Excess carbon: the relationship with phenotypical plasticity in storage and defense functions of plants

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Abstract

Photosynthates accumulating in plants in amounts exceeding those needed to saturate growth are considered as *excess carbon*. Enhancement of carbohydrate excretion by unicellular algae is the simplest phenomenon where *excess carbon* may be identified. Carbon storage and carbon-based defense are the functions alternative to growth for *excess carbon* allocation in higher plants. After revising literature definitions of storage and defense, a conceptual model that relates the phenotypical variation in the relative carbon allocation to each function with the source to sink ratio is developed. Environmental factors promoting the accumulation of total non-structural carbohydrates in source leaves, a parameter proposed as an estimation of the source to sink ratio, include nutrient stress, low temperature, water stress, sink removal, light intensity and CO_2-enrichment. The revision of the effect that nutrient stress, water stress, light intensity and CO_2-enrichment have on the concentration of some carbon-based defensive compounds, such as phenolic compounds and structural polysaccharides, in different plant organs shows an increasing effect by many of these environmental factors. However, whereas phenolic compounds concentration is increased by nutrient stress, light intensity and CO_2-enrichment, concentration of structural polysaccharides is increased by nutrient stress and maybe by light intensity, but clearly not by CO_2-enrichment. Although the conceptual model should be better redrawn for every environmental factor affecting source-sink balance and for each kind of compound, the general trend is the allocation of part of *excess carbon* to carbon-based secondary compounds such as condensed tannins. Finally we consider some ecological consequences of *excess carbon*.

Key words: Defense, *excess carbon*, growth, phenolic compounds, storage, structural polysaccharides, total non-structural carbohydrates.

Resum. *Excedents de carboni*: *relació amb la plasticitat fenotípica del magatzematge i de les defenses dels vegetals*

Es consideren excedents de carboni els fotosintats que s'acumulen als vegetals en quantitats superiors a les necessàries per a saturar el creixement. El fenomen més simple en el qual es poden identificar excedents de carboni és 1'excreció de carbohidrats per algues unicel·lulars. En plantes superiors, el magatzematge i la síntesi de compostos de base carbònica per a defensa són les funcions alternatives al creixement per l'assignació dels exce-

dents de carboni. Després de revisar als estudis les definicions de magatzematge i de defensa, es desenvolupa un model conceptual que relaciona la variació fenotípica en l'assignació relativa de carboni a cada funció amb la ràtio entre font i embornal. Proposem l'acumulació de carbohidrats no estructurals en fulles productores com una estima de la ràtio entre font i embornal. Els factors ambientals que promouen l'acumulació de carbohidrats no estructurals en fulles productores són 1'estrès nutricional, les baixes temperatures, 1'estrès hídric, la supressió dels embornals, la intensitat llumínica i l'enriquiment en CO_2. La revisió de l'efecte que 1'estrès nutricional, l'estrès hídric, la intensitat llumínica i l'enriquiment en CO_2 té en la concentració d'alguns compostos de base carbònica amb funcions defensives, com els compostos fenòlics i els polisacàrids estructurals, en diferents òrgans mostra en molts casos una tendència positiva. La concentració de compostos fenòlics, però, augmenta amb l'estrès nutricional, la intensitat llumínica i 1'enriquiment en CO_2, mentre que la concentració de polisacàrids estructurals augmenta amb 1'estrès nutricional, i potser amb la intensitat llumínica, però no amb 1'enriquiment en CO_2. Malgrat que el model conceptual hauria de construir-se per a cada factor ambiental que afecti el balanç font-embornal i per a cada tipus de compost, la tendència general és 1'assignació de part dels excedents de carboni a compostos secundaris de base carbònica, com els tanins condensats.

Paraules clau: carbohidrats no estructurals, creixement, defensa, excedents de carboni, fenols, magatzematge, polisacàrids estructurals.

Introduction

A central idea in the study of plant carbon economy is that photosynthesized carbon can be invested, as a general pattern, in four different functions: growth, reproduction, storage and defense, that are restricted to three in the vegetative phase. Carbon is used to build structural polymers (polysaccharides and lignin) and carbon skeletons for growth metabolism, and to construct polymers (polysaccharides, lipids, tannins, terpenes, hydrocarbons) and their precursors for storage and defense. A trade-off among the three functions arises from the impossibility of spending the same atom of carbon in more than one function.

This paper aims to discuss alternatives for carbon allocation in environmental contexts where growth is limited by a factor other than carbon supply. Limitations in growth refer to actual growth rates below the maximum growth rate of the species under optimal conditions.

Excess carbon

Photosynthates can accumulate in plants in amounts exceeding those needed to saturate growth. This occurs because when a resource different than carbon (e.g. nutrients) is limiting growth, the inhibitory effect on growth is more intense than the inhibitory effect on photosynthesis (Chapin III, 1980). As a consequence of carbon acquisition exceeding growth requirements, the products of photosynthesis accumulate primarily as carbohydrates. This phenomenon leads to what is known in literature as *excess carbon* (or also as *carbon overflow*) (Baas, 1989b; Bryant et al., 1983b; Dubinsky, 1994b; Herms and Mattson, 1992b; Lambers and

Poorter, 1992b; Lawlor, 1994b; Mague et al., 1980b; Smetacek and Pollenhe, 1986b; Tuomi et al., 1991b), and it has been described for terrestrial (Bryant et al., 1983) as well as for marine plants (Mague et al., 1980).

Excess carbon *in unicellular algae*

Although the concept of *excess carbon* has been widely used, it has not been treated in a quantitative way due to its difficult identification. As a starting point we want to focus in the simplest photoautotroph organisms in which it can be studied: unicellular algae. The choice is based on the conceptual simplicity that these plants present because of their unicellularity: 1) the whole organism contained in a single cell implies total identity between cell processes and whole plant processes, and 2) life cycle restricted to a single cell give an easy perception of growth by identification with cellular division.

But the most attractive characteristic trait of unicellular algae for the study of *excess carbon* is the excretion of carbohydrates to the external medium conducted by some of them. Carbohydrates are excreted in a dissolved form and can form polysaccharides with a variety of morphological forms known as extracellular polymeric substances or mucilages to which defense and survival functions have been attributed (Smetacek and Pollenhe, 1986). However, a physiological basis has also been invoked to explain the excretion: the internal carbohydrate pool is saturated and leads to the efflux of excess carbohydrates because of an imbalance between production and utilization of photosynthate (Mague et al., 1980; Soeder and Bolze, 1981).

Excretion of polysaccharides to the external medium by phytoplankton is accepted as an usual trait both in cultures (Jensen, 1984) and in natural habitats (Mague et al., 1980). The release of dissolved organic matter by healthy phytoplankton is a general phenomenon (Fogg, 1991), but the percent of photosynthetic carbon excretion is smaller when cultures are in logarithmic phase than in growth limited stationary phase (Myklestad and Haugh, 1972; Myklestad et al., 1989). Increases in excretion from 10% of photosynthesized carbon in the logarithmic phase to 60% in the stationary phase have been reported (Myklestad et al., 1989). In planktonic ecosystems excretion reaches 10% of primary production (Jackson, 1993). Excretion of carbohydrates is enhanced under culture conditions limiting growth such as nutrient stress (de Philpps et al., 1993; Ignatiades and Fogg, 1973; Jensen, 1984; Myklestad, 1977; Myklestad, 1974; Obernosterer and Herndl, 1995; Soeder and Bolze, 1981; Vieira and Myklestad, 1986), salinity stress (Giordano et al., 1994) and culture conditions increasing the availability of energy such as high light (Mague et al., 1980). In natural conditions the highest percentages of excretion have been observed in samples exposed to high light and in samples from oligotrophic areas (Mague et al., 1980). In oligotrophic habitats excretion reaching 50% of photosynthetic carbon have been measured (see Mague et al., 1980). In marine oligotrophic environments excreted carbohydrates may form aggregates in a phenomenon known as «marine snow» (Herndl, 1992).

The benefit of excretion could be the by pass of absorbed irradiance exceeding the amount needed for growth (Fogg, 1991; Fogg, 1983; Wood and van Valen, 1990). Reduced carbon would be used as a carrier of excess light energy converted into chemical energy. Thus, to provide a «safety valve» for excess photosynthate (Dring, 1982) and to dissipate energy exceeding demands for growth as well as storage and photorespiratory capacities (Wood and van Valen, 1990) seems to be a physiological explanation consistent enough to explain increases in excretion under growth limiting conditions, without the need of involving other survival functions. However, excretion has been also considered as a continuous loss by passive permeation through the cell membrane (Bjornsen, 1988). Enhancement of excretion of carbohydrates does not compete with growth when it is limited, nor with reproduction, thus having no cost in terms of fitness reduction. Excretion in unicellular algae provides a clear evidence of photosynthetic apparatus being able to work at excess rates and of photosynthates being produced by photoautotrophic organisms at rates exceeding their demands. It also provides a good tool for a quantitative approach to *excess carbon* phenomenon under different environmental contexts.

Difficulties in identifying excess carbon

However, scaling up from single cell algae to more complex higher plants complicates the identification and measurement of *excess carbon* as well as of plant functioning. First complication is found in the greater spatial complexity of pluricellular plants with differentiation among cell types, tissues and organs. Specialization implies a reduction in the physiological processes realized in a cell, tissue or organ that are then spread in different parts of the plant. There is spatial separation between resource capture and resource use, which are connected by a transport system. As a result, physiological processes are integrated in spatially wider units. Second complication is derived from longer life spans in higher plants than in unicellular plants. Life spans are often longer than climatic annual seasons. Availability of resources is variable in time and there is asynchrony between resource capture and its use, which results in more complex patterns of storage. As a result, balances occur in longer periods of time. Ontogeny and phenology introduce large species spatial and temporal variation in allocation for growth of different organs and tissues (Kozlowski, 1992) and for other functions. In synthesis, the difficulties come from the variety of growth forms and life strategies in higher plants.

In unicellular algae, reproduction can be identified with growth, which is expressed as number of cell divisions per day. In higher plants, growth (cell division and cell enlargement and its translation into rate of biomass accumulation) does not correspond with reproduction although it is used as an estimation of reproduction (or fitness) (Kozlowski, 1992). In higher plants, reproductive structures are stronger sinks than vegetative structures (Cannell, 1985; Kozlowski, 1992) and reproduction becomes the most important function over growth, storage and defense. Significant amounts of stored reserves, and even defense and growth re-

sources, are mobilized to reproduction. In the extreme case of semelparous plants, reproductive effort is absolute and the plants die. The important changes in carbon economy between vegetative and reproductive stages of higher plants are not discussed in this essay which centers the discussion of *excess carbon* in the vegetative stage.

Storage and defense

In higher plants at vegetative stage, with no excretion to the external medium, storage and defense are the two alternatives for carbon allocation when growth is limited. The temporal and spatial complexity, as well as life strategy, make difficult to discern between constitutive storage or defense that divert resources from growth at the time of formation, and *excess carbon* in form of storage or defense that does not. Thus, a previous review of definitions of both functions is needed to analyze their role as alternatives. The following definitions are not only valid for carbon, but for other resources such as nutrients.

Storage

Storage is defined as the pool of resources that builds up in the plant and can be mobilized in the future to support biosynthesis for growth or other functions (Chapin III et al., 1990). Regarding carbon the main storage products are polysaccharides and sugars, but also organic acids and probably other compounds such as lipids (Chapin III et al., 1990). Four different classes of storage have been recognized:

Reserves. 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 (Chapin III et al., 1990)

Interim deposition. Storage compounds cycling on a short-time basis (e.g. day-night) (Heilmeier and Monson, 1994).

*Recycling. R*eutilization of compounds whose immediate physiological function contributes to defense (e.g. alkaloids) but which can subsequently be broken down to support future growth (Chapin III et al., 1990).

Accumulation. Increase in compounds that do not directly promote growth. It occurs because resource supply exceeds demands for growth and maintenance (Millard, 1988).

For discussion of *excess carbon*, storage interim deposition will be obviated since it cycles with a periodicity shorter than the required to develop source-sink balance and represents transitory storage. Recycling class is mostly described for nutrient storage and will be also avoided as it represents a small fraction of carbon (Chapin III et al., 1990). In any case, recycling represents a link between storage and defense through multifunctional compounds.

Chapin et al. (1990) differentiation between reserves and accumulation is dependent on whether there is or there is not diversion of resources (carbon) from growth, although from chemical and cellular localization points of view both are identical. As defined by Chapin et al. (1990) accumulation represents exactly a fraction of *excess carbon*.

Defense

Plant defenses against herbivores and pathogens may be physical or chemical. For our aims we only review the chemical ones. Chemical defenses are those components of secondary metabolism with properties useful for protection against other organisms such as herbivores or pathogen fungi and bacteria. They can be nitrogen-based defenses (containing N atoms: alkaloids, cyanogenic glicosides, toxic aminoacids) or carbon-based defenses (non-N containing phenolics, terpenes, resines...). The latter can be linked to *excess carbon* and will be taken into account in this essay. Thus, in the next sections when we refer to defenses we are referring to carbon-based defenses. Two different classes of chemical defenses have been described:

Induced defenses. Chemical defenses synthesized *de novo* after a damage produced by an herbivore or pathogen or in front of its presence. The new synthesis raises the constitutive level or provides a new defense that was not previously present (Zangerl and Bazzaz, 1992).

Constitutive defenses. Chemicals that are not affected by the presence of herbivores or pathogens. Constitutive defenses show phenotypic variation that has been attributed to variations of resource pool (Bryant et al., 1983) and related to *excess carbon* when the defenses are carbon based (Bryant et al., 1983; Herms and Mattson, 1992; Tuomi et al., 1991; Tuomi et al., 1988).

The following discussion will be centered on constitutive defenses which do not require to introduce specific biotic interactions.

The Balance Hypotheses

Two complementary hypotheses have been formulated to relate *excess carbon* and constitutive defense: the Carbon Nutrient Balance (CNB) (Bryant et al., 1983; Tuomi et al., 1988) and the Growth Differentiation Balance (GDB) (Herms and Mattson, 1992; Loomis, 1932; Lorio, 1986) hypotheses.

The CNB hypothesis predicts that concentration of carbon-based secondary compounds (CBSC), mainly with defensive function, is positively correlated with plant carbon/nutrient ratio (C/N), whereas concentration of nitrogen-based secondary metabolites is negatively correlated with this ratio. Nutrient limitations that lead to accumulation of carbohydrates exceeding growth requests, generate increases of C/N and increases of CBSC concentration. On the other side light

limitations that decrease carbon availability, and consequently diminish C/N, decrease CBSC concentration.

The GDB hypothesis (Loomis, 1932; Lorio, 1986) states that secondary metabolism expression is a function of the budget between cell growth (cell division and enlargement) and cell differentiation. Growth dominates over differentiation while it is favored by internal and external factors because the resources are mostly channelled to it. When growth is limited, resources are diverted towards secondary metabolism. Herms and Mattson (1992) revised the capacity of this hypothesis to explain phenotypic variations of constitutive defense and CBSC in general. The GDB hypothesis includes the CNB hypothesis and extends the predictions to any environmental factor affecting photosynthesis and growth with different intensity. They state that secondary metabolism is a function of available resource pool and the availability is a function of source as well as sink.

Growth relationships with defense and storage

The relationships between growth and defense have had two opposite approaches. One considers that defenses divert resources from growth and consequently have a negative impact on growth rate (Rhoades, 1979). The other approach considers defenses to have no cost in terms of growth rate (Bryant et al., 1988; Tuomi et al., 1988). The latter is based on the mentioned CNB hypothesis (Bryant et al., 1983) relating phenotypical variation in the level of carbon based defenses with *excess carbon*, and considering all constitutive defenses as *excess carbon* (Tuomi et al., 1988).

Assuming the trade-off between growth and defense, several models have been proposed to quantify the impact of defenses on growth. In addition to the direct costs of biosynthesis and maintenance, Gulmon and Mooney (1986) took into account the indirect costs. The indirect costs involve the reductions in plant growth (and reproduction) at some future time because of the allocation of carbon to defense during the present time. In addition to indirect costs, some models also include the benefits of defense in terms of herbivory reduction (Coley and Bryant, 1985; Fagerström, 1989; Gulmon and Mooney, 1986; Lerdau, 1992; Zangerl and Bazzaz, 1992).

The possibility of producing defenses «free» in growth terms or defenses without indirect costs is explicitly contemplated in one model that analyzes phenotypical variation of defense (Fagerström, 1989; Skogsmyr and Fagerström, 1992). Fagerström (1989) defines a parameter to quantify the degree of overlap between the resources required for growth and defense. The parameter ranges between 1 (total overlap) and 0 (no overlap) depending on whether growth and defense are limited or not by the same resource. Under a nitrogen limited context, the investment of nitrogen for purposes other than growth has a negative impact on growth, but the investment of carbon (a non-limiting resource) to increase carbon-based defenses (non-nitrogen consuming) above constitutive level does not have any negative impact on growth. Thus, when the resource taken into account

is carbon, the degree-of-overlapping parameter is also a measure of the fraction of the carbon pool that can be assigned to *excess carbon*.

Other authors also contemplate the existence of constitutive defenses not competing with growth (Chapin III et al., 1990; Herms and Mattson, 1992). Chapin et al. (1990) considered phenolics, tannins, lipids and lignin as compounds that can be used for non-storage accumulation.

As far as we know, there are few explicit models extending to storage cost-benefit analysis in similar terms than those for defense (e.g. Bloom et al., 1985). However, there is no doubt that concepts such as indirect costs and benefits can be also extended to storage as well as the degree-of-overlapping parameter. Similarly to carbon based defenses, increases in carbon storage above constitutive levels under nitrogen limited growth clearly do not compete with growth.

The revision of definitions and classifications of storage and defense in literature revealed an interesting common point between storage and defense functions that is fundamental for a phenotypical approach to *excess carbon*: when the resource limiting growth is different from the resource required for defense or is not the resource to be stored, increases in both defense and storage above constitutive levels can be considered as not competitive with growth.

Storage, defense and *excess carbon* (SDEC) integration

Each plant species has an specific pattern of partitioning of carbon among the three functions of growth, storage and defense, that is genetically determined and have an evolutive meaning (Bloom et al., 1985; Poorter and Bergkotte, 1992). For example, in a survey of published data related to defense it is concluded that quantitative production of secondary compounds is heritable in more than 50% (Berenbaum and Zangerl, 1992). We consider the genetically fixed percentage of carbon allocation to each function the one found when growth is equally limited by all the resources (Bloom et al., 1985), or what is similar, when there is a source-sink balance.

Deviations from balanced source-sink relationships cause variation of partitioning of carbon to growth, storage and defense above and below the balanced level. The SDEC conceptual model described in Figures 1 summarizes these variations and includes terminology used in literature. The X axis of Figure 1 represents the relative importance of each one of the three functions of a plant organ (e.g. leaves) in the vegetative stage: growth, storage and defense measured as percentage of allocation of carbon. The Y axis of Figure 1 represents a gradient of source-sink relationships. The model is conceptual and does not imply quantification of percentages which are dependent on species ecology and evolution (species specific).

In source-sink balanced conditions (line B-B'), the percentage allocation to each function is the genetically determined balanced amount. We call these percentages balanced storage and balanced defenses.

In source-sink unbalanced conditions, phenotypic deviations from balanced storage and defense take place. When sink overcomes source (line C-C'), stor-

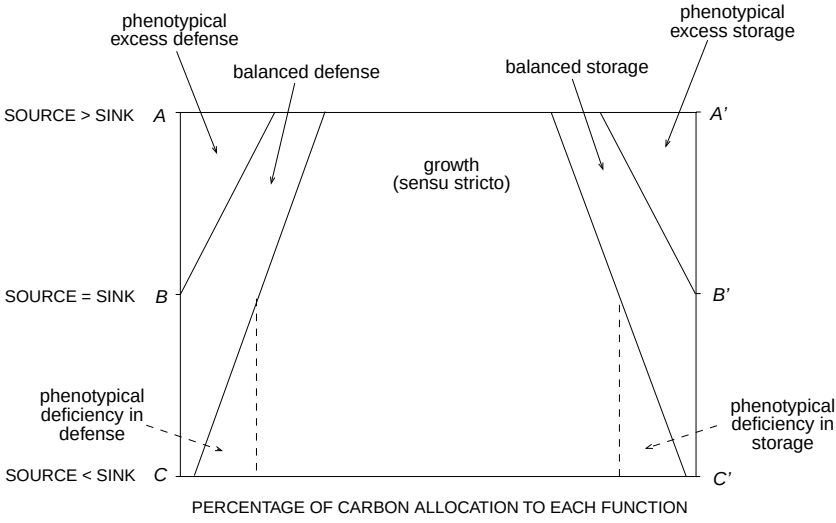

Figure 1. Conceptual model representing the relationship between the percentage of carbon allocated to each of the three functions of a plant in the vegetative stage (growth, storage and defense) and the plant source to sink ratio. For a detailed explanation see text in section **Storage, defense and excess carbon (SDEC) integration**.

age and defenses are considered to be below the balanced level. Thus, a deficiency in storage and defense can be defined as the difference between the balanced and the actual percentage.

When source overcomes sink (line A-A'), both defense and storage are overinvested relative to the balanced level. Two fractions can be defined: the balanced and the excess fractions. The balanced fraction, as defined previously, is a genetically fixed percentage of growth. Across de Y axis, balanced fraction keeps constant relative to growth from source-sink balance (B-B') to the top end (A-A'), but because of the existence of the considered excess fraction, its percentage of the total allocated carbon pool is lower. The excess fractions are the percentages of defense and storage synthesized from resources not diverted from growth. They are defined as total defense or storage minus the balanced percentage.

The relations between *excess carbon* and excess storage and defense are clear. Given that there is a limitation in growth, carbon allocated to both classes is *excess carbon*. Excess storage fraction corresponds to the accumulation class defined by Millard (1988). Excess defense fraction corresponds to non-storage accumulation as used by Chapin et al. (1990) and the resources diverted to it have no overlap with growth according to Fagerström (1989).

Because balanced percentages are genetically fixed percentages of growth, limitations in growth are also limitations in balanced storage and defense. Somatic

growth or growth on a *sensu lato* includes growth *sensu stricto* (cell expansion and division) and the fractions of storage and defense that are associated (balanced fractions of storage and defense). Phenotypical *excess carbon* can be redefined as phenotypic accumulation of carbon exceeding the needed to saturate growth *sensu lato*. Thus, we can talk about phenotypic *excess carbon* in storage form (or accumulation storage) and phenotypic *excess carbon* in defense form (or accumulation defense).

Values assigned to storage and defense in Figure 1 are arbitrary as well as it is the slope of the lines separating growth and storage and defense. These lines define phenotypical plasticity and the slope must be determined for each species.

Assuming that balanced storage and defense are formed from resources completely diverted from growth (in the sense of reducing growth rate) the model closes the considerations about *excess carbon.* In this case balanced storage corresponds with reserves in Chapin et al. (1990) terms. Resources invested in balanced defense should have a total overlap with growth according to Fagerström (1989). According to this author terminology the degree of overlap between defenses and growth is the ratio of balanced defense to total defense (balanced plus excess defense).

The assumption that balanced storage and defense divert resources from growth may be questioned by evolutive considerations relative to the biotic (e.g. herbivore pressure) and abiotic (e.g. nutrient availability) environment in which each plant species have evolved. It must be studied whether the chronic *excess carbon* in plants evolved under poor nutrient environments could generate defense sinks with strict no diversion of resources from growth, as it has been suggested (Bryant et al., 1988; Tuomi et al., 1988), or not. If such was the case a fraction of *excess carbon* should be included as balanced defense. However, in the present paper we are only discussing the phenotypical aspects. For evolutive considerations the reader is refereed to Herms and Mattson (1992).

No differences exist between balanced and excess storage and defense in cellular localization or chemical nature. Our objective is not to introduce new compartmentations where nature does not. Thus, the definitions here introduced only search to clarify the concepts. We think it will be helpful specially for cost-benefits analyses of defense (and storage), which must take into account the environmental context where plants grow, or even where they had evolved.

Environmental factors affecting source-sink balance

Source-sink unbalances are primarily detected by variations in total non-structural carbohydrate concentration (TNC) in source leaves. TNC in source leaves is a function of carbon exchange rate (CER) and carbon export rate (CEpR). (Hendrix and Huber, 1986). CEpR is determined by the demand for photosynthate and may be assimilated to sink demand of carbon for growth and storage outside leaves. CER includes gross photosynthesis and leaf respiration and may be assimilated to source strength. Thus, TNC in source leaves can be used as an estimation of the source-sink balance, and in absence of whole plant measurements, the best approach to *excess carbon*.

Table 1. Primary effects of environmental factors on source and sink strengths and their consequences on concentration of total non-structural carbohydrates (TNC) on source leaves. Environmental factors are classified attending on whether they have a greater effect on source or sink. A reference example is provided for each factor.

Factor	Primary effect over Source	Sink	TNC conc.	Reference examples
Greater impact on sink				
Nutrient stress	-	--	+	Radin and Eidenbock, 1986
Low temperature	0/-	-/--	+	Körner and Pelaez, 1989
Water stress	-?	--?	+ ?	Wardlaw, 1993 (moderate stress)
Sink removal (e.g. defruiting)	0	-	+	Gucci et al., 1991
Greater impact on source				
Light intensity and duration	+ + / +	+/0	+	(duration) Layne and Flore, 1993
CO_2-enrichment	+ +	+/0	+	Farrar and Williams, 1991
source removal (e.g. defoliation)	-	0	-	Layne and Flore, 1993

Accumulation of TNC is the result of the uncoupling between photosynthesis and growth. Regardless of ontogenetical factors (source to sink transition during development (Baysdorfer and Basshan, 1985)), the environment-dependent uncouplings can be classified depending on whether the factor promoting the uncoupling has stronger effect on source or in sink. Factors like nutrient stress, low temperature, and moderate drought as well as sink removal affect source-sink balance by having greater effects on sink strength. On the other side, light intensity, CO_2-enrichment and source removal affect the balance by having greater effects on source strength. Table 1 summarizes the effect of some environmental factors on source and sink and on TNC concentration in source leaves.

Environmental factors with greater impact on sink

Sink-driven unbalances are due to low sensibility of primary steps of carbon gain to many environmental stresses which cause growth reductions (Chapin III, 1980; Körner and Pelaez Menendez-Riedl, 1989).

Nutrient stress has been the most studied factor. Increases in TNC concentration in source leaves of nutrient stressed plants are widely reported in higher plants (Ariovich and Cresswell, 1983; Fredeen et al., 1991; Gallaher and Brown, 1977; Radin and Eidenbock, 1986; Rufty et al., 1988; Thorsteinsson et al., 1987; Wilson and Brown, 1983). Based on direct evidences of N and P stress, a mechanism involving inhibition of leaf expansion has been proposed (Radin and Boyer, 1982; Radin and Eidenbock, 1986; Radin and Eidenbock, 1984).

Effects of low temperature on source and sink have been quantified by Körner and Pelaez (1989) by comparisons of high altitude plants having lower relative growth rate than low altitude plants. They stated that limitations of cell production by low temperature may be responsible of a 25% of the differences in growth rates between high and low altitude plants, whereas restrictions of photosynthetic carbon fixation by temperatures can account only for 5 % of the differences. Higher source to sink balance in high altitude plants is accompanied by their higher TNC concentration than low altitude plants ((Körner and Pelaez Menendez-Riedl, 1989) and references therein). Experimental results showing accumulation of TNC in plants grown at lower temperatures have also been reported (Smart et al., 1995).

Moderate drought has a greater impact on expansive growth than on photosynthesis (Bradford and Tsiao, 1982) and it has been associated with a general accumulation of TNC in leaves and stems (Herms and Mattson, 1992; Wardlaw, 1993). However, reported responses of TNC to water stress are confusing. Both increases (increase in starch and sucrose, (Massacci et al., 1996)) and decreases (higher decrease in starch than increase in sucrose, (Fredeen et al., 1991)) have been reported. In addition there are shifts from insoluble (e.g. starch) to soluble carbohydrates (e.g. sorbitol) for osmotic adjustment ((Wang et al., 1995) and references therein) which can represent a large amount of carbohydrates. A question warranting a deeper discussion is whether carbohydrates used for osmotic adjustment can be considered as competing with growth or not. The confusion on reported effects of water stress on TNC may be a consequence of the different responses found depending on the duration and the intensity of the stress and on the interaction with nutrient uptake. At present stage no clear effect on TNC can be confidently assigned to water stress without specifying all those other interacting conditions.

And finally, the most evident factor affecting sink strength is the removal of sinks. Fruit removal is reported to promote increase in leaf starch concentration (Gucci et al., 1991). Removal or damage of other sinks (e.g. root herbivory) might have similar effects.

Environmental factors with greater impact on source

Light provides the energy required to reduce atmospheric CO_2. The curve of response to light intensity is one of the most well known traits of photosynthesis. Prolonging the duration of the light period or increasing the light intensity (while below saturation intensities) the energy available to reduce carbon dioxide increase, resulting in TNC accumulation (e.g. Lyne and Flore,, 1993).

Experimental source leaf removal, as a simulation of herbivory, decreases the TNC of the remaining leaves (e.g. Layne and Flore, 1993). Similarly, shading part of plant leaves decreases the starch concentration in illuminated leaves (Thorne and Koller, 1974).

The effects of CO_2-enrichment on source-sink balance are receiving a special attention due to the anthropogenic global change. Increasing the atmospheric CO_2 concentrations, net photosynthesis increases by increasing the carboxylation ac-

tivity of the Rubisco enzyme. The accumulation of TNC in plants grown under CO_2-enriched atmospheres has been widely reviewed (Farrar and Williams, 1991).

Others

CEpR is suggested to depend also on phloem loading capacity. According to it, accumulation of TNC on source leaves promoted by factors increasing source such as CO_2-enrichment, have also been attributed to the saturation of phloem loading capacity, specially in symplastic loaders (Körner et al., 1995). If this was the case, TNC accumulation would not be only a consequence of source-sink unbalance but also of transport limitation, and considerations on *excess carbon* should be restricted to source organs instead of to the whole plant.

The capacity of environmental factors promoting source increase (light intensity and CO_2-enrichment) to also promote sink increases (e.g. Stitt, 1991), and the capacity of environmental factors promoting sink decreases (e.g. defruitting or nutrient supply) to also promote source decreases (e.g. Barrett and Gifford, 1995), have not been discussed because our interest is centered on the translation of source to sink ratios into the concentration of TNC, and thus on *excess carbon*. Because of the same reason we have not discussed photosynthetic acclimation due to the possible feedback inhibition of photosynthesis by accumulated carbohydrates (e.g. Rogers et al., 1996)

Phenotypical *excess carbon* in storage form (TNC)

TNC accumulation in source leaves is the most usual data on carbon storage that is available in the literature and a short review has been done in the previous section. A very clear example of how TNC accumulation in source leaves is dependent on source-sink balance was provided by the use of transgenic plants (Fichtner et al., 1995; Fichtner et al., 1993). Transgenic plants transformed with «antisense» *rbcS* to decrease the expression of genes of Rubisco and consequently the source strength, allow the manipulation of source-sink ratio without altering the environmental context in which plants develop (Quick et al., 1991). Figure 2, drawn from data of Fitchner et al. (1993), show how photosynthetic rates and nitrogen nutrition interact to determine the concentration of starch in source leaves. Nitrogen nutrition determined the sink strength, which is reflected in the potential relative growth rate (RGR) at each nitrogen level. Photosynthesis or source strength was determined by Rubisco content. At each nitrogen supply, increases in photosynthesis had a different impact on RGR and starch concentration. At high nitrogen supply there was a high demand of photosynthates for growth and starch accumulated at lower rates. As nutrient supply decreased the growth demand of photosynthates decreased and plants became *sink-limited* as photosynthesis increased. Sink limitation was reflected in the accumulation of starch promoted by increasing photosynthesis without remarkable effects on RGR at medium and especially at low nitrogen supplies. The experiment provided an example of the de-

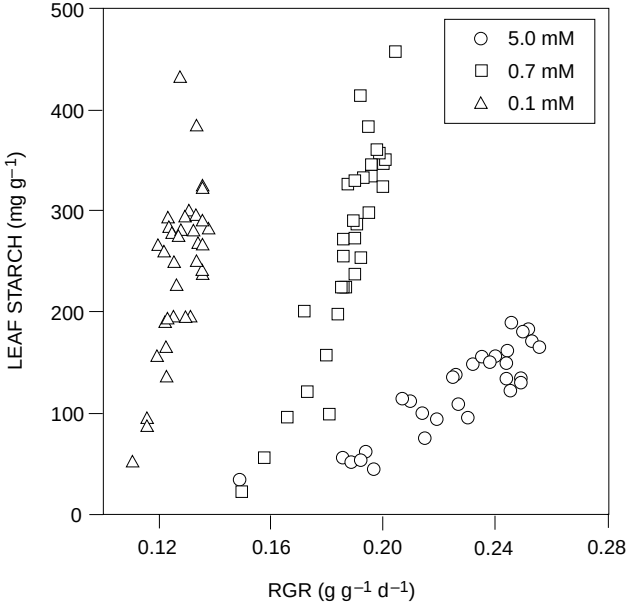

Figure 2. Starch concentration (mg g^{-1}) on a dry weight basis in leaves as a function of relative growth rate (RGR, g g^{-1} d^{-1}) in transgenic tobacco plants transformed with «antisense» *rbcS* to decrease the expression of genes of Rubisco and in wild-type tobacco plants. Transgenic and wild-type are not differentiated in the figure. The plants were watered once a day with a complete nutrient solution containing 0.1 (triangles), 0.7 (squares) and 5.0 mM NH_4NO_3 (circles). Redrawn from data of Fichtner et al. (1993).

pendence of carbon storage on source-sink relationships. At a same RGR, medium nitrogen plants with complete expression of Rubisco (i.e. high source to sink ratio) may accumulate as much as 700 % more starch than high nitrogen plants with low expression of Rubisco (i.e. low source to sink ratio). The starch accumulated at saturated RGR is a clear example of *excess carbon* in storage form.

Although both parameters are directly linked, for a quantitative approach whole plant TNC is a more real measurement of storage than leaf TNC. A study conducted on *Phaseolus lunatus* showed that whole plant storage depended on availabilities of resources favoring sink strength (nitrogen supply) or source strength (light intensity) (Mooney et al., 1995). Decreasing the nitrogen supply (i.e. decreasing the sink strength) whole plant TNC concentration increased (g_{TNC} g_{plant}^{-1}) at both high and low light intensities. Increasing the light intensity (i.e. increasing the source strength) whole plant TNC concentration increased (g_{TNC} g_{plant}^{-1}) at both high and low nitrogen supplies.

The experiments of Fichtner et al. (1993) and Mooney et al. (1995) reflected that when plant source-sink balance is shifted to source, carbon storage (TNC con-

centration) increases in plant tissues. At the light of the SDEC conceptual model (figure 1), a percentage of this carbon is not diverted from growth, but is exceeding growth requirements, and can be considered as *excess carbon*. Measuring which amount of carbon accumulated as storage can be assigned to *excess carbon* is difficult. The experiment with transgenic plants (Fichtner et al., 1993) provided some light to the problem of *excess carbon* quantification because it quantitatively showed accumulation of carbohydrates having minor or no impact on growth (measured as RGR).

A clear relation among storage and *excess carbon* is provided again by unicellular algae. Depending on the species, nutrient limitation may promote intracellular accumulation, or storage, of carbohydrates (Harrison et al., 1990) instead of excretion to the extracellular medium. In nitrogen depleted cultures of diatoms whereas for some species between 30 to 50% of the carbohydrates were found extracellularly, for other species under the same culture conditions almost all the carbohydrates were found intracellularly (Myklestad, 1974). Similarly, at high N/P ratios, whereas cultures of the diatom *Chaetoceros affinis* produced large amounts of extracellular polysaccharides (under extreme P-deficiency this production likely constituted the main photosynthetic activity), cultures of the diatom *Skeletonema costatum* under same conditions produced only small amounts of extracellular carbohydrates and large amounts of intracellular carbohydrates (Myklestad, 1977).

Phenotypical *excess carbon* in defense form

Defense has been one of the most studied of the functions attributed to secondary metabolites. The presence or absence of nitrogen in the molecule allows to separate secondary metabolites in two groups. Compounds such as alkaloids, non-protein aminoacids or cianogenic glycosides are nitrogen containing defensive compounds. Among the non-nitrogen containing compounds, the so-called carbon-based secondary compounds (CBSC), terpenes and phenolic compounds can represent an alternative for carbon allocation because carbon is the only resource required for their synthesis.

Phenolic compounds

In order to study the possibility of *excess carbon* being allocated to CBSC we surveyed literature reporting the effects of environmental factors on phenotypical variation of phenolic compounds concentration. Among the factors affecting source-sink balance and promoting the accumulation of TNC (Table 1), the survey yielded data on the effects of nutrient limitation, water stress, CO_2-enrichment and light intensity on concentration of several phenolic compounds. The results of the literature search are listed in the annexed tables (Table A.1 and A.2) and summarized in Table 2a,b,c. Among nutrient limitations, nitrogen limitation has been the most studied, either as the only limiting nutrient or in combination with other nutrients (reported as «several» in Table 2). Table 2 displays a clear tendency of phenolic compounds in general, condensed tannins and perhaps lignin

Table 2. Summary of the effects of environmental factors on concentration of *a)* phenolic compounds excluding condensed tannins and lignin, *b)* condensed tannins, *c)* lignin and *d)* structural polysaccharides. They are fully listed in Tables A.1, A.2 and A.3. Effects are summarized by counting the number of species presenting the same response (increase (+), decrease (–) or no effect (=)) to an environmental factor. Whenever the effects were different among plant organs or compounds, the effects are summarized with two symbols (+ / = , = /–, + /–). The effects are separated for different organs, being the first amount for leaves, the second for other organs and the third for leaf litter. ❶ comparison of the average of 27 species (Poorter et al. 1997). ❷ comparison of the average of trees growing in the shade with the average of conspecific trees growing in the sun for 16 species of trees in a dry deciduous forest of Madagascar (Ganzhorn, 1995).

a)	**Effect on phenolic compounds concentration**					
Environ. factor	+	+ / =	=	= /–	–	+ /–
Nutrient limitation						
Several	8/3/1	3/·/·	4/2/·	…	1/·/·	·/1/·
N	3/2/·	·/2/·	3/1/·	…	…	…
P	…	…	2/2/·	…	·/1/·	…
Water stress	·/1/·	·/1/·	1/·/·	…	2/1/·	…
CO_2-enrichment	6❶/1/·	2/·/·	4/1/·	1/·/·	1/·/·	2/1/·
Light intensity	7❷/2/·	…	…	…	…	…

b)	**Effect on condensed tannins concentration**					
Environ. factor	+	+ / =	=	= /–	–	+ /–
Nutrient limitation						
Several	9/2/1	2/·/·	4/3/·	…	1/·/·	…
N	1/2/·	…	1/·/·	…	·/1/·	…
P	…	…	·/1/·	…	1/1/·	…
Water stress	1/·/·	…	…	…	…	1/·/·
CO_2-enrichment	81❶/·/·	2/·/·	1/1/·	…	1/·/·	…
Light intensity	4❷/1/·	…	2/2/·	…	…	…

c)	**Effect on lignin concentration**					
Environ. factor	+	+ / =	=	= /–	–	+ /–
Nutrient limitation						
Several	2/1/·	·/1/·	1/·/·	·/1/·	…	…
N	1/·/·	…	1/·/3	…	…	·/1/·
Water stress	1/·/·	…	2/2/·	1/2/·	2/1/·	1/·/·
CO_2-enrichment	1/·/1	1/·/·	1❶/1/12	1/1/·	1/1/1	…
Light intensity	1/·/·	…	1/1/·	…	…	…

d)	**Effect on structural polysaccharides concentration**					
Environ. factor	+	+ / =	=	= /–	–	+ /–
Nutrient limitation						
Several	2/1/·	…	3/·/·	…	…	…
N	5/·/·	·/·/1	3/·/2	…	…	…
Water stress	1/·/·	1/·/·	…	3/2/·	2/3/·	…
CO_2-enrichment	…	2/·/2	4❶/1/8	…	1/·/·	…
Light intensity	5/3/·	…	2❷/3/·	…	…	…

to accumulate in plant tissues under general nutrient limitation, or under specifically nitrogen limitation, whereas when limiting nutrients are specifically different from nitrogen, such as P, the few data available do not show this tendency. The tendency is similar for CO_2-enrichment and increasing light intensity although lignin clearly does not respond to CO_2-enrichment and the data of light effect are too scarce to be conclusive. All kind of water stress effects on phenolic compounds concentration have been reported. The reported effects of temperature on phenolic compounds concentrations are also contradictory. Lignin concentration in five forage plant species was clearly higher in plants grown in the field at higher temperatures (Wilson et al., 1991). In contrast, accumulation of anthocyanin is a known response to cold stress (Christie et al., 1994; Leyva et al., 1995) as reviewed in the next section on regulation of phenylpropanoid metabolism.

Regulation of the phenylpropanoid pathway

In addition to the metabolic machinery involved in photosynthate synthesis and TNC accumulation as carbon storage, the accumulation of *excess carbon* as phenolic compounds requires the additional activation of the metabolic machinery of the phenylpropanoid pathway. The key enzymes in the regulation of the phenylpropanoid pathway are phenylalanine ammonia-lyase (PAL, the entry point enzyme) as well as 4-coumarate: CoA ligase (4CL) and chalcone synthase (CHS). Several examples of the activation of phenylpropanoid metabolism under conditions promoting the accumulation of *excess carbon* have been reported. Increases in transcription of genes of CHS and of two other enzymes of the flavonoid pathway have been reported under nitrogen stress (Bongue-Bartelsman and Philips, 1995). Increase in PAL activity has been reported as an acclimation response to low temperatures (Solecka and Kacperska, 1995). Increases in transcription of genes of PAL, CHS and 4CL have been described in response to cold stress, a response that was reversible and disappeared when plants were returned to control conditions (Christie et al., 1994). Similarly, cold stress increased the transcription of PAL and CHS but not in plants that were previously adapted to dark (Leyva et al., 1995).

Data on the regulation of phenylpropanoid pathway support the idea that *excess carbon* may also accumulate in phenolic compounds. No direct mechanism has been proposed to relate accumulation of carbohydrates with phenylpropanoid metabolism. However, nitrogen and phenylpropanoid metabolism have been related by an hypothesis suggesting that deammination of phenylalanine by PAL enzyme act as a mechanism to enhance availability of ammonia in N deficient plants, and this results in carbon skeletons that accumulate as flavonoids (Margna et al., 1989).

Among the factors involved in the regulation of phenylpropanoid metabolism, the most studied ones have been UV-light, blue-light and pathogen derived elicitors (Hahlbrock and Scheel, 1989), and specific light receptors have been postulated (Kubasek et al., 1992). In fact, the properties of phenolics against pathogens and of flavonoids as UV screens are well known (Waterman and Mole, 1994).

The dependence on light (Leyva et al., 1995) and the reversibility (Christie et al., 1994) of the increase in transcription of genes of phenylpropanoid enzymes in response to cold stress, as well as the response to N stress (Bongue-Bartelsman and Philips, 1995), suggest that, in addition to developmental and photoreceptor mediated regulations, carbohydrate status can also be involved in the regulation of phenylpropanoid pathway. In summary, the mentioned aspects of the regulation of the phenylpropanoid metabolism are in agreement with the accumulation of carbohydrates being linked to increase in phenolic compounds concentration. However, it is needed to further study which aspect of the carbohydrate metabolism, alone or in combination with some aspect of nitrogen metabolism, may be linked to the synthesis of phenolic compounds.

Multifunctional compounds: the case of structural polysaccharides

Lignin and structural polysaccharides are the main components of the cell wall. Thus their main function in plants is structural. However, both kinds of compounds have, in addition, defensive functions (Coley, 1986; Coley and Bryant, 1985; Turner, 1994). Lignins are polymers of phenolic nature and we considered them in the previous section on defense without paying attention to their structural function. Structural polysaccharides is the name given to the cell wall polysaccharides pectin, hemicellulose and cellulose. They do not contain nitrogen atoms and are also carbon-based compounds. Similarly to CBSC with only defensive functions, it has been hypothesized that structural polysaccharides concentration in plant tissues may show phenotypical variation related to *excess carbon* (Lincoln et al., 1993; Schulze, 1982); contrarily Chapin et al. (1990) in a review based on published data did not consider the possibility. Although available data on phenotypical variation of structural polysaccharides are more scarce than on phenolic compounds some reviews have already been published (Buxton and Casler, 1993; Buxton and Fales, 1994).

Table A.3 in the annex lists responses of structural polysaccharides to the environmental factors promoting accumulation of *excess carbon*: nutrient limitation, CO_2-enrichment, water stress and light intensity. These effects are summarized in Table 2d. From these data it can be concluded that both nutrient stress and light intensity tend to increase structural polysaccharides concentration. CO_2-enrichment seems to have no effect, and water stress tends to decrease structural polysaccharides concentration. In addition to the effects of resource supply, increasing temperature, a factor that can be considered to reduce *excess carbon* accumulation has been reported to increase the concentration of structural polysaccharides [(Buxton and Fales, 1994) and references therein].

Phenotypical *excess carbon* in other forms

CBSC of non-phenolic nature may have functions different from specifically defense against herbivores and pathogens, that are generally considered as survival functions. Some of those non-phenolic CBSC can also accumulate in conditions

favoring the accumulation of *excess carbon*. Unicellular algae, which lack a large part of the phenolic metabolism present in higher plants (Mole and Joern, 1994; Waterman and Mole, 1994), provide some examples. The green colonial *Botyrococcus braunii* accumulates from 25 to 80% of its dry weight as hydrocarbons, that promotes buoyancy, depending on the physiological state (Wolf, 1983). The relation ships between growth and secondary metabolism have also been pointed out in the green alga *Dunaliella bardawil*. This algae accumulates (-carotene (that protects against damaging radiation) under conditions that retard cell division including nutrient deficiency, salt stress, extreme pH or temperatures ((Ben-amotz and Avron, 1983) and references therein). The accumulation is also related to the integral quantity of light to which the culture is exposed during a division cycle (Bhom, 1987).

Overview on the SDEC conceptual model

The SDEC conceptual model proposed in figure 1 postulates that phenotypical variation in the allocation of carbon to carbon-based storage and defense functions is dependent on the source to sink ratio, and that when source>sink a fraction of *excess carbon* is allocated to defense in addition to storage.

In the depicted way (figure 1), the SDEC model assumes the same phenotypic plasticity for storage and defense functions. However, the slopes of the lines separating growth from storage and defense remain to be determined for each species and do not necessarily have to be the same for all kind of compounds. As carbohydrates are the starting point of any situation with *excess carbon*, it is likely a greater slope in the line separating growth from storage than in the line separating growth from defense.

Within defense function, different kinds of compounds: phenolic compounds (flavonoids, lignins, condensed tannins, lignin and other phenolic compounds), structural polysaccharides and even the non reviewed terpenes, may have different responses depending on the strengths of their biochemical regulation and the environmental factor. The effect of CO_2-enrichment is a clear example: there is a tendency to increase the concentration of phenolic compounds in general and condensed tannins whereas lignin and structural polysaccharides are not affected and terpenes are reported to present diverse responses (Peñuelas and Llusià, 1997). Conversely, nutrient deficiency, and probably high light intensity, tend to promote increased phenolics and structural polysaccharides concentrations.

Thus, as stated when discussing the regulation of the phenylpropanoid pathway, aspects of plant physiology other than carbohydrate availability may be involved in determining the response of different kinds of carbon-based compounds to source to sink ratios. Such is the case of temperature: cold stress activates the phenylpropanoid pathway but concentration of structural polysaccharides in forages is positively correlated with temperature.

The exact response to source to sink ratio is different for different environmental factors and different defense compounds, and the SDEC model should be considered in the framework of characteristic effects of each environmental fac-

tor affecting source-sink balance and of the particular biochemical traits of each kind of compound. However, the possibility of *excess carbon* being allocated to compounds having defense functions has been clearly demonstrated. This possibility has been found to materialize for several CBSC, such as the phenolic compounds (excluding lignin Table 2a,b), which present a general increasing trend in response to environmental factors promoting *excess carbon*.

Some final remarks

The *excess carbon* resource not required for growth may be allocated to storage, defense, structural or survival compounds, that, in agreement with other authors previously cited, are proposed to act as carbon sinks alternative to growth when growth is limited. We want to highlight that although in this essay we centered the discussion in plant functions, the phenotypic plasticity in allocation of carbon to storage and defense is not primarily dependent on the function but on the chemical nature of the compounds. The excretion of carbohydrates by unicellular algae reflects that the cause of *excess carbon* generation is alien to the function that *excess carbon* may have if it is accumulated as compounds of several chemical nature. The «decision» of which function/s (and compound/s) are favored must depend on how every function improves plant fitness under the environmental conditions that promote *excess carbon*, but an overall response involving all compounds (and thus functions) is not discarded.

Current studies on the regulation of photosynthesis (acclimation) under sink limited conditions involving sucrose, phosphor recycling, and nitrogen reallocation from photosynthetic machinery (Stitt, 1991; Wang and Nobel, 1996) will provide new insights on the physiological factors regulating accumulation of *excess carbon*. In any case, accumulation of *excess carbon* is shown as an intrinsic property of photoautotrophy under growth limiting conditions. The nature of the primary «function» assigned to *excess carbon*, such as the dissipation of excess energy, seems difficult to be elucidated. Independently of the cause of the growth-photosynthesis uncoupling, the recognition of the existence of *excess carbon* is interesting for its ecological (e.g. Baas, 1989) and evolutionary (e.g. Tuomi et al., 1988) consequences.

Appendix tables (tables A.1, A.2 and A.3)

Table A.1. List of literature surveyed reports on quantitative response of concentration of phenolic compounds to the following environmental factors: nitrogen and other nutrients availability, water stress and light availability. Effects are described as increases (+). decreases (–) or no clear effect (=) in the concentration of each kind of compounds. When the effects included more than one compound or organ, or contradictory reports irom different literature sources, the effects are summarized in the last column (S.). The table also includes the name of the species, the organ in which concentration of phenolic compounds were measured, the class of phenolic compound and the literature reference. When there were more than one nutrient involved (usually including nitrogen) the nutrient stress is not specified.

Environ. factor	Species	Organ	CBSC	Effect	Reference	S.
Nutrient limitation						
	Picea sitchensis	leaves	total phenolics condensed tannins	+ +	Hartley et al., 1995	PH + CT +
	Pinus muricata	leaves	total phenolics tannins	+ +	Northup et al., 1995	PH + CT +
		leaf litter	total phenolics tannins	+ +	Northup et al., 1995	PH + CT +
	Pinus contorta	leaves	total phenolics tannins	+ +	Northup et al., 1995	PH + CT +
N	*Pinus sylvestris*	shoots and roots	total phenolics resin acids	+ / = +	Holopainen et al., 1995	PH + / =
	Cupressus pygmaea	leaves	total phenolics tannins	+ +	Northup et al., 1995	PH + CT +
	Eucaliptus tereticornis	leaves	total phenolics condensed tannins lignin	+ = =	Lawler et al., 1997	PH + CT = LI =

Table A.1. Continuation

Environ. factor	Species	Organ	CBSC	Effect	Reference	S.
	Calluna vulgaris	shoots	total phenolics condensed tannins lignin	= = +	Hartley et al., 1995.	PH = CT = LI +
N	*Populus tremuloides*	leaves	total phenols tremuloiden + salicin condensed tannins	+ + + +	Bryant et al., 1987a	PH + CT +
	Betula resinifera	internodes	total phenolics papyriferric acid + condensed tannins	+ = =	Bryant et al., 1987b	PH + CT =
P			total phenolics papyriferric acid condensed tannins	– = –	Bryant et al., 1987b	PH – CT –
N			total phenolics papyriferric acid condensed tannins	+ +	Bryant et al., 1987b	PH + CT +
	Betula pendula	leaves	salidroside dehydrosalidroside CT precursors flavonoids condensed tannins lignin	= = + + + +	Lavola and Julkunen-Tiito, 1994 Cotrufo and Ineson, 1996	PH + / = CT + LI +
		stems	salidroside dehydrosalidroside betuloside CT precursors condensed tannins	+ – = = / – =	Lavola and Julkunen-Tiito, 1994	PH + / – CT =

	Alnus crispa	internodes	total phenolics pinosylvin derivatives condensed tannins	= = 	Bryant et al., 1987b	PH = CT +
P			total phenolics pinosylvin derivatives condensed tannins	= = 	Bryant et al., 1987b	PH = CT =
N			total phenolics pinosylvin derivatives condensed tannins	= = 	Bryant et al., 1987b	PH = CT +
	Salix lasiolepsis	shoot tips	total phenolics phenolic glycosides	+ +	Price et al., 1989	PH +
N	*Salix dasyloclados*	leaves	phenolic compounds	=	Larsson et al, 1986	PH =
	Salix alaxensis	twigs	total phenolics condensed tannin	+ +	Bryant, 1987	PH + CT +
	Salix aquatica	leaves	tannins lignin	+ +	Waring et al., 1985	CT + LI +
	Liriodendron tulipifera	leaves	total phenolics hydrolizable tannins condensed tannins	= = =	Dudt and Shure, 1994	PH = CT =
	Cornus florida	leaves	total phenolics hydrolizable tannins condensed tannins	= = =	Dudt and Shure, 1994	PH = CT =
	Cecropia polystachia	mature and immature leaves	total phenolics condensed tannins	= 	Folgarait and Davidson, 1995	PH = CT =
	Cecropia membranaceae	mature (m) and immature (i) leaves	total phenolics condensed tannins	= (m)/ + (i) +	Folgarait and Davidson, 1995	PH + / = CT +
	Cecropia engleriana	mature (m) and immature (i) leaves	total phenolics condensed tannins	= (m)/ + (i) = (m)/ + (i)	Folgarait and Davidson, 1995	PH + / = CT + / =

Table A.1. Continuation

Environ. factor	Species	Organ	CBSC	Effect	Reference	S.
	Cecropia ficifolia	mature (m) and immature (i) leaves	total phenolics condensed tannins	= = (m)/ + (i)	Folgarait and Davidson, 1995	PH = CT + / =
	Cecropia sp. A	mature (m) and immature (i) leaves	total phenolics condensed tannins	+ +	Folgarait and Davidson, 1995	PH + CT +
	Cecropia sp. B	mature (m) and immature (i) leaves	total phenolics condensed tannins	+ +	Folgarait and Davidson, 1995	PH + CT +
	Rhizophora mangle	leaves	total phenolics condensed tannins	– –	Feller, 1995	PH – CT –
N			total phenolics condensed tannins	= =	Feller, 1995	PH = CT =
P			total phenolics condensed tannins	– =	Feller, 1995	PH = CT –
N	*Larrea tridentata*	leaves	resin (mainly phenolic)	=	Rundel et al., 1994	PH =
	Plantago lanceolata	leaves	iridoid glycosides phenylpropanoid glycosides	+ +	Fajer et al., 1992	PH +
	Plantago erecta	shoot root	lignin lignin	= –	Chu et al., 1996	LI = / –
N	*Zostera marina*	leaves	total phenolics	+	Buchsbaum et al., 1990	PH +
N	*Capsicum annuum*	leaves	total phenolics	+	Estiarte et al., 1994; Estiarte and Peñuelas, unp.	PH +
P	*Lycopersicon esculentum*	leaves and roots	flavonoids	=	Zornoza and Esteban, 1984	PH =
B		leaves and roots	flavonoids	+	Zornoza and Esteban, 1984	PH +
Mn		leaves	flavonoids	=	Zornoza and Esteban, 1984	PH =

		roots	flavonoids	–	Zornoza and Esteban, 1984	PH –
N	*Lotus corniculatus*	shoots	condensed tannins	–	Briggs, 1990	CT –
N	*Oryza sativa*	leaves	lignin	+	Matsuyama, 1975	LI +
N	*Andropogon gerardii*	leaf litter	lignin	=	Kemp et al., 1994	LI =
N	*Poa pratensis*	leaf litter	lignin	=	Kemp et al., 1994	LI =
N	*Sorghastrum nutans*	leaf litter	lignin	=	Kemp et al., 1994	LI =
	Avena fatua	shoot root	lignin lignin	= +	Chu et al., 1996	LI + / =
N	*Triticum aestivum*	leaves	lignin	=	Peñuelas et al., 1996	LI =
		shoots	total phenolics lignin	+ +	Brown et al., 1984	PH + / = LI + / –
		roots	total phenolics lignin	– =	Brown et al., 1984	
Cu		leaves	lignin	–	Robson et al., 1981	LI –
Mn		shoots roots	total phenolics lignin total phenolics	– – –	Brown et al., 1984	PH = / – LI –
N	*Fucus vesiculosus* (seaweed)	fronds	total phenolics	+	Yates and Peckol, 1993	PH +
Water stress						
	Pseudotsuga menziesii	leaves	condensed tannin	+ / –	Horner, 1990	CT + / –
	Salix lasiolepsis	shoot tip	total phenolics phenolic glycosides	+ +	Price et al., 1989	PH +
	Populus tremuloides	plant tissues	catechol salicin salicicortin	– – –	Kruger and Manion, 1993	PH –

Table A.1. Continuation

Environ. factor	Species	Organ	CBSC	Effect	Reference	S.
	Rumex cyprius	leaves	condensed tannin	+	Hegazy and Ismail, 1992	CT +
	Digitalis lanata	leaves	cardenolides	–	Stuhlfauth et al., 1987	PH –
	Larrea tridentata	leaves	resin (mainly phenolic)	=	Rundel et al., 1994	PH =
	Medigago sativa	leaves	lignin	=	Halim et al., 1989 Peterson et al., 1992	LI =
		stem	lignin	= / –	Peterson et al., 1992	LI = / –
	Lotus corniculatus	leaves and stem	lignin	–	Peterson et al., 1992	LI –
	Astragalus cicer	leaves stem	lignin lignin	– =	Peterson et al., 1992 Peterson et al., 1992	LI – LI =
	Trifolium pratense	leaves and stem	lignin	=	Peterson et al., 1992	LI =
	Macroptilium atropurpureum	leaves	lignin	+	Wilson, 1983	LI +
	Sorghum bicolor	leaves and stems	lignin	= / –	Akin et al., 1994	LI = / –
	Triticum aestivum	leaves	flavonoids	–	Estiarte et al. unp	PH –
		leaves of 32-day old plants	lignin	=	Akin et al., 1995a	LI + / –
		flag leaves of 105-day old plants	lignin	= / +	Akin et al., 1995a	
		mature flag leaves	lignin	–	Akin et al., 1995a	
	Vigna unguiculata	seedlings	anthocyanin = total phenol	+ +	Balakumar et al., 1993	PH + / =
Light intensity						
	Picea sitchensis	shoots of seedlings	total phenolics condensed tannins	+ +	Hartley et al., 1995.	PH + PH +

Eucaliptus tereticornis	leaves	total phenolics condensed tannins lignin	+ + +	Lawler et al., 1997	PH + CT + LI =
Betula resinifera	internodes	total phenolics papyriferric acid condensed tannins	+ + =	Bryant et al., 1987b	PH + CT =
Salix dasyloclados	leaves	phenolic compounds	+	Larsson et al, 1986	PH +
Salix aquatica	leaves	tannins lignin	= +	Waring et al., 1985	CT = LI +
Salix alaxensis	twig	total phenolics condensed tannin	+ +	Bryant, 1987	PH + CT +
Calluna vulgaris	shoots	total phenolics condensed tannin = lignin	= = =	Hartley et al., 1995.	PH = CT = LI =
Liriodendron tulipifera	leaves	total phenolics hydrolizable tannins condensed tannins	+ + +	Dudt and Shure, 1994	PH + CT +
Cornus florida	leaves	total phenolics hydrolizable tannins condensed tannins	= + +	Dudt and Shure, 1994	PH + CT =
Barteria fistulosa	leaves	total phenolics condensed tannins	+ +	Waterman et al., 1984	PH + CT +
Zostera marina	leaves	total phenolics	+	Verger et al., 1995	PH +
trees of dry deciduous forest	leaves	condensed tannins	+	Ganzhorn, 1995	CT +

Table A.2. List of literature surveyed reports on quantitative response of concentration of phenolic compounds to atmospheric CO_2-enrichment. Effects are described as increases (+). decreases (–) or no change (=) in the concentration of compounds and are summarized in the last column (S.). The table includes the name of the species, the atmospheric $C0_2$ concentrations under which plants were grown, the organ in which concentrations of phenolic compounds were measured, the class of phenolic compound and the literature reference.

Species	CO_2 (µmol mol^{-1})	Organ	CBSC	CO_2 effects	Reference	S.
Picea sitchensis	350 and 700	leaves	lignin	+	Cotrufo et al., 1994	LI +
Pinus strobus	350 and 650	leaves	condensed tannins	+	Roth and Lindroth, 1994	CT +
Pinus eldarica	400, 550, 680 and 810	leaves	total phenolics condensed tannins	– –	Peñuelas et al., 1996	PH – CT –
Quercus rubra	369 and 700 350 and 650	leaves	gallic ac. derivatives hidrolisable tannins condensed tannins	= + / – =	Roth and Lindroth, 1995, Lindroth et al., 1993	PH + / – CT =
Quercus pubescens	379 and 518	leaves	tannins	+	Johnson et al., 1996	CT +
Castanea sativa	350 and 700	leaf litter	lignin	–	Coûteaux et al., 1996	LI –
Eucaliptus tereticornis	352 and 793	leaves	total phenolics condensed tannins lignin	+ + –	Lawler et al., 1997	PH + CT + LI –
Fagus sylvatica	350 and 600	leaves	total phenolics	=	Docherty et al., 1996	PH =
Populus tremuloides	369 and 700 350 and 650	leaves	phenolic glycosides (salicortin and tremulacin) condensed tannins	+ / = + / =	Roth and Lindroth, 1995; Lindroth et al., 1993 Lindroth et al., 1997	PH + / = CT + / =
Betula papyrifera	369 and 700 369 and 700 350 and 650	leaves	condensed tannins	+	Roth and Lindroth, 1995; Lindroth et al., 1995; Roth and Lindroth, 1994	CT +

Betula pendula	350, 700, 1050 and 1400	leaves	salidroside dehydrosalidroside CT precursors flavonoids condensed tannins	+ = = + / = +	Lavola and Julkunen-Tiito 1994	PH + / = CT +
		stems	salidroside dehydrosalidroside betuloside CT precursors condensed tannins	= – + = =		PH + / – CT =
	350 and 600	leaf litter	lignin	+	Cotrufo and Ineson, 1996	LI +
Betula pubescens	350and 700	leaf litter	lignin	=	Cotrufo et al., 1994	LI =
Betula populifolia	350 and 700	leaves	condensed tannins	+	Traw et al., 1996	CT +
Betula allegheniensis	350 and 700	leaves	condensed tannins	+	Traw et al., 1996	CT +
Salix myrsinifolia	350, 700 and 1050	leaves	phenolic glycosides (salicortin and salicin) catechin proanthocyanidins	= / – + / = + / =	Julkunen-Tiito et al., 1993	PH + / – CT + / =
Acer saccharum	369 and 700 350 and 650	leaves	hidrolisable tannins condensed tannins	+ +	Roth and Lindroth, 1995, Lindroth et al., 1993	PH + CT +
Acer pseudoplatanus	350 and 700	leaf litter	lignin	=	Cotrufo et al., 1994	LI =
Fraxinus excelsior	350 and 700	leaf litter	lignin	=	Cotrufo et al., 1994	LI =
itrus aurantium	370 and 670	leaves	total phenolics	=	Peñuelas et al., 1996	PH =
Cecropia peltata	350 and 640	leaf litter	lignin	=	Hirschel et al., 1997	LI =
Ficus benjamina	350 and 640	leaf litter	lignin	=	Hirschel et al., 1997	LI =
Lindera benzoin	370 and 710	leaves and stems	total phenolics	+	Cipollini et al., 1993	PH +

Table A.2. Continuation

Species	CO_2 (µmol mol^{-1})	Organ	CBSC	CO_2 effects	Reference	S.
Elettaria cardamomum	350 and 640	leaf litter	lignin	=	Hirschel et al., 1997	LI =
Artemisia tridentata	270, 350 and 650	leaves	coumarins sesquiterpene lactone flavonoids	= = =	Johnson and Lincoln, 1990	PH =
Capsicum annuum	350 and 700	leaves	total phenolics	+	Estiarte and Peñuelas, unp.	PH +
Digitalis lanata	350 and 1000	leaves	cardenolides	=	Stuhlfauth et al., 1987	PH =
Mentha piperita	350, 500 and 650	leaves	mono–and sesquiterpenes	=	Lincoln and Couvet, 1989	
Nicotiana tabacum	350 and 700	leaves	chlorogenic acid rutin total polyphenols	+ + +	Rufty et al., 1989	PH +
Plantago lanceolata	350 and 700	leaves	iridoid glycosides phenylpropanoid glycosides	= / – = / –	Fajer et al., 1991, 1992	PH = / –
Plantago erecta	350 and 700	shoot and root	lignin	–	Chu et al., 1997	LI –
Spartina patens	360 and 700	leaf litter	lignin	=	Ball and Drake, 1997	LI =
Scirpus olneyi	360 and 700	leaf litter	lignin	=	Ball and Drake, 1997	LI =
Sorghum bicolor	370 and 550	leaves and stems	lignin	=	Akin et al., 1994	LI =
Triticum aestivum	370 and 550	leaf blades	total phenolics flavonoids alkali soluble aromatics + lignin	+ + + = / – (depending on phenology)	Peñuelas et al., 1996 Estiarte et al. unp. Akin et al., 1995a	PH + LI = / –
		stems	aromatic carbon alkali soluble aromatics	= =	Akin et al., 1995b	PH =

Avena fatua	350 and 700	shoot root	lignin lignin	= –	Chu et al., 1997	LI = / –
Andropogon gerardii	390 and 780	leaf litter	lignin	=	Kemp et al., 1994	LI =
Poa pratensis	390 and 780	leaf litter	lignin	=	Kemp et al., 1994	LI =
Sorghastrum nutans	390 and 780	leaf litter	lignin	=	Kemp et al., 1994	LI =
Agrostis canina	350 and 700	leaves	lignin	+ / =	Fordham et al., 1997	LI + / =
Carex curvula	350 and 640	leaf litter	lignin	=	Hirschel et al., 1997	LI =
Average of 27 C_3 sp.		leaves	phenolics + lignin	= =	Poorter et al., 1997	PH + LI =

Table A.3. List of literature surveyed reports on quantitative response of concentration of structural polysaccharides to the following environmental factors: nitrogen availability, water stress, atmospheric CO_2 enrichment and light intensity. Effects are described as increases (+). decreases (–) or no change (=) in the concentration of compounds and are summarized in the last column (S.). The table includes the name of the species, the organ in which concentration of phenolic compounds have been measured, the class of structural poiysaccharide and the literature reference.

Env. factor	Species	Organ	Parameter	Effect	Reference	S.
Nutrient limitation						
	Rhizopora mangle	leaves	NDF / ADF	=	Feller, 1995	=
N	*Rhizopora mangle*	leaves	NDF / ADF	=	Feller, 1995	=
	Eucaliptus tereticornis	leaves	cellulose non-cellulose structural carbohydrates	+ +	Lawler et al., 1997	+
	Calluna vulgaris	shoots of seedlings	ADF	+	Hartley et al., 1995	+
	Betula pendula	leaves	cellulose	+	Cotrufo and Ineson, 1996	+
	Helianthus annuus	leaves	crude cell wall	=	Fredeen et al., 1991	=
	Artemisia tridentata	leaves	NDF	=	Johnson and Lincoln, 1991	=
N	*Amaranthus sp.* (5 species)	leaves	NDF	+ (3 sp.) / = (2 sp.)	Walters, 1988	3 + 2 =
N	*Capsicum annuum*	leaves	total fiber	+	Estiarte and Peñuelas, unp.	+
N	*Triticum aestivum*	leaves	ADF / cellulose	+	Peñuelas et al., 1996	+
N	*Andropogon gerardii*	leaf litter	cellulose	+ / =	Kemp et al., 1994	+ / =
N	*Poa pratensis*	leaf litter	cellulose	=	Kemp et al., 1994	=
N	*Sorghastrum nutans*	leaf litter	cellulose	=	Kemp et al., 1994	=

Picea sitchensis	leaves	cellulose	=	Cotrufo et al., 1994	=
Betula pendula	leaf litter	cellulose	=	Cotrufo and Ineson, 1996	=
Betula pubescens	leaf litter	cellulose	=	Cotrufo et al., 1994	=
Fraxinus excelsior	leaf litter	cellulose	=	Cotrufo et al., 1994	=
Acer pseudoplatanus	leaf litter	cellulose	=	Cotrufo et al., 1994	=
Castanea sativa	leaf litter	hemicellulose cellulose	+ =	Coûteaux et al, 1996	+ / =
Eucaliptus tereticornis	leaves	cellulose non-cellulose str. carb.	= =	Lawler et al., 1997	=
Plantago lanceolata	leaves	NDF / ADF	=	Fajer et al., 1991	=
Spartina patens	leaf litter	cellulose hemicellulose	= =	Ball and Drake, 1997	=
Scirpus olneyi	leaf litter	cellulose hemicellulose	= =	Ball and Drake, 1997	=
Capsicum annuum	leaves	total fiber	=	Estiarte and Peñuelas, unp.	=
Artemisia tridentata	leaves	NDF	–	Johnson and Lincoln, 1991	–
Triticum aestivum	leaves of 32-day old plants flag-leaves of 105-day-old plants mature flag leaves	NDF ADF / cellulose NDF / ADF / cellulose NDF / ADF / cellulose	= + = +	Akin et al., 1995a	+ / =
Sorghum bicolor	leaf blades leaf sheats and stems	NDF ADF NDF / ADF	+ =	Akin et al, 1994	+ / = = =

Table A.3. Continuation

Env. factor	Species	Organ	Parameter	Effect	Reference	S.
	Andropogon gerardii	leaf litter	cellulose	+ / =	Kemp et al., 1994	+ / =
	Poa pratensis	leaf litter	cellulose	=	Kemp et al., 1994	=
	Sorghastrum nutans	leaf litter	cellulose	=	Kemp et al., 1994	=
	Average of 27 C_3 sp.	leaves	total structural carbohydrates	=	Poorter et al., 1997	=
Light intensity						
	Eucaliptus tereticornis	leaves	cellulose non-cellulose str. carb.	= =	Lawler et al., 1997	=
	Calluna vulgaris	shoots of seedlings	ADF	=	Hartley et al., 1995	=
	Barteria fistulosa	leaves	ADF	=	Waterman et al., 1984	=
	Panicum clandestinum	leaf blades non -laminar herbage	NDF NDF	+ =	Kephart and Buxton, 1993	+ =
	Phalaris arundinacea	leaf blades non-laminar herbage	NDF NDF	+ =	Kephart and Buxton, 1993	+ =
	Festuca arundinacea	leaf blades and non-laminar herbage	NDF	+	Kephart and Buxton, 1993	+
	Andropogon gerardii	leaf blades and non-laminar herbage	NDF	+	Kephart and Buxton, 1993	+
	Panicum virgatum	leaf blades and non-laminar herbage	NDF	+	Kephart and Buxton, 1993	+
	Trees of dry deciduous forest in Madagascar	leaves	ADF	=	Ganzhorn, 1995	

Water stress

Medicago sativa	leaves	NDF / ADF cellulose hemicellulose	= / – – =	Peterson et al., 1992 Halim et al., 1989	= / –
	stems	NDF / ADF cellulose hemicellulose	– – =	Peterson et al., 1992 Halim et al., 1989	= / –
Lotus corniculatus	leaves and stems	NDF / ADF	–	Peterson et al., 1992	–
Astragalus cicer	leaves and stems	NDF / ADF	–	Peterson et al., 1992	–
Trifolium pratense	leaves stems	NDF / ADF NDF / ADF	= / – –	Peterson et al., 1992	= / – –
Helianthus annuus	leaves	crude cell wall	+	Fredeen et al., 1991	+
Sorghum bicolor	leaf blades, leaf sheats and stems	NDF ADF	= –	Akin et al., 1994	= / –
Triticum aestivum	leaf blades of 32-day old plants	NDF / ADF / cellulose	=	Akin et al, 1995a	+ / =
	leaf blades of 105-day old plants	NDF / ADF / cellulose	+ / =		
	mature flag leaves	NDF / ADF / cellulose	=		

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