
Funding the bud bank: a review of the costs of buds

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Retaining a reserve of buds or meristems for recovery from occasional damage is widespread among plants. Yet possession of a bud bank is not ubiquitous. Presumably there are costs to maintaining buds and for some species these costs outweigh the benefits. This paper has two themes. We estimate carbon costs of constructing and maintaining buds, and review other costs and benefits of buds in different situations. Second, we develop a framework for thinking quantitatively about the costs and benefits. Given available data and some reasonable assumptions, the absolute carbon costs of buds seem small. So the fact that many species do not maintain bud banks suggests that the benefits of buds may be negligible for them. Alternatively, buds may carry other costs. Costs of bud protection or of reserves that are coordinated with buds seem likely candidates.

Perennial plants achieve indeterminate growth by possession of persistent meristems (Raunkiaer 1934, Bond and Midgley 2001). If shoot apical meristems differentiate into reproductive structures, or if they are damaged or lost to some form of disturbance, then growth can resume from a bank of reserve meristems or buds. Additionally, sprouting from reserve meristems facilitates opportunistic use of space and resources, for instance if a light gap appears. Possession of a bud bank appears highly useful and common (Del Tredici 2001, Bond and Midgley 2003). Phylogenetic analyses have found that sprouting is mixed within species and between species in the same clades, and is broadly spread across clades of seed plants, thus demonstrating that sprouting is a highly labile trait (Schutte et al. 1995, Keeley and Zedler 1998, Ojeda 1998, Bond and Midgley 2003, Vesk and Westoby 2004).

However, sprouting is position dependent; different types and intensities of disturbance can lead to sprouting from different parts of the plants (Gill 1981, Bellingham and Sparrow 2000). Not all species can sprout from all parts of the plant. While in some species high proportions of plants sprout whether plants are clipped or burnt, in other species high proportions sprout after clipping but substantially lower proportions sprout after

burning (Hodgkinson 1998, Vesk et al. 2004, Vesk and Westoby 2004). In a comparative field experiment of 45 species, sprouting after clipping required buds below the clipping point, ca 5 mm above ground (Vesk et al. 2004). A burning treatment prevented sprouts from emerging from shallower than 6 mm below ground. So plants that could sprout after clipping, but not after burning, have buds below 5 mm above ground but lack buds deeper than 6 mm below ground (Vesk et al. 2004). So then, why do those plants that can survive clipping but not burning not have deeper buds?

More generally, why do some plants have many epicormic buds while others do not; and why do some plants generate aerial shoots from roots yet others do not? Or more generally still, why do not all plants have buds everywhere? It must be something about the costs of making and maintaining buds relative to their potential benefits. Buds have been rather overlooked, compared to belowground storage (James 1984, Pate et al. 1990). Logically, both meristems and reserves are required for sprouting. This paper briefly reviews costs and benefits of maintaining a bank of meristems.

We first outline major bud types and important differences between them. Second, using a compilation of bud sizes we estimate their construction and maintenance costs in terms of forgone net carbon assimilation using two different methods. Third, we perform a risk-based cost-benefit analysis of buds for recovery from possible damage. Finally, we examine other costs and benefits, addressing how some situations lead to buds being more or less costly to the plant.

All buds are not equal

Different bud types carry different costs and benefits. We can broadly distinguish preformed buds, persistent meristems and adventitious bud formation and growth.

The bud types may be differentiated on at least four criteria: size; timing; architectural control; location and protection. Preformed buds are generally larger than persistent meristems, as they include leaf primordia or prophylls. Preformed buds represent a relatively large upfront investment in construction and maintenance, with relatively low activation costs and rapid releafing response upon activation. There may also be turnover costs if buds have limited lifespan and need to be replaced periodically. Adventitious budding defers upfront costs until disturbance, but de-differentiation into meristematic tissue and formation of adventitious buds results in larger activation costs at a time when the plant has low carbon income. This extra development upon activation retards the rate of releafing. Persistent meristems would be intermediate in both upfront and activation costs and in releafing rate. The majority of leaf flushing in woody plants following unfavourable seasons (frigid winters or summer drought) and post-disturbance is from preformed buds (Zimmermann and Brown 1971, Del Tredici 2001). Perhaps this is because preformed buds allow rapid releafing with low activation costs.

Preformed buds and persistent meristems may also allow sprouting responses to be more specific and tied to general architectural form. Reliance on totipotency and adventitious budding may be less controllable, and result in inefficient regrowth architecture. This may carry greater opportunity costs for tall, long-lived and woody species than for low-growing, short-lived herbaceous species. Multi-stemmed plants are generally shorter than single-stemmed plants because their stems are narrower and often lean away from each other, so risking buckling (McMahon 1973, Chamberlin and Aarssen 1996, Midgley 1996). Coexistence between such growth forms can occur through trade-offs of growth rate and fecundity (Kohyama 1992). Adventitious root buds would be favoured where lateral expansion is useful as an active foraging strategy or for reducing the risk from patchy disturbances (Peterson and Jones 1997).

In a review of sprouting in temperate trees, Del Tredici (2001) distinguished sprouts by their origin: stem collar and epicormic; underground stems (rhizomes and lignotubers); roots; opportunistic stem sprouts. Differences in location and protection of buds are clearly important. Belowground buds may be protected by soil, but are of limited use for re-establishing a tall canopy following disturbance because so much height needs to be recovered. By contrast, aboveground buds enable rapid recovery of elevated canopy but may require protection by thick bark or wood. For the rest of this paper we concentrate on preformed buds and suppressed meristems on aboveground stems. We focus mainly on woody plants, though results may be relevant to herbaceous species.

Nutrition and metabolic costs of suppressed buds

Partitioning studies using radiocarbon-labelled photo-assimilate have produced some evidence of bud costs. In grasses (*Lolium temulentum*, *L. multiflorum*) and cereals (*Triticum aestivum*) ca 1–2% of a leaf's assimilate is allocated to the repressed tiller bud that it subtends (Jewiss 1972). Leaves immediately above and below that each contribute ca 1%, suggesting that ca 3% of leaves' assimilate is allocated to repressed buds. Tiller buds are relatively large (ca 3 mm long) compared to axillary buds in dicots so should represent the upper end of the cost range.

In woody plants, *Pinus radiata* shoots accumulated 0.8% of photo-assimilated ^{14}C per lateral bud (Ross et al. 1984). *Prosopis glandulosa* (honey mesquite) allocated 0.7–10% of leaf-assimilated radiocarbon to the root crown seasonally (Fick and Sosebee 1981). The high end of this range reflected active storage, i.e. reserves rather than bud costs. The low end of the range reflected the normal running costs of the total bud bank and storage tissue. Broadly, these photo-assimilation studies of monocots and woody dicots suggest that ca 1–2% of a leaf's export might go to buds. But this may be greater where buds are large (e.g. monocot tiller buds) or when active storage occurs.

Estimating carbon costs of manufacture and maintenance from bud sizes

We now turn to estimating the costs of buds using their volumes together with published estimates of construction costs and maintenance respiration. Bud volumes were calculated from measurements on micrographs in published studies. Two orthogonal axes through the bud were measured, and the volume estimated as an ellipsoid with two equal short diameters and one long. This is a rough approximation, but it indicates the scale of bud sizes (Fig. 1). Undifferentiated meristems were distinguished from preformed buds. The volumes of undifferentiated meristems ranged 10^{-4} – 10^{-2} mm³ and preformed buds ranged 10^{-3} – 10^{-1} mm³ (Fig. 1, n = 43 species). Over-wintering buds of woody deciduous species extend to even larger sizes. A table of species and sizes appears in Appendix 1.

Costs of constructing tissues are remarkably invariant across organs, species and environments despite three-fold difference in the costs of different organic constituents; approximately 1.5 g g⁻¹ DM (1.25–1.75, 10th and 90th percentiles) for roots, stems and leaves (Lambers et al. 1998, p. 129). If buds are located where there would otherwise be no tissue, then the costs may be absolute, i.e. as costs per gram multiplied by the tissue mass. On the other hand, if buds are located where there would otherwise be parenchyma, then the bud has costs only by

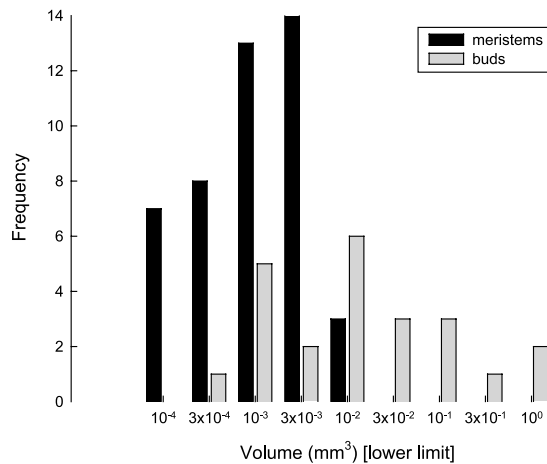


Fig. 1. Volumes of meristems and axillary and adventitious buds from 43 plant species. Estimated and compiled from photographs in published papers (Appendix 1). Volumes were estimated as ellipsoids. Buds include prophylls, and buds at the upper end of size range generally had more prophylls.

comparison to the parenchyma that would otherwise fill the space of the bud. If the costs do not vary between tissues, then we would assume there is no cost to the bud. But if density differs substantially between bud tissues and parenchyma, then there may be a construction cost difference. Visually, meristematic tissues appear denser than parenchyma due largely to the large vacuoles in parenchyma and abundant organelles in meristematic cells. Measurements of tissue densities may help to unravel this question.

Estimates of maintenance respiration rates are much less certain (Lambers et al. 1998, p. 125), but range 3–6% dry mass (DM) d^{-1} . Therefore maintenance costs become equivalent to the construction costs cited above after ca 20–60 days. Unless bud turnover is that rapid, maintenance costs will be larger than construction costs. If maintenance costs differ consistently between tissues, then this twofold range may be significant. Protein turnover and ion gradient maintenance are the primary contributors to maintenance costs (Penning de Vries 1975, Bouma et al. 1994, Amthor 2000, Cannell and Thornley 2000). Bud tissues, which are composed of cells with dense cytoplasm and abundant organelles, would thus be expected to have higher maintenance costs than parenchyma, which is composed of largely vacuolate cells with few organelles. Amino acid incorporation into proteins was no different between pea buds that were dormant, buds that were actively growing and buds in transitional states (Stafstrom and Sussex 1988). This implies that in *Pisum sativum* at least, protein turnover is relatively constant.

Estimates of dry matter construction costs and maintenance appear in Table 1. Based on the upper end of these estimates, we can carry out two calculations, firstly the cost of a single axillary bud to the leaf it subtends;

secondly, the cost to a whole plant of keeping 10 buds for a rare disturbance. A single bud of 0.1 mm^3 would cost 0.09 mg DM to construct and $0.003 \text{ mg DM } d^{-1}$ to maintain (Table 1). If we assume a net assimilation rate (NAR) of $0.008 \text{ mg DM mm}^{-2} \text{ leaf } d^{-1}$ (from seedling growth experiments, range 0.003–0.014, median 0.008 $\text{mg mm}^{-2} d^{-1}$ from 24 herbaceous and 33 woody species: Poorter and Remkes 1990, Wright and Westoby 1999), we can calculate that construction of a single 0.1 mm^3 bud would require the net assimilation from 7.5 mm^2 of leaf area for one day. Maintenance would require the net assimilation from 0.34 mm^2 of leaf area per day.

We can also calculate costs from direct measurements of dark respiration rates on the large overwintering leaf- and flower- buds of fruit crops. McPherson et al. (1997) cited values of $0.8\text{--}3.5 \text{ nmol CO}_2 \text{ s}^{-1} \text{ g}^{-1}$ fresh mass (FM) among various fruit crop buds (kiwifruit, pears, peach, apricot). First, we calculate the equivalent gross photosynthesis needed to fund bud respiration. Then, noting that leaf area also respire, we calculate the potential carbon assimilation (photosynthesis minus dark respiration) that the bud respiration represents and hence, the leaf area equivalent of funding bud maintenance.

Buds of 0.1 mm^3 would respire $0.007\text{--}0.03 \text{ } \mu\text{mol CO}_2 \text{ d}^{-1} \text{ bud}^{-1}$, let us assume $0.02 \text{ } \mu\text{mol CO}_2 \text{ d}^{-1} \text{ bud}^{-1}$. If the photosynthetic rate, A , is $10 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (median of 80 species, range $5\text{--}20 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ from (Wright et al. 2001), over a 10 h day of saturated photosynthesis this is $0.36 \text{ } \mu\text{mol CO}_2 \text{ mm}^{-2} \text{ d}^{-1}$ (range $0.18\text{--}0.72$). Thus the respiration of a single axillary bud is equivalent to the gross photosynthesis of ca 0.06 mm^2 of leaf area (range $0.01\text{--}0.17 \text{ mm}^2$ using the opposite ends of the photosynthesis and bud respiration ranges cited, respectively).

Now, using an estimate of leaf dark respiration rate, R_D , of $1.4 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (median of 80 species, range $0.3\text{--}6.9$ from Wright et al. (2001), we can calculate the potential carbon assimilation over a day (10 h of saturated photosynthesis minus 24 h leaf dark respiration) as $0.21 \text{ } \mu\text{mol CO}_2 \text{ mm}^{-2} \text{ d}^{-1}$ (median of 78 species, range $0.02\text{--}0.66$ calculated from Wright et al. (2001). So respiration of a single axillary bud requires allocation of the potential carbon assimilation of 0.095 mm^2 of leaf area ($0.01\text{--}1.5 \text{ mm}^2$ using the opposite extremes of bud respiration and leaf potential carbon assimilation rate ranges respectively).

The estimates for maintenance of a 1 mm^3 bud from the two methods of calculation (0.1 and 0.3 mm^2 leaf area net assimilation) agree closely, and suggest that a single axillary bud should require allocation of the potential carbon assimilation from ca 0.2 mm^2 of a single leaf. Similarly, 10 reserve buds should require dedication of ca 2 mm^2 of leaf area to their maintenance. A plant with leaf area of $10\,000 \text{ mm}^2$ ($10 \times 10 \text{ cm}$, herb

Table 1. Calculation of possible construction and maintenance costs of reserve buds. Based upon size estimate from published micrographs (Fig. 1). Assumes no shrinkage in specimen preparation, fresh mass (FM) per volume 1 mg FM mm^{-3} , and dry matter (DM) content $0.6 \text{ g DM g}^{-1} \text{ FM}$. Cost estimates in terms of dry matter for construction ($1.5 \text{ g g}^{-1} \text{ DM}$) and maintenance ($45 \text{ mg g}^{-1} \text{ DM d}^{-1}$) based on Lambers et al. (1998, pp. 125 – 129). Bud dark respiration rates (median 2.3, range 0.8–3.5 $\text{nmol CO}_2 \text{ g}^{-1} \text{ FM s}^{-1}$) from McPherson et al. (1997).

	Buds			
	low	mid	high	
	Meristems			
	low	mid	high	
Volume (mm^3)	10^{-4}	10^{-3}	10^{-2}	10^{-1}
Fresh mass (FM, mg)	10^{-4}	10^{-3}	10^{-2}	10^{-1}
Construction cost (mg DM bud^{-1})	9×10^{-5}	9×10^{-4}	9×10^{-3}	9×10^{-2}
Maintenance cost ($\text{mg DM bud}^{-1} \text{d}^{-1}$)	2.7×10^{-6}	2.7×10^{-5}	2.7×10^{-4}	2.7×10^{-3}
Bud respiration ($\text{nmol CO}_2 \text{ s}^{-1} \text{g}^{-1} \text{ FM}$)	2.3×10^{-3}	2.3×10^{-2}	2.3×10^{-1}	2.3
Daily respiration ($\mu\text{mol CO}_2 \text{ bud}^{-1} \text{d}^{-1}$)	2×10^{-5}	2×10^{-4}	2×10^{-3}	2×10^{-2}

sized) would allocate 0.02% of the leaf area to maintaining a reserve of ten buds.

If leaves are only retained for a short growing season, e.g. three months, then this allocation of leaf assimilation may be increased four times, ignoring temperature dependence, which would tend to reduce respiration in cold climates. Conversion into storage forms and transport inefficiencies may further increase costs. If we assume that together, transport, conversion to storage forms and a short growth season increase the respiration costs tenfold, then a single axillary bud may require the potential carbon assimilation of 2 mm^2 of leaf area.

This does not seem like a very large outlay. Moreover, these estimated costs are absolute. As mentioned previously, if buds or meristems are embedded in stem tissue, then the relevant cost is that beyond the cost of parenchyma filling the space if the buds were absent. Variation in NAR between species is only fourfold (Poorter and Remkes 1990, Wright and Westoby 1999), and would either halve or double these cost estimates. NAR declines as plants mature and accumulate stem and root mass. According to the idea that respiration costs limit achievable plant height, as stem and root structures accumulate through height growth the total costs approach the total photosynthesis (Givnish 1995). As the margin between photosynthesis and total costs narrows, perhaps these seemingly small costs of bearing buds become uneconomical against the benefits of investment in reproduction. If many buds are maintained throughout a long-lived plant, then clearly the costs will accumulate—but maintaining enough to resprout from should be a small cost. These estimates indicate that buds are metabolically inexpensive. For those species that do not have the capacity to resprout, this suggests either that the benefits of maintaining buds are negligible or that other costs need to be considered. We next address cost–benefit calculations.

Risk and reserve

Here we use an approach from standard microeconomic theory to ask what is the maximum cost a plant should be prepared to pay to avoid a risk of death from severe disturbance.

Risk aversion and utility functions of wealth

Risk can be defined as the variation in possible outcomes of chance events (Dorfman 1994). Greater risk is due to greater variation around an average expected outcome. Risk reduction then, is a decrease in the variance of an event. For most but not all people, the marginal value of wealth declines with increasing total wealth. One dollar is worth less (has less utility) to someone when they already have \$10 000 than when they have only \$10. A graph of utility against wealth can be used to describe the risk profile of a person, firm or in this case, individuals of a plant species. A straight line describes a risk-neutral firm. Risk aversion is described by utility functions that are concave-down (steep at low wealth with diminishing returns to increased wealth). Risk-seeking behaviour is described by a concave-up utility function. For a risk-averse firm, the declining utility of wealth implies that at any point, the utility from an increment of wealth gained is less than the disutility caused by loss of an equal increment (Frank 1994).

Plants would be expected to be risk-averse. This is because fitness over successive generations is multiplicative, e.g. $N_t = N_{t-1} (r_t + s_t)$, where N is the population number, r_t is the recruitment rate in year t and s_t is the survival rate in year t (Higgins et al. 2000). Thus, evolutionary models over time use geometric rather than arithmetic means for fitness (Lewontin and Cohen 1969, Venable 1989, Simons 2002). Risk reduction in a fitness context aims to minimise the probability of having the

sum of survivors and recruits equal zero. As variance in fitness increases, the geometric mean decreases. Sprouting may reduce the arithmetic mean fitness (through bud costs to seed production) but increases the geometric mean by reducing the variance in survivorship (especially the chance of failing to reproduce). This is the basis for the often-observed trade-off between sprouting and seeding (Keeley 1977).

How risk-averse are plants? The magnitude of risk aversion in people may be determined by the 'certainty equivalent' of a gamble. That is, one determines how high would the expected return on a gamble have to be before a person would prefer that gamble to a smaller (but certain) gift. The difficulty is in offering a gamble to a plant and determining preference. But we can turn the question around and ask what would a plant be prepared to pay (the certainty equivalent) in order to avoid a possible loss (disturbance damage)?

This problem is similar to that of asking what is the most that a consumer would be prepared to pay for insurance against a loss (Frank 1994). Insurance is not strictly analogous because insurance is the case where risks are (a) transferred to another party and (b) reduced by the law of large numbers. Plants cannot transfer the risk to another party, nor can they benefit from the law of large numbers reducing variance around the expected outcome in the way that insurers do. However, the exercise is useful to determine what a plant should be prepared to pay to reduce the risk of zero fitness.

First, we need to define a utility function for plants. Leaf area may represent wealth. Utility we might think of as seed output. Within a generation, seed output is directly proportional to leaf area (Henery and Westoby 2001). But because of the multiplicative effect noted above, fitness over a series of generations is best thought of as the sum of the logs of seed output. Thus we can consider utility as a logarithmic function of leaf area.

Consider a plant with an initial leaf area, L_0 (wealth), and fitness (utility) function, $F(L) = \text{seed output} = \log \text{leaf area}$ (curve, Fig. 2). If there is prospect of damage D to the leaf area with probability p , then the expected value (or leaf area) is: $E(L_0 - D) = p(L_0 - D) + (1 - p)L_0$; but the expected utility (or fitness) is: $E(F(L_0 - D)) = p F(L_0 - D) + (1 - p) F(L_0)$.

If R is the reserve kept, then the fitness is $F(L_0 - R)$, whether or not loss occurs. The plant is indifferent to keeping or not keeping a reserve when the fitness of keeping a reserve equals the expected fitness. $L_0 - R$ is the certainty equivalent of the gamble of getting $L_0 - D$ with probability p and L_0 with probability $(1 - p)$. $L_0 - R$ is less than the expected value because the plant is risk-averse and is willing to pay a premium to avoid the possibility of a large loss. R is the maximum reserve that the plant should keep.

We can use this model to determine how the reserve should vary as a function of the probability of damage

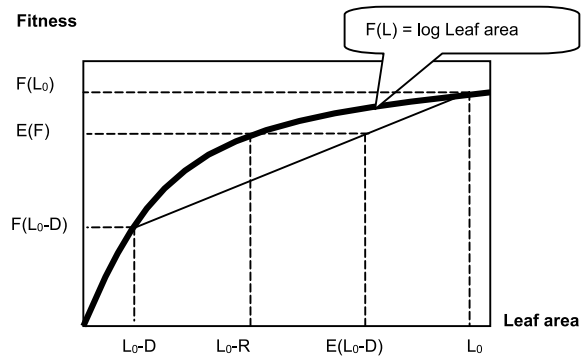
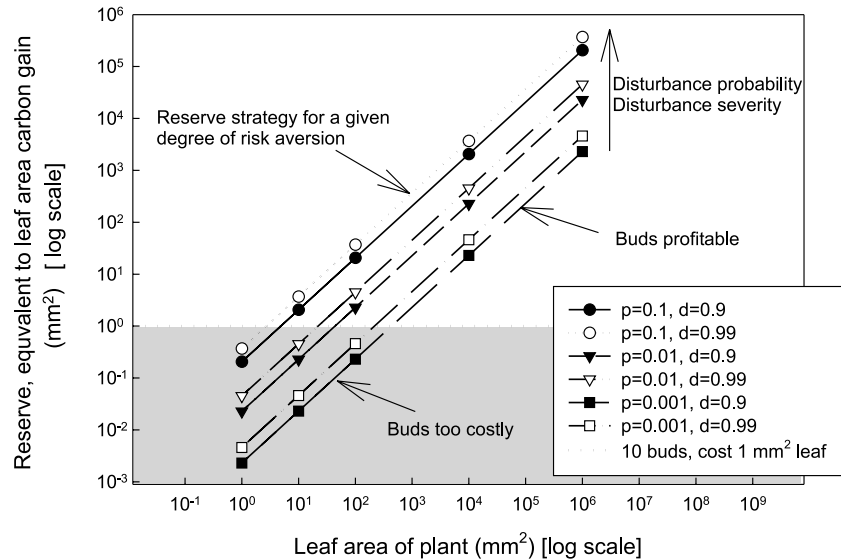


Fig. 2. Model for maximum reserve to be kept by a plant due to risk aversion. Curve represents utility or fitness $F(L)$ as a function of current leaf area. L_0 is initial leaf area. The possibility of damage (D) results in expected leaf area $E(L_0 - D)$. But expected fitness $E(F)$ corresponds to a lower leaf area ($L_0 - R$) than the expected leaf area because the plant is risk-averse and prefers a small but certain loss to the possibility of a much larger one. R is the certainty equivalent of the possible damage. R represents the maximum the plant should pay for recovering from possible damage. Based on Frank (1994, p. 230).

and the magnitude of the damage. In Fig. 3 we have presented some results from this model. For a given utility function (here fitness = $\log(\text{leaf area})$), the maximum reserve kept for different probabilities and severities of disturbance appear as parallel lines. The region above the horizontal line is where the maximum that the plant is prepared to pay exceeds the cost of ten buds in terms of potential carbon gain of leaf area (1 mm^2). Below this line, the plant is not prepared to pay the cost of keeping ten buds. The intersections indicate the size of plant that is just able to afford funding the bud bank. For this example, a small herb (435 mm^2 leaf area) would be prepared to fund a bud bank for recovery from a rare disturbance (probability 0.001) causing damage to 90% of leaf area (long dash, filled squares). But no smaller plant would keep a bud bank for this disturbance scenario. At the other extreme, a plant with only 5 mm^2 leaf area (a tiny asterid, *Actinobole uliginosum* perhaps) would not fund a bud bank if the disturbance was less likely than one in ten and would result in less than 90% leaf area loss. If we have underestimated the cost of buds (e.g. deciduous leaves, storage and conversion inefficiencies), then the horizontal line would be shifted upward and the minimum size plant that should allocate potential carbon assimilation to buds reserves will increase. As disturbances become less predictable, uncertainty about the probability or severity of damage increases. Hence variation in outcomes, or risk, increases. This would tend to shift the reserve strategy lines upward. The slopes of reserve strategy lines reflect the degree of risk aversion. Steep lines result from risk aversion, while risk neutrality would appear as a horizontal line. That is, a risk-neutral

Fig. 3. Example results from a model of the maximum reserve a plant should be prepared to keep aside for recovering from disturbance, based on risk aversion, see Fig. 2 and text. Utility function was: fitness = log (leaf area). Symbols and lines represent maximum proportion of leaf area devoted to maintenance of buds for recovery from disturbances that differ in probability and severity. Each line represents a strategy adapted to a particular combination of disturbance probability and severity. The slope of the lines increases with increasing risk aversion. Horizontal line represents leaf area cost of maintaining ten buds, calculated as equivalent potential carbon gain. The part of the strategy line below the horizontal line represents where the cost of ten buds exceeds the maximum the plant is prepared to pay. The part of the strategy line above that intersection represents where the cost of ten buds is less than the maximum the plant is prepared to pay and so the plant will keep a bud bank.



plant makes no change to its willingness to pay for buds because of changes in total leaf area. Hence, the risk profile could have an effect on this analysis. But with moderate degrees of risk aversion, the probability and severity of damage have more effect on maximum reserve. This analysis suggests that most plants should keep buds.

This is a static calculation and might be thought of as a per day or per year payment. The limitation of a static approach is that it cannot assess the long term opportunity cost that a risk-averse strategy incurs from not investing in current growth and so increasing wealth (Chapin III et al. 1990, Frank 1994). This will act in opposition to benefits of maintaining a reserve when opportunities for growth are unrestricted, but will tend to favour reserves in slow-growing species (Kobe 1997). Opportunity costs would also be affected by competitive interactions between species (Bond and Midgley 2003). The balance of the trade-off between current growth and reserve will depend upon growth rate and lifespan as well as the probability, scheduling, and severity of disturbance. This requires a dynamic model, beyond the scope of this paper. Storage enables evening out supply and demand (Chapin III et al. 1990), and was most favoured in a dynamic model of sprouting under high productivity and moderately frequent disturbance (Iwasa and Kubo 1997). The dynamic model supports our result that most plants should keep buds and reserves for sprouting

(Iwasa and Kubo 1997). Bellingham and Sparrow (2000) proposed a shift to non-sprouting at low productivity sites that are frequently and severely disturbed (herbaceous species) and at productive sites subject to infrequent but severe disturbances (trees).

What other costs and benefits do buds have?

We have shown that photosynthetic costs of constructing and maintaining buds are small—both in absolute terms and relative to benefits for damage recovery. So explaining why some species do not retain buds requires either minimal benefits, other costs, or that costs and benefits are modified under different conditions. Stafstrom (1995) thought that the costs of making and maintaining buds would be most apparent in “harsh environments”. Citing work on *Betula* at the tree line that rely upon buds (Maillette 1987), he inferred that the “costs must be minimal relative to their value”. While strictly this is true for that situation, it obscures the general point that if the potential benefit of buds is high then this will offset the costs, leading to obvious bud use. Evidence for the costs of buds would be better sought by comparing situations that are similar in most respects but deliberately contrasted in one way that affects the relative benefit of buds. Costs and benefits of buds may be affected in a few broad ways, outlined in Table 2. Several of these are self-explanatory, but two will be discussed further below.

Table 2. Ecological factors affecting costs and benefits of increased bud numbers. B is benefit, C is cost, arrows indicate higher or lower.

Factor favouring buds	Examples	Effect
Higher probability of bud use	Frequent disturbance, intense disturbance, long plant lifespan, long bud lifespan	B ↑
Lower probability of bud loss	Low risk of bud predation, disturbance intensity not too high	C ↓
Harsh post-disturbance conditions for seedling recruitment	Intense competition, harsh environment, possibility of long extension of lifespan	B ↑
Low opportunity cost of not investing in growth	Short vegetation, plants in dimly lit understorey	C ↓
Collateral benefit	Clonal expansion favoured over seeds	B ↑
Factor disfavouring buds		
Coordination with reserves required	Ongoing respiration costs of roots when canopy is damaged	C ↑
Coordination with protection required	Bark, embedded in wood, belowground location	C ↑
Collateral costs	Physical interference of buds and/or bud traces with vascular function or support	C ↑

Does coordination with reserves, in effect represent a cost of buds?

Most literature on sprouting after herbivory and fire has emphasized limitation by carbohydrate and nutrient reserves (Wright 1972, Stoddart et al. 1975, James 1984, Pate et al. 1990, Canadell and López-Soria 1998). Variation within and between individuals, especially between seasons, has been particularly emphasized (Stoddart et al. 1975, Malanson and Trabaud 1988). Later work showed that leaf area of sprouts quickly changed from a sink to a source of carbohydrates and that the storage reserve was not greatly drawn down (Richards and Caldwell 1985, Chapin III et al. 1990, Briske and Richards 1995). Other work showed that reserves and regrowth were uncorrelated (Sparks and Oechel 1993, Cruz et al. 2003a). The emphasis in range management shifted to the availability of meristems for regrowth (Richards and Caldwell 1985, Briske and Richards 1995).

One expects buds and reserves to be coordinated, such that neither are limiting (or both are, depending upon one's perspective). This is the economic principle of equalisation of marginal returns (Bloom et al. 1985, Frank 1994, Westoby et al. 2002). To explain this, suppose that a species consistently stored more resource than was necessary to fund resprouting by the buds. In this case, buds would be considered limiting to sprouting success, because at the point when plants could no longer resprout they would still have reserves, but no buds. Now, if a mutant arose that stored a little less, it would be more successful by being able to reallocate the extra reserve and consequently would invade the population. If the resident strategy stored much less, such that when plants failed to resprout they consistently had remaining buds, then a mutant that stored a little more could invade. Hence a balance of buds and reserves should be established. This does not say that buds and storage are perfectly aligned at each individual disturbance event. Under certain conditions, it may be that buds are more limiting than reserves because the bud

bank is exhausted relatively more easily than the reserves, or if buds are relatively less effective under those conditions (Bell and Pate 1996, Canadell and López-Soria 1998, Cruz et al. 2003a, b). For instance, burning following a clip may reduce the available buds to a greater degree than the reserves.

Need the reserves and buds be spatially coordinated? Should a plant maintain a single protected store of reserve but have buds in a number of places, not knowing which might be needed? There is no point in storing reserves in a location that is susceptible to damage and loss. Similarly, bud locations should be commensurate with disturbance type and intensity (Bellingham and Sparrow 2000). Work by Pate et al. (1990) showed that a wide range of fire-resprouter species had high starch concentration and swollen organs below ground. However, Myrtaceae species had high starch concentration above ground, not below ground. This suggests the hypotheses that (1) Myrtaceae stems survive the fire (as do many *Eucalyptus*; Burrows 2002), and (2) that starch mobilization from belowground to aboveground structures is costly. Similarly, in the tree *Euptelea polyandra*, found growing on unstable slopes, substantial reserves of starch are found in aboveground stems (Sakai et al. 1997). In the event of landslips, stems are often knocked down without being snapped, and reserves are then translocated to the site of new sprouts. In cutting experiments, few sprouts arise from the stump (Sakai et al. 1997, Sakai and Sakai 1998). Transport inefficiencies and susceptibility of reserves to predation or other loss would tend to act against centralised reserves and dispersed buds.

Concluding remarks

The contribution of Raunkiaer (1934) in drawing attention to the ecological significance of buds is felt to this day. Yet progress on mechanistic understanding of the costs of buds and why they vary among species and environments has languished. This paper has produced

estimates for costs and hopefully will stimulate researchers to better quantify the costs of buds to improve understanding of trade-offs in life-history and architecture of plants. Given available data and some reasonable assumptions, both in absolute and relative terms bud costs were estimated to be small. So the fact that many species do not maintain bud banks suggests that the benefits of buds are negligible for them. Alternatively, buds carry other costs. Costs of protection and/or reserves with which buds are coordinated are likely candidates.

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