixes to allow it to work properly out of water. What did the first land plants encounter in their new surroundings? Faced with high light, warm temperatures and enhanced availability of CO₂ at the plant surface, conditions in which incontinent photosynthesis was not disadvantageous, they must have found themselves awash with fixed C, which would explain the relative rapidity with which conquest of the land was followed by establishment of forests. It is likely that early plants could not avoid promiscuous photosynthesis; in the words of (Harper 1977, p. 656), ‘the green plant may indeed be a pathological overproducer of carbohydrates.’ This being so, there would have been selective pressure to develop ways of restraining photosynthesis and offloading excess C. At the macro-evolutionary level, this is consistent

with the ideas of Vermeij (1995), who has suggested that elevated nutrient and energy fluxes through the biosphere that occurred during episodes of submarine volcanism during the early Palaeozoic and late Mesozoic, for example, were driving forces for increases in evolutionary innovation and diversity. In any event, feedback mechanisms that slow down photosynthesis are widespread (Evans 1993). This is of current interest in relation to the effects of increasing atmospheric CO₂ concentration. Most studies agree that, over the long term, plants acclimate to high CO₂ by reducing C-fixation capacity. For example, Drake, González-Meler & Long (1997) reported decreases of up to 15% in amount and 24% in activity of Rubisco when plants were grown under elevated CO₂. Studying historic records of wheat and rice production, Amthor (1998) concluded that the increase in global CO₂ concentration in the past 200 years has had a minor effect on crop yields.

Evolution of programmed senescence

Returning to the significance of photosynthetic compensation point in deciding the fate of leaves in the canopy, if the evolutionary argument is correct and the origins of the photosynthetic apparatus really do imply a general requirement for gratuitous C disposal, then it would not be surprising to find a C overdraft horizon to be a common feature of many canopies. Let us consider further the disposable nature of plant parts. If terrestrial autotrophs are, as suggested, dedicated to unloading surplus C by a whole range of means, then such apparently profligate phenomena as autumnal leaf fall may be understandable. But when and how was this kind of lifestyle evolved? Cell separation and death, the major means by which the external architecture of plants is reconfigured, are ancient features of plant behaviour. The lytic potential of even single-celled or filamentous plants such as *Chlamydomonas* and *Chara* is high by virtue of their lysosome-like vacuole system (Moriyasu 1995; Park *et al.* 1999). The evolutionary origins of lysigeny and schizogeny may lie with the ancestral tendency to secrete highly aggressive hydrolases and oxidases from the cytoplasm into the ‘inner space’ of the vacuole and the ‘outer space’ of the extracellular matrix. A set, or genetically determined, lifespan was probably not a critical feature of the leaves of the earliest terrestrial plants, which were growing in virtually season-proof parts of a world into which evolution had yet to introduce fungal and invertebrate pathogens and predators. Nevertheless a deciduous *Glossopteris* flora was already well established in Gondwanaland during the Carboniferous era (Plumstead 1958). Abscission of lower megaphylls in primitive trees such as *Archaeopteris* (359–349 million years ago) probably played a role in controlling canopy morphology (Raven 1986). Abscission may have also been important in dehiscence of sporangia even before it became

significant in vegetative shaping of plants (Raven 1986). Green tissues of modern cryptogams certainly have the capacity to run through a yellowing process indistinguishable in its major features from angiosperm foliar senescence (Matile, Hörtensteiner & Thomas 1999). The habit of leaf turnover would have evolved as seasonal factors including colder temperatures and decreased daylength became part of the yearly cycle. The archetypal terrestrial plant form is the tree, and smaller herbaceous species with shorter life cycles, including the major crop plants, are thought to have developed from trees by colonization of more unstable habitats away from the even environment of the primeval forest (Corner 1964). From comparisons between extant and fossil plants, Raven (1986) concluded that no tracheophytes prior to the Jurassic were ruderals or ephemerals with life cycles of less than 1 year. Fast-growing land plants, such as annuals (relative growth rate up to 0.3 d^{-1}) evolved from slow-growing trees (relative growth rate about 0.03 d^{-1}) primarily by increasing the allocation of plant material to photosynthetic tissue. It should be noted that these views are at odds with Tilman (1988), who proposed that slow-growing plants evolved from rapidly growing plants.

Modern tropical forests may provide a glimpse of how life was in the earliest plant communities. Even here, patterns of leaf turnover are well established (Longman & Jenik 1987). Trees with continuously growing shoots shed leaves continuously. Typically leaf lifespans are in the range of 3–15 months. Flush growth is common (but often difficult to associate with any particular environmental cue). There are even some species, mostly monocots, which senesce in the monocarpic fashion. Although the bright autumnal colours of temperate deciduous woodlands are largely absent, ageing leaves of tropical forests usually lose chlorophyll and become yellowish and there is considerable recovery of mobile nutrients, indicating that abscission is preceded by a recognizable senescence-like process (Richards 1957; Chapin & van Cleve 1989). The general conclusions to be drawn from considering the likely evolutionary origins of programmed senescence are that the phenomenon is an ancient and probably near-universal feature of the genetic repertoire of higher plants, but it is variable in its emphasis during the life cycles of different species.

Senescence and C overcapacity

From the utilitarian agronomic perspective, the value of senescing leaves rests largely with their function in nutrient remobilization, and the canopies of modern crop varieties generally combine a prolonged presence phase followed by a fast and efficient senescence that reallocates a high proportion of biomass and mineral nutrients in the harvested fraction. Seed of mature sunflower, for instance, accounts for 55%

of the plant dry matter and 70–75% of its N (Sadras *et al.* 1993). Non-domesticated species would be expected to be less efficient at recovering materials from leaves before or during senescence. In a sense, the foliage of grain crop species shares the desirable (from the point of view of agricultural production) physiological features of the seeds, sequestering raw, mobilizable biomass to the point of hypertrophy. This connection may be a pleiotropic consequence of the operation of genetic programmes common to leaves and seeds (Thomas 1984). Although there are exceptions, it is broadly true that crop plants yielding small seeds with meagre reserves do not display emphatic patterns of foliar senescence, whereas senescence is most dramatic in species with large, energetically costly reserves (e.g. soybean and sunflower).

In the wider ecological context, senescing leaves are significant in other ways. The amounts and nature of compounds remaining in fallen leaves are important for ecosystem functioning by affecting, for instance, the rate of litter decomposition (Grime *et al.* 1996). The striking colours of autumn foliage bear more than a passing resemblance to those of showy flowers. Similar phytochemical components occur in petals and senescing leaves – anthocyanins, carotenoid derivatives, flavonoids – and the organelles characteristic of the highly coloured state, chromoplasts and gerontoplasts, are closely related in the plastid family tree (Sitte 1977). In many species, for example *Sorbus*, the brilliant colours of senescing foliage appear to supplement the attractiveness of the brightly pigmented fruit which ripens at that time, and may enhance the chances of fruit dispersal by animals. This has been referred to as ‘fruit flagging’ (Stiles 1982). Even species that simply turn yellow without apparently accumulating new richly coloured compounds may become more intensely photoactive in the non-visible regions of the spectrum. *Ginkgo*, for instance, accumulates a highly fluorescent compound in the epidermis that acts like an optical brightener (Matile *et al.* 1992).

From deploying highly visible leaves attractive to animal dispersers, it is a short step in developmental and evolutionary terms to organizing colourful leaf-like structures into insect-pollinated flowers. Programmed foliar senescence was probably well established in cryptogams long before flowers appeared on the scene. Was the chloroplast–gerontoplast transition appropriated during the evolution of angiosperm flowers and fruits, which owe their colours to chromoplasts? It may be that the evolution of flower form and pigmentation originates with the characteristic metabolism of senescing leaves. The comparative biochemistry of chlorophyll catabolism is informative in this respect (Matile *et al.* 1999). The pathway of chlorophyll breakdown up to at least the ring-opening enzyme phaeophorbide *a* oxygenase is known to be encoded in the genomes of unicellular algae such as *Chlorella* and *Chlamydomonas* (Doi *et al.* 1997; Engel

et al. 1991), and the activity of the next enzyme in the sequence, RCC reductase, has been observed in *Selaginella* (Hörttensteiner *et al.* 1999). The fact that mosses, ferns and conifers are genetically competent to carry out the conversion from chloroplast to gerontoplast suggests that this capability either predates the appearance of chromoplasts in evolution, or is at least derived from some common ancestral plastid form. Chromoplast differentiation (Camara *et al.* 1995), a key process in entomophily, fruit dispersal and angiosperm evolution, is possibly a variation on the more ancient theme of plastid transition leading to gerontoplasts. The corolla was an innovation of mid-Cretaceous rosids (Crepet *et al.* 1991). Before this, the stimulus that attracted insects to flowers was probably not visual. This suggests that an elaboration of plastid differentiation pathways happened somewhere around the late Cretaceous period, a time of rapid angiosperm diversification.

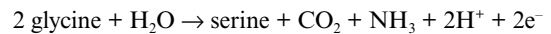
The general message from this speculation is that the propensity for biochemical improvisation, evident throughout the plant kingdom from the extent of secondary product elaboration, including foliar and floral pigmentation, is perhaps another manifestation of C overcapacity, permitting speculative metabolic doodling which has a negligible impact on fitness but occasionally has a significant evolutionary payoff.

Nitrogen in relation to offloading resources

If we start from the position that a plant generally has more fixed C than it knows what to do with, following the fate of this C can lead to instructive and often unexpected conclusions. To take an example from nutrition, many (but by no means most) higher plants have a voracious appetite for N. Conditioned by human experiences with crop species, it is customary to consider N as a serious limiting factor for growth. Nitrogen assimilation processes are high consumers of energy and C skeletons. But one could equally well regard N as a metabolic sink for excess ATP, reducing power and reduced C. For example, symbiotic root nodules make a large contribution to resource dumping in legumes (40–50% of each day's photosynthate is processed by the nodules, and about 50% of this C is respired away; Gordon *et al.* 1987), while simultaneously enhancing the metabolic sink function of reduced N. Nitrogen could also take reduced C out of the osmotic and metabolic picture by, for instance, sequestering it in a high-molecular-weight form undergoing minimal turnover, perhaps as an enzyme with a rather low catalytic activity. If that enzyme could itself eject C from the cell as one of its properties, so much the better. All of which adds up to an accurate description of Rubisco. This view of N as a sink for reduced C, and of carbohydrates not often being limiting for plant growth, is consistent with observations made by (Stitt & Schulze 1994) in experiments with tobacco (*Nicotiana tabacum*) transformed with

antisense *rbcS* to decrease expression of Rubisco. These authors pointed out (i) the key role of Rubisco as an N store; (ii) a weak association between Rubisco activity and C assimilation in wild plants; (iii) the lack of consistent association between C assimilation and plant growth; and (iv) the downregulation of nitrate assimilation associated with decreased availability of carbohydrates.

An important example of N metabolism functioning as a sink for excess C concerns the reassimilation of ammonia liberated during photorespiration, which consumes a large proportion of the ATP and reduced ferredoxin generated by photosynthetic reactions in the chloroplast of C₃ plants (Wallsgrave *et al.* 1983). A major, often neglected, aspect of photorespiration is the stoichiometric release of NH₃ in the mitochondria:



The flux of N through this pathway could be up to 10 times the rate of primary N assimilation (Wallsgrave *et al.* 1983). The photorespiratory N cycle (Keys *et al.* 1978), involving release of NH₃ in mitochondria and its reduction in chloroplasts, is consistent with the putative role of N as a sink for photosynthetic products. Photorespiration has long been regarded as a wasteful and agronomically undesirable process. From an evolutionary perspective, the oxygenase function of Rubisco was likely to have been selectively neutral when it was operating at very low O₂ tensions in Precambrian cyanobacteria (Raven 1986), but it could be argued that once atmospheric O₂ started to increase at about the Ordovician, the fortuitous photorespiratory function of this enzyme became increasingly significant as a mechanism for re-emitting C at the point of fixation. According to this point of view, trying to disable photorespiration is a risky, perhaps unattainable, goal for crop improvement. Apparent exceptions to the principle of C avoidance, such as the C₄ syndrome, may be regarded as instances of *post post hoc* add-ons.

Futile cycles and other physiological extravagances

Metabolic pathways in plants have a noticeable tendency towards making futile cycles and other mechanisms for the seemingly aimless consumption of resources. A central feature of cellular C relations is the loading of sucrose into the central vacuole. This organelle is also the primary intracellular location of invertase, a sucrose-catabolizing enzyme that hydrolyses the glucose–fructose bond without recapturing the released energy as nucleoside triphosphate. The result is a futile cycle (Scholes *et al.* 1996). By organizing sucrose turnover in this way, metabolism can idle while retaining the flexibility to respond quickly when homeostasis is disturbed, for example by altered source–sink conditions (Geigenberger & Stitt

1991). The terminal oxidase system of mitochondria is another distinctive feature of plant metabolism. All angiosperms, many algae, a few fungi, but probably no animals have mitochondria capable of passing electrons not only to the cytochrome chain, but also to an alternative oxidase that reduces molecular oxygen to water (McIntosh 1994). The alternative pathway is non-phosphorylating and, in tissues such as the spadix of aroid flowers, generates the heat that volatilizes chemical attractants for pollinators (Hoefnagel & Wiskich 1996; Meeuse 1975). As in the case of the sucrose-invertase cycle, the alternative oxidase system functions as an energetically expensive metabolic engine that can even out physiological imbalances (Vanlerberghe & McIntosh 1997).

A further illustration of the way in which plants employ conspicuous-consumption redundancy for cellular regulation concerns the stoichiometry of membrane complexes. Correct assembly of thylakoid pigment proteolipids requires accurately matching the supplies of all the components. In general this is not controlled by balanced gene transcription. Instead proteins, pigments and lipids are produced in excess, complexes are generated by self-assembly, and surplus materials or malformed products are mopped up by post-translational catabolic systems (Thomas 1997). This is an effective way of making the fabrication of complicated structures highly responsive to cellular and environmental conditions; but only energy- and resource-rich organisms can indulge in such luxury on the scale that plants do.

Morphological implications of overabundance

Morphology also plays a role in dealing with C surfeit. Plant form is generally defined by redundant shoots and reproductive structures (Sachs *et al.* 1993; Stephenson 1981) and also by storage organs. Accumulation of reserve substances (starch, oils, sucrose) is usually interpreted as having arisen as a way of evening out supply-demand relations over time in a fluctuating environment. It could equally well be argued that reserves originated as resource dumps, and only subsequently became exploited as investments for the future. To account for these seemingly divergent perspectives, Chapin, Schulze & Mooney (1990) distinguished between reserve formation competing with growth, and accumulation of storage when growth is limited by other factors. Similarly, wood can be looked at in two contrasting ways. Rigid, compression-resistant lignin was exploited early in the evolution of terrestrial plants as a means of resisting implosion of the water-conducting xylem elements (Raven 1986). On the other hand, what is a tree if not a colony of autotrophs living on the surface of a large deposit of excreted C in the form of cellulose? The general lesson we take from these observations is that developing novel functions for offloaded assimilate could be an effective evolutionary tool.

Roots may have a particularly significant function in balancing incoming resources with limited capacity to utilize them. In many ecosystems, net primary production of roots exceeds that of the above-ground fraction (Caldwell 1987). Resource allocation to roots generally reduces, and allocation to leaves increases, when growth conditions are unfavourable for photosynthesis (low light, low CO₂) and/or when soil resources are high (Evans 1989; McConnaughay & Coleman 1999). The physiological mechanisms underlying the functional equilibrium between shoot and root are complex (Aerts & Chapin 2000), but an important factor is tissue turnover. In general, turnover of leaves and roots is low in nutrient-poor environments, a pattern of behaviour usually rationalized in terms of the need for nutrient conservation (Eissenstat & Yanai 1997). But it could as well be argued that high resource availability drives root and leaf turnover, a strategy for offloading excess resources.

Plants that are adapted to N-limited environments often demonstrate a characteristic kind of resource rejection. Forest communities exposed to polluted atmospheres, resulting in high loads of wet and dry N deposition, can protect themselves against overnutrition. Rennenberg *et al.* (1998) showed that the nitrophobic species *Picea abies* and *Fagus sylvatica* respond to excessive N by reducing root uptake of NO₃. There is also smaller investment of C below-ground, with consequences for root growth and mycorrhizal associations. Lee & Caporn (1998) have described another example of adaptive resource rejection by natural communities, showing that the nitrate reductase activity of *Calluna vulgaris* from pristine sites generally tracks deposition events, whereas the enzyme of mosses from locations with a history of exposure to atmospheric pollution is inhibited, thereby limiting N uptake. Nitrogen fertilization might tend to extend leaf lifespans, but in a phosphorus-limited environment, say, the need to mobilize and recycle P would be overriding and leaves may senesce without wholesale protein breakdown. *Arabidopsis*, a non-mycorrhizal nitrophobe, shows just this kind of foliar senescence pattern under some circumstances. Plenty of species shed leaves when they still contain considerable amounts of potentially recoverable N, for example alder (*Alnus glutinosa*, an N-fixer) and some genotypes of *Fraxinus excelsior* (Bortlik, Gut & Matile 1987; Neave, Dawson & DeLucia 1989). These are examples of overnutrition regulated by dumping raw materials. Resources that are discontinuously distributed in the environment, such as phosphorus (spatially patchy) and water (availability fluctuating in space and time), really do seem to pose capture problems for plants, and ecophysiological measures (mycorrhizal associations, for example) have clearly been adopted during evolution to cope with the limitations in supply. But C and N, which are everywhere, and just a few enzymatic conversions away from entry to metabolism, are different.

Conclusion

From the perspective of the evolutionary origins of resource capture in plants, notions of 'efficiency' and 'economy' applied to cellular energy or C relations, if they are meaningful at all, do not necessarily have the adaptive significance they may have for heterotrophs. In particular, to look at the physiology of fundamental plant processes from the standpoint of crop species and the demands and priorities of agricultural production is often to invert the imperatives that shaped the design in the first place. When this happens, attempts to 'improve' a particular attribute, such as breeding for increased C assimilation rate or lower photorespiration, will always end up swimming against the evolutionary tide – which may account for the conspicuous lack of success of such strategies (Evans 1993). It appears that when plants took to the land they encountered a problem of surplus. They consequently developed habits not unlike those of the citizens of affluent societies: dumping, hoarding, freedom from subsistence, the pursuit of often frivolous objectives, great diversity of lifestyle, conspicuous consumption, and complicity in the rise of opportunist parasites. Every time the sun comes up it presents the green plant with a dilemma arising from material excesses, the legacy of half a billion years of evolution.

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