

CONSTRUCTION COSTS AND PAYBACK TIME OF BIOMASS: A WHOLE PLANT PERSPECTIVE

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Abstract

Literature data were compiled on the construction costs of plant biomass, that is, the amount of glucose required to construct one gram of biomass. No evidence was found for more than a slight variation in construction costs, with leaves of herbaceous species somewhat more expensive to produce than stems or roots. There is little or no variation due to environmental differences, or in construction costs between ecologically contrasting groups of species. However, most research in this area has focused on leaves. Differences between woody and herbaceous species may become apparent when construction costs of whole plants are considered.

It has been suggested that the payback time of leaves, *i.e.*, the time a leaf requires to meet its own construction costs, rather than the construction costs themselves, vary for ecologically contrasting species. Although correct, such an approach ignores the relevance of stem and roots and their associated costs for the functioning of a leaf. From a whole plant perspective, payback time is identical to the relative growth rate of a plant. As such, this concept is closely related to part of Grime's plant strategy theory, where relative growth rate is considered to be one of the differentiating key factors.

1. Introduction

Plants differ widely in their chemical composition, both qualitatively and quantitatively (Table 1). These differences may be partly phenotypic (*e.g.*, Waring *et al.* 1985, Diamantoglou *et al.* 1989) and partly genetic (*e.g.*, Kramer 1979, Poorter & Bergkotte 1992). Just as the biosynthetic pathways for the construction of the vast array of chemical constituents vary, so may the amount of ATP and NAD(P)H required to drive these biosynthetic reactions. The amount of carbon needed for the C-skeletons of one gram of the various compounds also differs. Therefore the construction costs, the total input of glucose required to construct one gram of plant biomass, are subject to variation. In this paper I first briefly discuss methods to estimate the construction costs of plant biomass. Secondly, intra- and interspecific variation in the construction costs are analyzed. Finally, I deal with some aspects of payback time, the ratio between construction costs and net carbon gain.

2. Methods for the determination of construction costs

There are several methods to assess the construction costs of plant tissue. The ideal analysis would be to determine all chemical constituents in a plant and analyze the biosynthetic pathways for each of these. Practically, this is not feasible and the closest one can get is to assess costs of various groups of compounds. Penning de Vries *et al.* (1974) used this approach to determine the construction costs of a maize plant. From the most likely biosynthetic pathways they calculated costs of various classes of compounds: lipids, lig-

Table 1. Construction costs (g glucose/g compound) for different groups of constituents according to Penning de Vries *et al.* (1974, 1983) and concentrations (mg (g DW)⁻¹) normally found for each of these compounds. For the construction cost calculation, cellulose and hemicellulose were assumed to be present in equal amounts, and non-structural carbohydrates to be starch:sucrose:glucose in a weight ratio of 1:1:1. The ranges of concentrations in leaves, stems, roots and seed/fruits are the 10th and 90th percentiles of a compilation of data from a large number of literature sources.

Compound	Construction Costs	Concentration					
		herbaceous			woody		seed/fruit
		leaves	stem	roots	leaves	stem	
Lipids	3.030	15-70	15-40	10-25	20-100	20-75	15-460
Lignin	2.119	10-80	25-60	20-50	40-195	90-250	40-130
Protein (with NO ₃)	2.475	100-350	40-250	45-230	50-220	30-140	70-370
Protein (with NH ₄)	1.623						
(Hemi)cellulose	1.220	130-530	180-620	170-310	40-300	45-605	
Non-structural carbohydrates	1.090	70-260	80-315	200-330	40-255	10-135	150-880
Organic acids	0.906	40-125	30-100	5-55	15-55	?	10-95
Minerals	-	85-205	60-185	40-190	30-120	0-70	20-65

nin, organic N-compounds, (hemi)cellulose/starch/sugars, organic acids and minerals. As an example of this approach the costs of the various steps in the production of protein from NO_3^- and glucose are outlined in Appendix 1. Although different constituents within each of the above-mentioned classes of organic compounds may have different construction costs, Penning de Vries *et al.* concluded that variation within each group was small compared to the variation between groups. The values, as calculated by Penning de Vries *et al.*, are given in Table 1. Compared to glucose, compounds such as lipids, lignin and protein are costly to produce, whereas organic acids are less expensive. Although the mineral fraction does not require C-skeletons for synthesis, some ATP is needed for uptake from the root environment and transport within the plant. However, as these costs are often considered to be independent of energy required for growth (cf. Van der Werf *et al.* 1988), I assume that no glucose is required for their "construction". The calculated values should be considered with some care. For example, based on recent information on the process of amino acid polymerization, De Visser *et al.* (1992) suggest that total glucose costs for protein synthesis may actually be 0.3 g g^{-1} higher than those given in Table 1.

The chemical determinations necessary for this type of analysis are rather laborious and total recovery often is less than 100% (e.g., Merino *et al.* 1984, Lafitte & Loomis 1988, Poorter & Bergkotte 1992). Therefore, quicker and easier methods were sought based on the observation that expensive compounds are generally more reduced than glucose, whereas cheap compounds are relatively more oxidized. McDermitt & Loomis (1981) analysed C, H, N, O and S in the plant biomass. From the elemental composition, and knowledge about the form of N- and S-supply, they calculated the reduction state of the plant material thus allowing the total amount of NAD(P)H required to provide reducing equivalents to be determined. The amount of ATP needed to drive the various reactions cannot be measured, but is estimated by a correction factor. The determination of O by pyrolysis may give rise to problems, due to the formation of oxides (Lafitte & Loomis 1988).

A second method estimates the construction costs of plant material by determining N-concentration, heat of combustion and ash content (Williams *et al.* 1987). Again, the amount of ATP required in the chemical reactions is a complicating factor. Williams *et al.* concluded that a fixed correction factor brings estimates within 6% of the "true value", depending on chemical composition. Another complication could have been that ash content is not necessarily similar to mineral content. During the ashing process, both NO_3^- and organic acids turn into oxides (Baumeister 1958). Ignoring this may normally lead to additional errors. However, considering the range in mineral content generally found (Table 1), the effect of the ash correction in the equation of Williams *et al.* is so small (less than 1% of the total construction costs of normal plant material), that it does not seem worth the effort to determine mineral content anyway.

Vertregt & Penning de Vries (1987) proposed a further simplification. Given that the reduction state of the different compounds is coupled to their carbon content, they claim that determining ash and carbon content of the plant material yields a satisfactory estimate. They illustrate this method for a range of fruits and seeds, which show a large variation in lipid content, the constituent with the highest concentration of C and the highest construction costs (Table 1). Lambers & Rychter (1989) questioned this method, calculating that the observed relationship between C-content and construction costs did not hold for diplacol, a flavonoid. However, they did not select the proper regression equation from Vertregt & Penning de Vries (1987), using one where ATP requirements for synthesis were not considered. The relationship of C-content and construction costs of a number of compounds is shown in Fig. 1. As can be seen, diplacol fits the calculated regression line reasonably well. This applies also to a range of other secondary com-

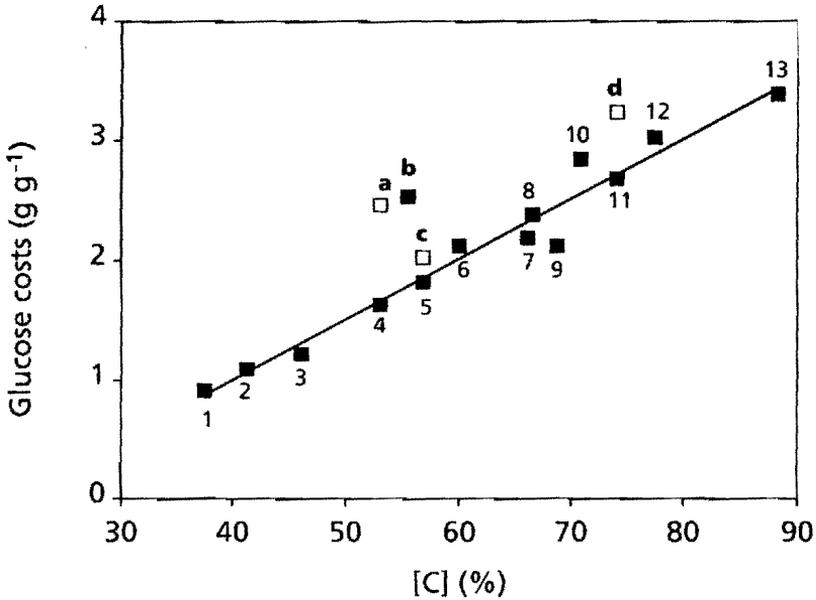


Fig. 1. Relationship between construction costs and the carbon content of model compounds of the various groups of constituents of plant biomass. 1. Organic acids; 2. Starch/sucrose/glucose; 3. (Hemi)cellulose; 4. Protein (with NH_4); 5. Prunasin (a cyanogenic glucoside); 6. Caffeic acid (a phenol); 7. Narrengenin chalcone (a flavonoid); 8. Umbelliferon (a coumarin); 9. Lignin; 10. Diplacol (a flavonoid); 11. Nicotine (with NH_3 , an alkaloid); 12. Lipids; 13. Limonene (a monoterpene); a. Protein (with NO_3); b. Ellagic acid (a tannin); c. Prunasin (with NO_3); d. Nicotine (with NO_3). The regression line is fitted through 1–13. Construction costs are derived from Penning de Vries *et al.* (1974, 1983), Merino *et al.* 1984 and Lambers & Rychter (1989). The costs for ellagic acid are tentative (Lambers & Rychter 1989).

pounds, like an alkaloid, a cyanogenic glucoside, a flavonoid, a monoterpene, and a phenol (Fig. 1). Unfortunately, an important assumption underlying this method is that NH_4^+ is the source of protein N. If NO_3^- is the source, the relationship is no longer valid, as the costs of protein lay well above the regression line in this case (Fig. 1). In such situations, organic N must be determined separately. Extending the approach of Vertregt & Penning de Vries to NO_3^- -fed plants and using the relationship of Fig. 1, construction costs are then given by the formula:

$$\text{CC} = (-1.041 + 5.077 * C_{\text{om}}) * (1 - M) + (5.325 * N_{\text{org}}) \quad (1)$$

where CC is the total cost to produce one gram of plant biomass (g glucose/g dry weight), C_{om} the carbon content of the organic biomass (g/g), M and N_{org} the mineral and organic nitrogen content of the total dry weight (g/g), respectively. The first part of the first term of equation 1 is calculated from a regression through all the numbered points of Fig. 1. The second part of the first term corrects for the mineral content of the biomass, assuming a separation of costs for nutrient uptake and for growth. The second term adds the additional cost for nitrate reduction to the total glucose costs, assuming all of the organic N to be protein. In this equation, mineral content forms an essential part and cannot be omitted.

Using data on the seasonal pattern of the chemical composition of kiwifruit (*Actinidia*

sinensis) and assuming that NH_4^+ was the N-source, Walton *et al.* (1990) compared the different methods. Basically, they all yielded similar results, with the Vertregt & Penning de Vries method 4% lower than average, and the method of Williams *et al.* (1987) 3% higher. As all of the simpler methods have correction factors or regression estimates based on Penning de Vries *et al.* (1974), this may not come as a surprise. It also implies that, if indeed the cost of protein synthesis is higher than listed in Table 1 (De Visser *et al.* 1992), all of the correlative methods need correction. A consequence for the Vertregt & Penning de Vries analysis would be that nitrogen content has to be included as an independent variable in the regression equation regardless of whether NO_3^- or NH_4^+ is the source of protein-N.

As they stand now, the last three procedures are relatively easy and quick to use, and do not suffer from the problem of the proximate analysis of Penning de Vries *et al.* (1974), where recovery may be significantly less than 100% (Chiariello *et al.* 1989), especially in leaves (see discussion in Poorter & Bergkotte 1992). However, the proximate analysis has the advantage that it provides insight into the biochemical differences underlying variation in construction costs. A nice example of the power of the proximate analysis approach is given in Walton *et al.* (1990), where ontogenetic trends in the glucose costs of kiwi fruit could be explained by variation in the concentration of sugars, organic acids and lipids over time.

3. Limitations to the concept of construction costs

The concept of construction costs has some limitations and uncertainties. Firstly, the concept is static. Construction costs are estimated from the chemical composition at the moment of harvest, so that energy expenditure for the maintenance of concentrations of compounds subject to turnover is not taken into account (Penning de Vries *et al.* 1974). Similarly, redistribution of compounds later in a leaf's life may cause calculated costs to be different from real costs (Chapin 1989).

Secondly, there is uncertainty about the costs of N-assimilation. This is related to both the proportion of N taken up as NO_3^- , and the site of NO_3^- -reduction. The high costs of NO_3^- -reduction may only apply to roots. In the shoot, nitrate reduction may depend partly on the reducing power generated in the chloroplasts (Layzell 1990). These costs of reduction would not show up in respiration and could therefore, seen from the perspective of the carbon balance of the plant, be considered as nil.

A third point of concern is that the concentration of the various compounds listed in Table 1 are not necessarily mutually independent. For example, most biosynthetic conversions require enzymes and therefore, synthesis of, say, lignin also requires synthesis of some protein. In the formation of amino acids from glucose and NO_3^- , OH^- is formed (see appendix 1), which is partly neutralized by accumulation of organic acids. Thus, in assessing the effect of a change in concentration of one compound, changes in other compounds may have to be included as well.

Lastly, it should be noted that construction costs can always be calculated, but that this does not imply that the production of glucose is the factor limiting growth.

4. Variation in construction costs

What is the range in construction costs to be expected in plant material? In compiling data from the literature, I assumed that the various methods gave similar values. The form in which the plant obtains its nitrogen is a complicating factor, because as mentioned above, there is a large difference in the construction costs of protein derived from

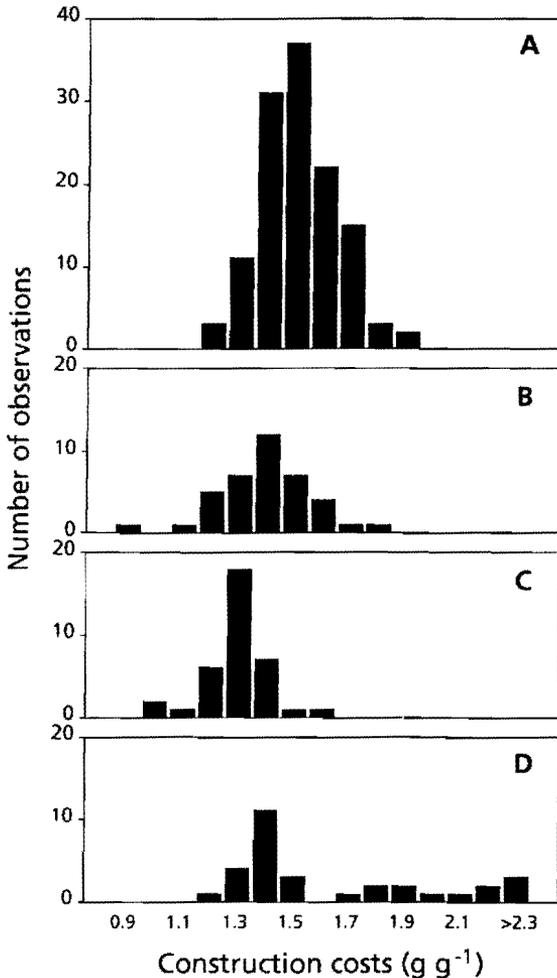


Fig. 2. Distribution curve of construction costs of plant biomass, as compiled from the literature and supplemented with some additional data. A, leaves ($n = 123$); B, stems ($n = 38$); C, roots ($n = 35$); D, seeds/fruits ($n = 31$). All values are determined assuming NO_3^- to be the N-source. Data of Chung & Barnes (1977), Merino *et al.* (1984), Merino (1987), Berendse & Elberse (1989), Chapin (1989), Gower *et al.* (1989), Williams *et al.* (1989), Sims (1990), Walton *et al.* (1990), Sobrado (1991), Kull *et al.* (1992), Nobel *et al.* (1992); Poorter, H., Dijkstra, P., Den Hartog, J. & Lenssen, G. (on leaves of *Alnus glutinosa*, *Elymus athericus*, *Plantago major* ssp. *major*, *Solanum tuberosum*, *Spartina anglica*, *Triticum aestivum*, K.L. Griffin (on leaves, stem and roots of *Pinus teada*), Bouma, T. (on roots of *Solanum tuberosum*) and Baruch, Z. (on leaves and roots of *Melinis minutiflora*, *Hyparrhenia rufa*, and *Trachypogon plumosus*), unpublished; and derived from proximate analysis by Challa (1976), Lambers & Rychter (1989) and Poorter & Bergkotte (1992). Data of Miller *et al.* (1990) were not included, as they seem to have miscalculated the construction costs.

NH_4^+ and from NO_3^- (Table 1). Depending on the pH of the soil, some authors have assumed the N-source to be solely NH_4^+ , others NO_3^- . For the purpose of comparison, I have recalculated all data where NH_4^+ was considered to be the N-source, assuming that it was NO_3^- instead (Penning de Vries *et al.* 1983, Chapin 1989, Walton *et al.*

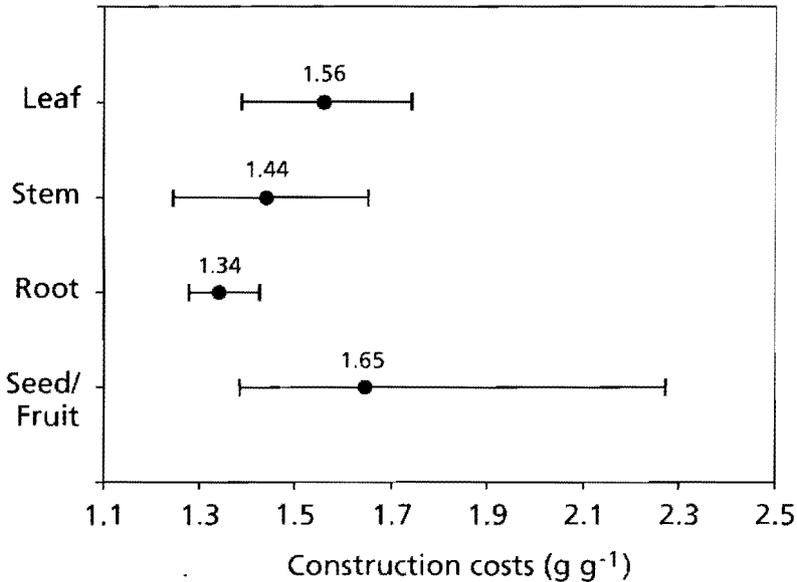


Fig. 3. Range of construction costs generally found for leaves, stem, roots and fruit/seeds (10th and 90th percentile of the data of Fig. 2). Numbers give the average value.

1990). Fig. 2 shows a distribution curve of the compiled values. Such a distribution is characterized by percentile values, which indicate the value below which a given percentage of the observations is found. From the 10th and 90th percentile of all of the data of Fig. 2, I conclude that construction costs of plant biomass generally range from 1.31 to 1.75. What factors contribute to this variation?

4.1. Variation between organs

The most obvious difference in construction costs is between various organs of a plant. On average, seeds are most expensive to produce (Fig. 3), partly caused by the high lipid and/or protein content in some species (cf. Penning de Vries *et al.* 1983). But there are also differences within the vegetative parts of herbaceous or woody species. From data of Challa (1976), Chapin (1989), Sims (1990), and Poorter & Bergkotte (1992), I calculated costs for stems and roots of each herbaceous species, relative to the glucose costs of leaves. On average, stems of herbaceous species had 12% lower construction costs than leaves ($p < 0.001$), whereas roots were 17% lower ($p < 0.001$). The higher construction costs of leaves are at least partly caused by their higher protein and lower mineral content (cf. Challa 1976, Poorter & Bergkotte 1992). The few data on woody species (Chung & Barnes 1977, Chapin 1989, Griffin *et al.* 1993), show that their stems and roots are almost as expensive to produce as leaves. Indeed, Berendse & Elberse (1989) found higher construction costs of shoots (mainly stem) and roots of an ericaceous shrub compared to a co-occurring grass species. Most likely, the lower protein costs of stems and roots are balanced by a high expenditure for lignin and/or lipids.

4.2. Changes with ontogeny

Merino *et al.* (1984) harvested leaves of different age classes on three shrubs of the chaparral. The two deciduous species showed a 10% decrease in construction costs with increasing age class, but no downward trend was found for an evergreen. Chapin (1989) did not find much of a difference either between leaves of different year classes in an evergreen shrub. In woody twigs, a slight decrease with age was observed (Kull *et al.* 1992), in rhizomes of *Podophyllum peltatum* a 3% increase (De Kroon, H., Geber, M.A. & Watson, M.A., unpublished results). Probably, from a whole plant perspective ontogenetic shifts in biomass partitioning between organs are more important in determining variation in whole plant costs, than developmental variation within each organ (cf. section 4.1.). As far as I know, this has not yet been tested.

4.3. Effect of mycorrhiza

In a study on the effect of mycorrhizal infection on the carbon costs of fibrous roots of *Citrus volkameriana*, Peng *et al.* (1993) found 8% higher construction costs for infected plants. The higher construction costs coincided with a 2 to 3 fold increase in the concentration of lipids in the roots. This could be explained by the extensive formation of lipid-rich vesicles by the fungus, even at high P-concentrations.

4.4. Variation between environments

Information concerning the effect of environmental variables on construction costs is scarce. Williams *et al.* (1989) compared leaf construction costs of individuals of two tropical tree species, growing either in gaps, or in the forest understorey. Plants grown at high light had 10–20% higher construction costs than low-light plants. However, in *Alocasia macrorrhiza* plants grown under high and low light conditions, Sims (1990) found low-light grown leaves to be more expensive (5%). Leaves (or shoots) of plants grown at high N availability were reported to have 5–7% higher construction costs than those grown at low nutrient concentrations (Lafitte & Loomis 1988 for *Sorghum bicolor*, Griffin *et al.* 1994 for *Pinus taeda*). However, fibrous roots of *Citrus volkameriana* grown at high P-levels were somewhat cheaper (6%) than those grown at low P-supply (Peng *et al.* 1993). In a field survey in the Mediterranean area, Merino (1987) did not find any systematic difference between leaves of individuals of several species, grown at nutrient-poor and nutrient-rich sites. No systematic difference between plants of xeric and more mesic sites was found either. In a study on 6 species grown at 350 and 700 $\mu\text{mol}\cdot\text{mol}^{-1}\text{CO}_2$, construction costs, determined with equation 1, were similar or slightly higher in leaves of the high CO_2 grown plants (Poorter, H., Dijkstra, P., Den Hertog, J. & Lenssen, G., unpublished results). For *Pinus taeda*, leaf construction costs were found to be 3% lower for the high CO_2 plants as compared to those grown at control levels (Griffin *et al.* 1994). Clearly, information on this subject is too scanty at present to allow more than the tentative conclusion that environmental effects on construction costs of leaves are either small or absent.

4.5. Variation between species

Miller & Stoner (1979) and Sobrado (1991) suggested that species with long-lived leaves (evergreens) have higher construction costs than species with a shorter leaf life-span (deciduous plants). However, there is hardly any evidence to support this claim. Miller & Stoner calculated construction costs of leaves of 3 species on the basis of an incomplete

proximate analysis (no determination of non-structural carbohydrates, organic acids and minerals) with a total recovery of 80% for the deciduous species and only 50% for the evergreen ones. From their table, they appear to have assigned this missing part proportionally over the compounds they did measure. However, if they had assumed the missing portion to be carbohydrates, hardly any difference between the two evergreens and the one deciduous species would have been observed. Clearly, total recovery is much too low in their case to support any claim. Sobrado (1991) compared 4 evergreens with 6 deciduous woody species and found that the construction costs for the evergreens were more than twice as high. However, she expressed all values on an area basis, thus confounding this parameter with the specific leaf area (leaf area:leaf weight ratio), which varies twofold between the groups. Although the specific leaf area is an important parameter in itself, I prefer to uncouple it from the dry weight composition, and thus from the construction costs per unit weight. Calculated on a weight basis, there is no significant difference in the glucose costs between these two groups. Gower *et al.* (1989) found leaves of a deciduous conifer to be 12% cheaper than those of an evergreen conifer. Merino *et al.* (1984), on the other hand, reported leaves of an evergreen to be less costly than those of two drought-deciduous shrubs. Also in this case recovery was low for the evergreen species. Clearly, those comparisons based on just a few species do not permit a general conclusion. In a comparison of 46 woody species growing in their natural habitat, Merino (1987) did not observe systematic differences between leaves of vines, shrubs and trees. However, on average the species with small leaves had 9% higher construction costs than species with larger leaves. There was a 7% difference between evergreens and deciduous species in this survey, but within the group of species with similar leaf size, this difference was no longer significant.

Not much of a difference between a number of woody rainforest species was found, after correcting for the difference in light climate between various individuals (Williams *et al.* 1989). Chapin (1989) did not observe any systematic difference between leaves of different classes of tundra species. From the proximate analysis of leaf material, he deduced that the underlying reason for the constancy in the construction costs across these tundra species was due to the accumulation of either protein or lignin, or tannin instead of lignin. Thus, one expensive component was "exchanged" for another, leaving the total concentration of expensive compounds at a similar level. A slightly different conclusion was reached by Poorter & Bergkotte (1992). They did not find any systematic differences in the construction costs of a range of potentially fast- and slow-growing herbaceous species. In their experiment, there was also a negative correlation between protein and lignin, but as variation in lignin content was small anyway, this negative correlation did not explain the relative constancy quantitatively. For these species, a high concentration of costly protein coincided with a high content of cheap compounds, especially minerals (Fig. 4).

Thus, from the literature available I conclude that there is hardly any evidence for interspecific differences in glucose costs of leaves between functional groups of plants. However, large-scale comparisons of species with contrasting life form and ecological strategy are not available, certainly not at the whole plant level. If indeed stem and root biomass of woody species are more costly to produce than those of herbaceous species, construction costs of whole plants might be higher in the first group.

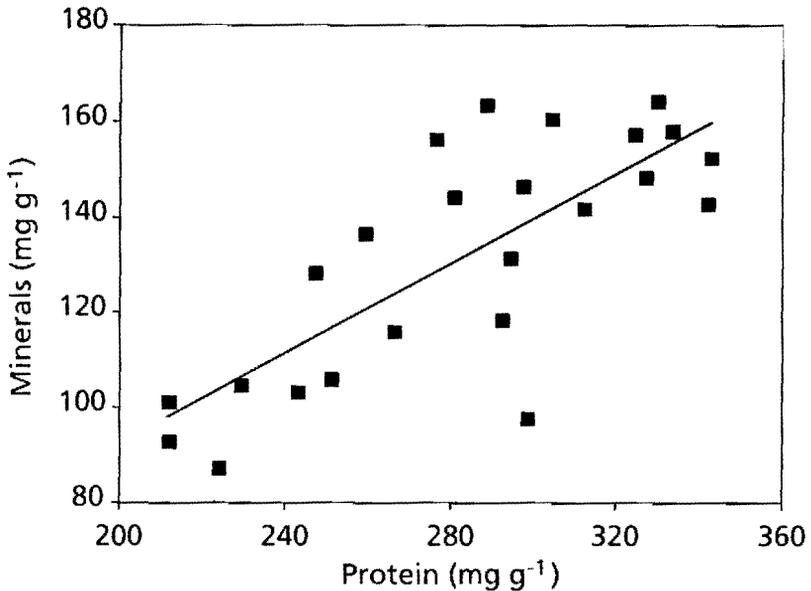


Fig. 4. Correlation between the concentration of protein and minerals for the whole plant biomass (dry weight) of 24 herbaceous species grown hydroponically. Data of Poorter & Bergkotte (1992). $p < 0.001$, $r^2 = 0.60$.

5. Ecological considerations

5.1. Differences in construction costs

The first publications in this field assumed that long-living evergreen leaves had higher construction costs than short-living deciduous ones (*e.g.*, Johnson & Tieszen 1976, Miller & Stoner 1979). The reason for the higher construction costs was supposed to be the high investment in expensive secondary compounds, like lignin and anti-herbivore compounds. However, as discussed above (section 4.5), very little experimental evidence supports this contention. Expressed on a weight basis, there is no significant difference between evergreen and deciduous species (Chapin 1989, Sobrado 1991). Differences between leaves of plants from contrasting environments are also small or entirely absent. Can we therefore dismiss construction cost as an ecologically important factor?

5.2. Payback time of a leaf

An alternative hypothesis was proposed by Williams *et al.* (1989), that the ratio of construction costs to carbon gain, rather than the absolute construction costs, differ for ecologically different species (see also Saeki & Nomoto 1958, Chabot & Hicks 1982). They found that species with leaves characterized by a long leaf longevity have a high ratio of construction costs over daily carbon gain, whereas the opposite was found for species with short-lived leaves. Based on estimates of daily rates of photosynthesis, respiration and construction costs they found that leaf payback time, the time required for a leaf to fix the same amount of glucose as required to construct that leaf, differed between 5 and 3000 days.

The arguments of Williams *et al.* are convincing, but their approach contains a number

of simplifications. Firstly, they related the construction costs to the net daily carbon gain, subtracting total night respiration of the leaf from the net carbon uptake during the day. Such an approach ignores that part of respiration (with a magnitude depending on the developmental stage of the leaves) is used to provide energy for the construction of biomass and in this way is already included in the construction costs. If one is interested in the time a leaf needs to fix the amount of CO_2 required to meet its construction costs, then subtraction of total leaf respiration, including that for growth, leads to an overestimation of payback time.

Secondly, Williams *et al.* (1989) assumed that for a leaf to pay back its construction costs, all photosynthates produced by the leaf are of equal weight. That is, photosynthates produced early in the life of a leaf have the same value for the payback of construction costs as photosynthates produced later by that leaf (see equation A2 in appendix 2). This seems an oversimplification, best illustrated by an economic analog. Suppose person A has borrowed 100 dollars from person B. Person A is able to set aside 1 dollar a day in order to pay back his debt. In doing so, he has roughly two options. He can keep his savings at home, in which case it will take him 100 days to accumulate the required 100 dollars. In this case, all dollars are of equal value. Alternatively, person A may daily bring his dollar to the bank. In that case, the first dollar will yield interest over the whole period required to accumulate the 100 dollars. The last dollar brought in does not provide any interest at all. Thus, the total time person A requires to pay back his debt is less than 100 days and the first dollar has been of relatively higher value than the last one. The second alternative seems most closely related to the functioning of a plant, where sugars are continuously re-invested in new material. Starting from the day when a leaf becomes a net exporter of sugars, the first photosynthates exported may be used to construct another leaf, which may then contribute to the payback of the first leaf as well (cf. Harper 1989). Photosynthates produced later in a leaf's life, although chemically identical, have not had the ability to undergo a similar number of "multiplication steps" and therefore contribute less to the total amount of sugars required for the payback of a leaf. A formula to calculate the payback time of the "average" leaf, taking into account this compounding effect, is derived in appendix 2 (equations A3–A6). Using this formula, the payback periods as found by Williams *et al.* (1989) are reduced by 30%.

5.3. Payback time of the whole plant

Lastly, the approach of Williams *et al.* (1989) focuses on carbon gain and construction costs of leaves only. However, a leaf does not function by itself. Without support structures and organs for uptake and transport of water and nutrients, CO_2 fixation is generally impossible, so their additional costs for construction and maintenance should also be calculated. A more realistic assessment of payback time then includes; a) respiration for growth is not subtracted from the daily carbon fixation, b) allowance is made for the compounding effect of partly paid-back carbon, and c) the payback time of whole plants is considered, instead of leaves only (see appendix 2, equation A8). To illustrate such an approach, I have calculated the payback time for 24 wild herbaceous species, with a wide range in potential growth rates. The growth rates and biomass allocation have been reported in Poorter & Remkes (1990), the rates of photosynthesis and ion uptake in Poorter *et al.* (1990 and 1991, respectively). Construction costs were calculated from the chemical composition given in Poorter & Bergkotte (1992) and the glucose costs of the various compounds as listed in Table 1. Respiration related to maintenance, growth and ion uptake was not determined directly. I therefore subtracted the value of maintenance respiration (in case of shoots and roots) and respiration related to ion uptake (in case of roots) as computed by Van der Werf *et al.* (1988) from the rate of photosynthesis,

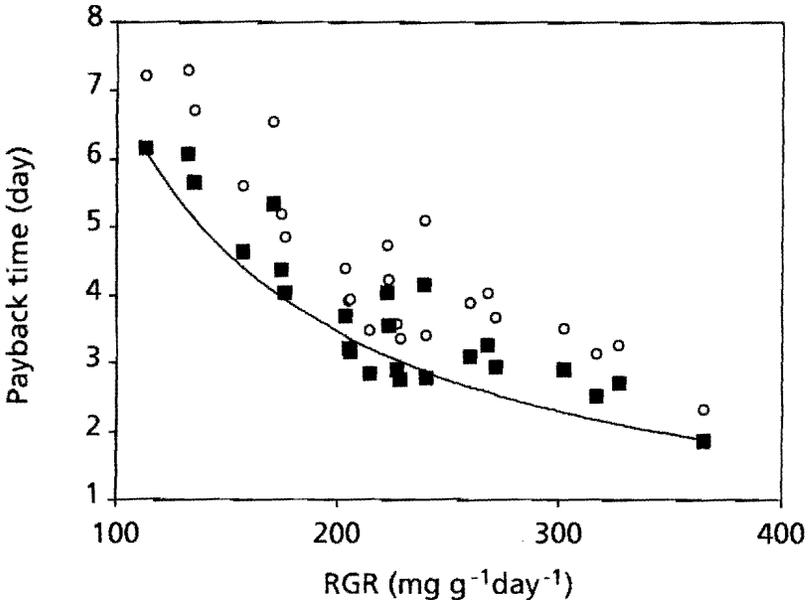


Fig. 5. Payback time of whole plants of 24 herbaceous species plotted against their relative growth rate. Payback time was calculated from measured rates of photosynthesis, allocation and chemical composition, an assumed maintenance respiration of $6.4 \text{ nmol CO}_2 (\text{g DW})^{-1} \text{ s}^{-1}$, and an assumed cost of ion uptake of $4 \text{ mol ATP mol}^{-1}$ anions. (○), NO_3^- reduction included in the costs; (■), nitrate reduction not included in the construction costs. The continuous line is the mathematical relationship between doubling time and relative growth rate.

assuming the remainder of respiration to be related to growth. Thus, I could estimate the time required for one gram of whole plant material to meet its own construction costs. For young, vegetative plants of the 24 species these values for the payback time are given in Fig. 5 as open circles. The values range from 2.3 to 7.3 days. For comparison, I have also calculated the payback time of leaves, which varied between 1.4 and 3.6 days under the conditions used in this growth room experiment.

Are these values realistic? As the payback time is the time for 1 gram of plant material to meet its construction costs, it is in fact the doubling time of plant material. And as doubling time is a variable which gives the growth rate of an organism, corrected for its weight already present, it is actually another way to express the relative growth rate (RGR). The mathematical relation between doubling time and RGR is given in Fig. 5 by the continuous line. This line does not fit the calculated payback times very well ($r^2 = 0.10$). Although the calculated values show the same general trend they are, on average, 35% higher than those derived from the measured RGR's. That may be due to the fact that nitrate reduction is included in the construction costs. As indicated above (section 3), NO_3^- -reduction occurring in the shoots does not (fully) show up in the carbon balance of the plant. If I assume nitrate reduction occurs at no glucose cost, calculated payback times (closed squares in Fig. 5) and doubling times come much closer ($r^2 = 0.76$). The goodness of fit depends on a number of assumptions, e.g., the ADP:O ratio of respiration, here assumed to be 3, may actually be less (cf. Poorter *et al.* 1991) and therefore increase glucose costs. However, a change in such an assumption does not severely affect the overall trend.

5.4. Generalizations

Starting from the biochemical background of variation in construction costs and following the line of Williams *et al.* (1989), we have arrived at the RGR of the whole plant. Thus, from the perspective of the whole plant, the concept of payback time is actually a physiological specification of part of the plant strategy theory of Grime & Hunt (1975) and Grime (1979), where RGR plays an important differentiating role between stress tolerators versus competitors or ruderals.

How can the observed differences between the potentially fast- and slow-growing species at the cellular and organ level best be arranged in a conceptual framework? A genetic difference causes slow-growing species to invest a large fraction of their leaf biomass in cell-wall constituents and quantitative secondary compounds like lignins, whereas fast-growing species invest relatively more in compounds related to the cytoplasm, especially protein, but also in minerals and organic acids (Niemann *et al.* 1992, Poorter & Bergkotte 1992). As a consequence, total construction costs are rather similar, but net carbon-gain per unit leaf weight is much higher for the fast-growing species (Poorter *et al.* 1990, Garnier 1991, Reich *et al.* 1991). And as interspecific variation in the fraction of plant biomass allocated to leaves is much smaller than variation in the physiological activity (cf. Garnier 1991), at least under conditions of optimum nutrient supply, a difference in carbon gain per unit leaf weight generally translates into a difference in net carbon gain per unit total plant weight as well, and therefore into a difference in relative growth rate. If this line of reasoning is correct, anatomical/biochemical features rather than the construction costs per unit leaf weight differentiate between ecologically contrasting species. Payback time of leaves, or the RGR of whole plants is then a mere consequence of these differences.

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References

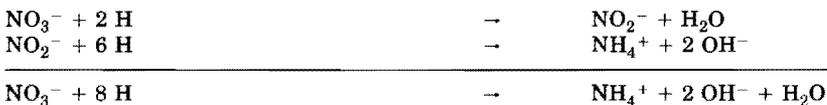
- Baumeister, W. 1958. Die Aschenstoffe. In: Michael, G. (ed), *Encyclopedia of Plant Physiology IV*, pp. 5–36. Springer-Verlag, Berlin
- Berendse, F. & Elberse, W.T. 1989. Composition and nutrient losses from the plant. In: Lambers, H., Cambridge, M.L., Konings, H. & Pons, T.L. (eds), *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants*, pp. 269–284. SPB Academic Publishing, The Hague
- Chabot, B.F. & Hicks, D.J. 1982. The ecology of leaf life spans. *Ann. Rev. Ecol. Syst.*, 13, 229–259
- Challa, H. 1976. An Analysis of the Diurnal Course of Growth, Carbon Dioxide Exchange and Carbohydrate Reserve Content of Cucumber. Agricultural Research Report 861. Pudoc, Wageningen
- Chapin, F.S. 1989. The costs of tundra plant structures: Evaluation of concepts and currencies. *Am. Nat.*, 133, 1–19
- Chiariello, N.R., Mooney, H.A. & Williams, K. 1989. Growth, carbon allocation and cost of plant tissue. In: Percy, R.W., Ehleringer, J.R., Mooney, H.A. & Rundel, P.W. (eds), *Plant Physiological Ecology: Field Methods and Instrumentation*, pp. 327–365. Chapman & Hall, London

- Chung, H. & Barnes, R.L. 1977. Photosynthate allocation in *Pinus taeda*. I. Substrate requirements for synthesis of shoot biomass. *Can. J. For. Res.*, 7, 106–111
- De Visser, R., Spitters, C.J.T. & Bouma, T.J. 1992. Energy cost of protein turnover: theoretical calculation and experimental estimation from regression of respiration on protein concentration of full-grown leaves. In: Lambers, H. & Van der Plas, L.W. (eds), *Molecular, Biochemical and Physiological Aspects of Plant Respiration*, pp. 493–508. SPB Academic Publishing, The Hague
- Diamantoglou, S., Rhizopoulou, S. & Kull, U. 1989. Energy content, storage substances, and construction and maintenance costs of Mediterranean deciduous leaves. *Oecologia*, 81, 528–533
- Garnier, E. 1991. Resource capture, biomass allocation and growth in herbaceous plants. *Trends Ecol. Evol.*, 6, 126–131
- Gower, S.T., Grier, C.C. & Vogt, K.A. 1989. Aboveground production and N and P use by *Larix occidentalis* and *Pinus contorta* in the Washington Cascades, USA. *Tree Physiol.*, 5, 1–11
- Griffin, K.L., Thomas, R.B. & Strain, B.R. 1993. Effects of nutrient supply and elevated carbon dioxide on construction cost in leaves of *Pinus taeda* seedlings. *Oecologia*, 95, 575–580
- Grime, J.P. 1979. *Plant Strategies and Vegetation Processes*. Wiley, Chichester
- Grime, J.P. & Hunt, R. 1975. Relative growth rate: Its range and adaptive significance in a local flora. *J. Ecol.*, 63, 393–422
- Harper, J.L. 1989. The value of a leaf. *Oecologia*, 80, 53–58
- Johnson, D.A. & Tieszen, L.L. 1976. Above-ground biomass allocation, leaf growth and photosynthetic patterns in tundra plant forms in arctic Alaska. *Oecologia*, 24, 159–173
- Kramer, T. 1979. Environmental and genetic variation for protein content in winter wheat (*Triticum aestivum* L.). *Euphytica*, 28, 209–218
- Kull, U., Herbig, A. & Otto, F. 1992. Construction and economy of plant stems as revealed by use of the BIC-method. *Ann. Bot.*, 69, 327–334
- Lafitte, H.R. & Loomis, R.S. 1988. Calculation of growth yield, growth respiration and heat content of grain sorghum from elemental and proximal analyses. *Ann. Bot.*, 62, 353–361
- Lambers, H. & Rychter, A. 1989. The biochemical background of variation in respiration rate: respiratory pathways and chemical composition. In: Lambers, H., Cambridge, M.L., Konings, H. & Pons, T.L. (eds), *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants*, pp. 199–225. SPB Academic Publishing, The Hague
- Layzell, D.B. 1990. N₂ fixation, NO₃⁻ reduction and NH₄⁺ assimilation. In: Dennis, D.T. & Turpin, D.H. (eds), *Plant Physiology, Biochemistry and Molecular Biology*, pp. 389–406. Longman Group, Harlow
- McDermitt, D.K. & Loomis, R.S. 1981. Elemental composition of biomass and its relation to energy content, growth efficiency and growth yield. *Ann. Bot.*, 48, 275–290
- Merino, J. 1987. The costs of growing and maintaining leaves of mediterranean plants. In: Tenhunen, J.D., C atarino, F.M., Lange, O.L. & Oechel, W.C. (eds), *Plant Response to Stress*, pp. 553–564. Springer Verlag, Berlin
- Merino, J., Field, C. & Mooney, H.A. 1984. Construction and maintenance costs of mediterranean-climate evergreen and deciduous leaves. *Acta Oecol./Oecol. Plant.*, 5, 211–229
- Miller, P.C. & Stoner, W.A. 1979. Canopy structure and environmental interactions. In: Solbrig, O.T., Jain, S., Johnson, G.B. & Raven, P.H. (eds), *Topics in Plant Population Biology*, pp. 428–458. Columbia University Press, New York
- Miller, P.M., Eddleman, L.E. & Kramer, S. 1990. Allocation patterns of carbon and minerals in juvenile and small-adult *Juniperus occidentalis*. *For. Sci.*, 36, 734–747
- Niemann, G.J., Pureveen, J.B.M., Eijkel, G.B., Poorter, H. & Boon, J.J. 1992. Differences in relative growth rate in 11 grasses correlate with differences in chemical composition as determined by pyrolysis mass spectrometry. *Oecologia*, 89, 567–573
- Nobel, P.S., Alm, D.M. & Cavellier, J. 1992. Growth respiration, maintenance respiration and structural-carbon costs for roots of three desert succulents. *Funct. Ecol.*, 6, 79–85.
- Peng, S., Eissenstat, D.M., Graham, J.H., Williams, K. & Hodge, N.C. 1993. Growth depression in mycorrhizal citrus at high-phosphorus supply. Analysis of carbon costs. *Plant Physiol.*, 101, 1063–1071
- Penning de Vries, F.W.T., Brunsting, A.H.M. & Van Laar, H.H. 1974. Products, requirements and efficiency of biosynthetic processes: a quantitative approach. *J. Theor. Biol.*, 45, 339–377
- Penning de Vries, F.W.T., Van Laar, H.H. & Chardon, M.C.M. 1983. Bioenergetics of growth of seeds, fruits, and storage organs. *Proc. Symp. Potential Productivity of Field Crops under Different Environments*, 1980, pp. 37–59. IRI, Manila
- Poorter, H. & Bergkotte, M. 1992. Chemical composition of 24 wild species differing in relative

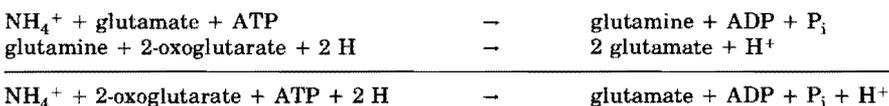
- growth rate. *Plant Cell Env.*, 15, 221–229
- Poorter, H. & Remkes, C. 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia*, 83, 553–559
- Poorter, H., Remkes, C. & Lambers, H. 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. *Plant Physiol.*, 94, 621–627
- Poorter, H., Van der Werf, A., Atkin, O.K. & Lambers, H. 1991. Respiratory energy requirements of roots depend on the potential growth rate of a plant species. *Physiol. Plant.*, 83, 469–475
- Reich, P.B., Uhl, C., Walters, M.B. & Ellsworth, D.S. 1991. Leaf lifespan as a determinant of leaf structure and function among 23 amazonian tree species. *Oecologia*, 86, 16–24
- Saeki, T. & Nomoto, N. 1958. On the seasonal change of photosynthetic activity of some deciduous and evergreen broadleaf trees. *Bot. Mag. Tokyo*, 71, 235–241
- Sims, D.A. 1990. The costs and benefits of photosynthetic acclimation to light environment in *Alocasia macrorrhiza*. Ph.D. dissertation, University of California, Davis. 165 p.
- Sobrado, M.A. 1991. Cost-benefit relationships in deciduous and evergreen leaves of tropical dry forest species. *Funct. Ecol.*, 5, 608–616
- Thornley, J.H.M. & Johnson, I.R. 1990. *Plant and Crop Modelling. A Mathematical Approach to Plant and Crop Physiology*, pp. 286–369. Oxford University Press, New York
- Van de Werf, A., Kooijman, A., Welschen, R. & Lambers, H. 1988. Respiratory energy costs for the maintenance of biomass, for growth and for ion uptake in roots of *Carex diandra* and *Carex acutiformis*. *Physiol. Plant.*, 72, 483–491
- Vertregt, N. & Penning de Vries, F.W.T. 1987. A rapid method for determining the efficiency of biosynthesis of plant biomass. *J. Theor. Biol.*, 128, 109–119
- Walton, E.F., De Jong, T.M. & Loomis, R.S. 1990. Comparison of four methods calculating the seasonal pattern of plant growth efficiency of a kiwifruit berry. *Ann. Bot.*, 66, 299–307
- Waring, R.H., McDonald, A.J.S., Larsson, S., Ericsson, T., Wiren, A., Arwidsson, E., Ericsson, A. & Lohammar, T. 1985. Differences in chemical composition of plants grown at constant relative growth rates with stable mineral nutrition. *Oecologia*, 66, 157–160
- Williams, K., Percival, F., Merino, J. & Mooney, H.A. 1987. Estimation of tissue construction cost from heat of combustion and organic nitrogen content. *Plant Cell Env.*, 10, 725–734
- Williams, K., Field, C.B. & Mooney, H.A. 1989. Relationships among leaf construction cost, leaf longevity, and light environment in rain forest plants of the genus *Piper*. *Am. Nat.*, 133, 198–211

Appendix 1

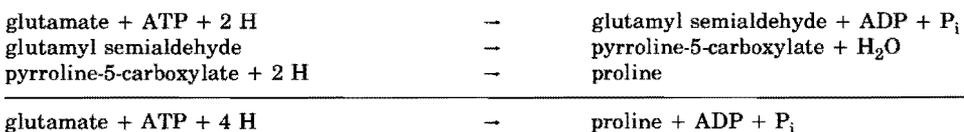
Nitrate reduction occurs in two steps:



Next, glutamate is formed:



Subsequently, either with or without transamination, other amino acids can be formed, mostly at additional cost. E.g.:



The last step is polymerization, at a cost of probably 4 ATP. Two ATP for the formation of tRNA, 1 ATP for the elongation of the peptide chain and 1 ATP for moving the ribosome to the next mRNA codon (Thornley & Johnson 1990):



Apart from these direct costs, there are indirect ones. The mRNA is occasionally hydrolysed and re-synthesis of one three-subunit codon requires 6 ATP. Furthermore, error correction by tRNA synthetases and signalling sequences may increase the costs of protein synthesis (De Visser *et al.* 1992). Finally, as different amino acids have different costs, total costs of the protein will depend on its amino acid composition. For further details see, *e.g.*, Thornley & Johnson (1990). Costs that are normally not considered in protein synthesis, but are of indirect nature as well, are those related to neutralization of the OH^- , formed during the above given reactions. This occurs partly by formation of organic acids.

Note: Partly depending on the organ and organelle where the above-given reactions take place, reducing power (H) may be provided by NADH, NADPH or Fd_{red} .

Appendix 2

Assuming no ontogenetic drift in the rates of photosynthesis and maintenance respiration, the net amount of sugars produced by one gram of leaf that can be re-invested in growth (GP, g glucose g^{-1} DW day^{-1}) over time t (days) is given by

$$\text{GP} = (\text{PS} - \text{LR}_m) \cdot t \quad (\text{A1})$$

where PS is the daily rate of photosynthesis (g glucose g^{-1} DW day^{-1}), and LR_m the maintenance respiration of the leaves (g glucose g^{-1} DW day^{-1}). Payback time is defined as the time at which GP equals the construction costs. If all the photosynthates produced by a leaf weigh equally, as assumed by Williams *et al.* (1989), payback time (PT, days) of one gram of leaf is given by

$$\text{PT} = \frac{\text{CC}}{\text{PS} - \text{LR}_m} \quad (\text{A2})$$

where CC are the construction costs to build one gram of material (g glucose g^{-1} DW).

Alternatively, photosynthates produced early in a leaf's life may be used to construct another leaf, which may then contribute to the payback time of the first leaf as well. In its simplest form, where sugars are invested in new leaves without delay, this would lead to an exponential increase in biomass. In formula, total biomass produced (BP, gram) over time t , starting from 1 gram of leaf is:

$$\text{BP} = e^{\frac{(\text{PS} - \text{LR}_m)}{\text{CC}} \cdot t} - 1 \quad (\text{A3})$$

Total glucose invested in biomass during that period is, by definition:

$$\text{GP} = \text{BP} \cdot \text{CC} \quad (\text{A4})$$

and thus, over a period t , the total amount of glucose that was available for growth is

$$\text{GP} = \text{CC} \cdot e^{\frac{(\text{PS} - \text{LR}_m)}{\text{CC}} \cdot t} - \text{CC} \quad (\text{A5})$$

Payback time is then given by

$$\text{PT} = \frac{\ln(2) \cdot \text{CC}}{\text{PS} - \text{LR}_m} \quad (\text{A6})$$

At the whole plant level, formula A5 converts into:

$$GP = CC \cdot e^{\frac{(PS - LR_m) \cdot LWR - SR_m \cdot SWR - (RR_m + RR_u) \cdot RWR}{CC} \cdot t} - CC \quad (A7)$$

where SWR and RWR are Stem Weight Ratio (biomass stems:total plant biomass) and Root Weight Ratio (biomass roots:total plant biomass), and SR_m , RR_m and RR_u the daily rates of stem maintenance respiration, root maintenance respiration and respiration related to uptake of nutrients (g glucose g^{-1} DW day^{-1}), respectively.

And thus, payback time of the whole plant becomes:

$$PT = \frac{\ln(2) \cdot CC}{(PS - LR_m) \cdot LWR - SR_m \cdot SWR - (RR_m + RR_u) \cdot RWR} \quad (A8)$$

Note added in proof:

As suggested in the legend of Fig. 2, the values of Miller *et al.* (1990) are not correct. The construction costs in their Table 2 should be: 1.21 ± 0.02 , 1.26 ± 0.04 , 1.33 ± 0.02 , 1.07 ± 0.02 , 1.18 ± 0.02 , 1.14 ± 0.03 and 1.23 ± 0.03 (P.M. Miller, personal communication).