

Acknowledgements

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Coping with herbivores and pathogens: a model of optimal root turnover

Because they live underground, we know very little about the life and death of roots. It is tempting to compare them to leaves, and to speculate, for example, that plants in nutrient-poor environments should maintain their roots for a long time, while plants in resource-rich environments or roots in fertile patches should turn over rapidly (Grime *et al.* 1991). It is not clear, however, that plants have as much control over root lifespan as they do over leaf lifespan. Roots observed in minirhizotrons are commonly seen to disappear rather than senesce and decompose in place (Johnson *et al.* 2001; Stevens *et al.*, in press). Insecticide and fungicide applied to soil can extend the lifespan of roots by 46–125 days in peach (Wells, Glenn & Eissenstat 2002a), and more than 500 days in sugar maple (Eissenstat *et al.* 2000). If herbivores and pathogens control the death of roots, then theories of optimal resource allocation may not prove predictive of root lifespan. Here we propose a theory of root lifespan that allows plants to exert a probabilistic control over root death by allocating resources to defence. Speculation in this area is almost entirely unfettered by observation, but might prove useful in directing future research.

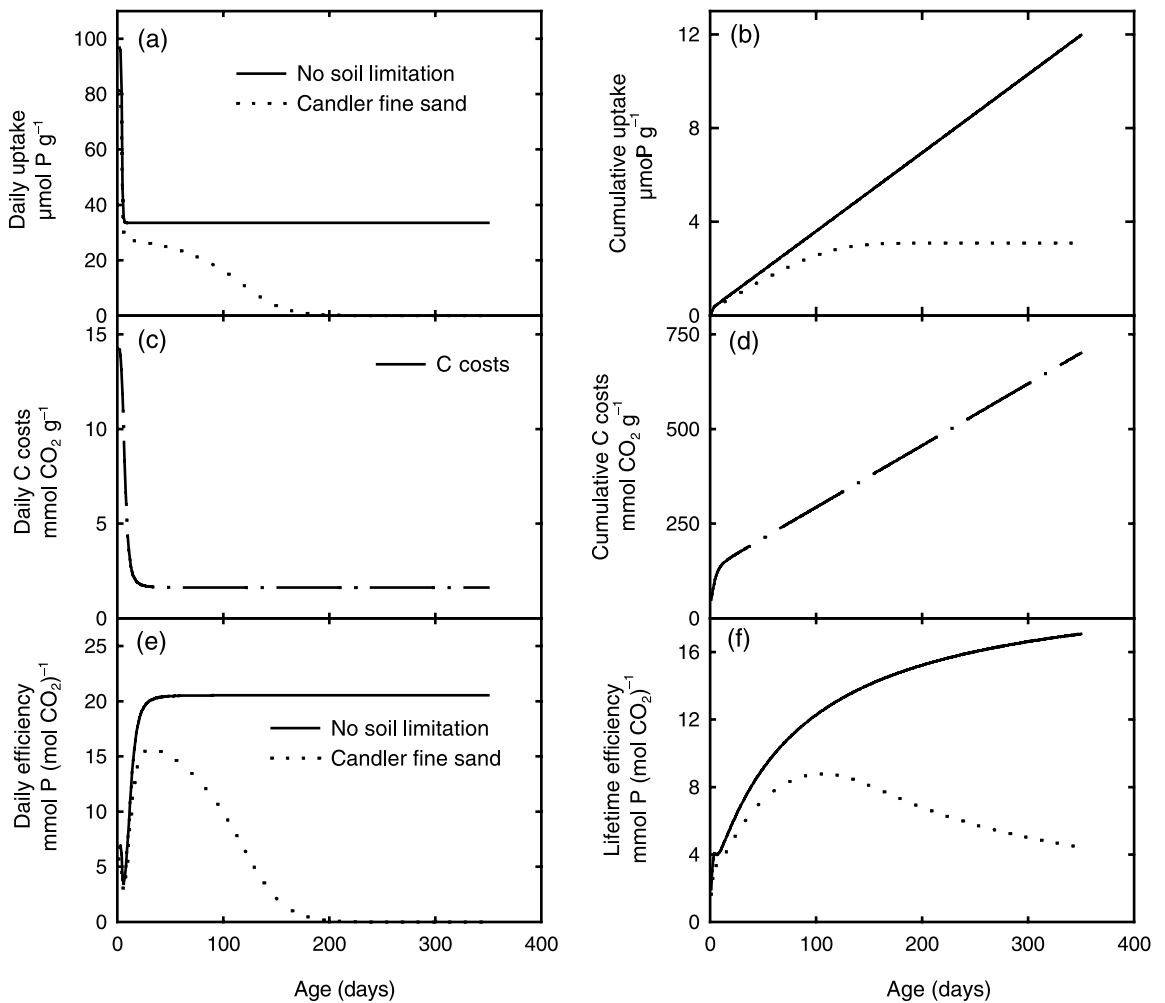


Fig. 1. Daily P uptake (a); lifetime P uptake (b); daily C cost (c); lifetime C cost (d); daily efficiency (e); and lifetime efficiency (f) of citrus roots. Solid line, simulated uptake with no soil depletion; dashed line, uptake with soil P depletion based on soil parameters of Chandler fine sand (see Bouma *et al.* 2001 for details). Data are slightly different from those presented by Bouma *et al.* (2001) because of a corrected value for the effective P diffusion coefficient ($4.1 \times 10^{-8} \text{ cm}^2 \text{ s}^{-1}$ instead of the published value of $4.1 \times 10^{-4} \text{ cm}^2 \text{ s}^{-1}$).

The theoretically optimal deployment of roots can be defined as that which maximizes the return on an investment. We can define the investment in terms of the carbon required to build and maintain a root, and the return as the uptake by that root of the limiting soil resource. This allows us to define the efficiency of the root in nutrient or water capture, E , as the ratio of return to investment. E can be calculated from the instantaneous rates of respiration and uptake, but this instantaneous E does not predict the optimal root lifespan. The theoretically optimal lifespan is that which maximizes the lifetime cumulative efficiency of the root, which is the cumulative uptake divided by the cumulative carbon cost (Yanai, Fahey & Miller 1995). To illustrate this approach, we will use root respiration from apple (not shown) and phosphorus uptake from citrus (Fig. 1), for reasons that will become clear below.

There are few data available to parameterize even this simple model of root efficiency. The predicted optimal lifespan is quite sensitive to the assumed pattern of respiration and uptake as a function of root age. It is easy to show that, if respiration and uptake

were constant with age, the optimal root lifespan would be infinite because the cumulative efficiency would increase continuously as the initial investments in root construction were amortized over a longer period (Yanai *et al.* 1995). We do know, however, that respiration and uptake are not constant over the lifetime of a root. One reason, presumably, that old roots are abandoned and new roots constructed is that they deplete the soil around them of nutrients, or they become less effective at nutrient uptake as they age (Bouma *et al.* 2001; Clarkson 1991; Van Rees & Comberford 1990). Respiration is also highest in young, rapidly growing roots, and declines with age and with the concurrent reduction in the number and metabolic activity of living cortical cells (Bouma *et al.* 2001; Comas *et al.* 2000). The peak in lifetime efficiency depends on the relative shapes of these two declining curves, both of which are likely to be poorly characterized.

A comparative study of citrus and apple produced observations of respiration rates and P-uptake capacity from excised root segments ranging in age from 0–80 days (Bouma *et al.* 2001). These data allowed us to

predict optimal root lifespan based on the efficiency model. The results, however, did not provide a very definitive test. Apple, which has fine, ephemeral roots, was predicted never to achieve an optimal lifespan, at least based on the efficiency of P acquisition, which is probably not the limiting nutrient. For citrus, which has coarse, long-lived roots, an optimal lifespan was indeed predicted (Fig. 1), and it could be adjusted to any desired value depending on the assumed rate of depletion of soil P (Bouma *et al.* 2001). The target value is generally the median lifespan reported from minirhizotron observations (30 days for apple, 300 days for citrus, for example). This brings us to another interesting point.

The various trials of the efficiency model to date (Bouma *et al.* 2001; Eissenstat & Yanai 1997; Yanai *et al.* 1995) have applied the theory to a single root, or to a root presumed to represent the median reported in minirhizotron measurements of longevity. If the plant had perfect control over root lifespan, and was optimizing efficiency of resource capture, then roots in similar environments should all have similar lifespans. Instead, roots exhibit a large range of lifespans, even along a single observation tube. This suggests, perhaps, that plant control of root death is imperfect, and also that a cohort approach to root efficiency and root lifespan might be appropriate.

In a cohort model, instead of focusing on the optimal lifespan of an individual, we seek to describe the optimal distribution of lifespans in a population. Consider exponential decay, in which each individual has an equal chance of dying at every point in time. For the population of roots undergoing decay, we can ask what decay rate k , or what root half-life, provides the maximum efficiency of resource acquisition to the plant. An advantage of the cohort model is that it has a strong evolutionary basis: natural selection for increased plant fitness operates at the level of the whole root system, not the individual root. The choice of exponential decay is convenient for illustration and is generally supported by observations (Wells, Glenn & Eissenstat 2002b); a more complex hazard function could include factors important in controlling root death, such as climate, phenology and herbivore pressure.

To illustrate the efficiency model applied to a cohort of roots, we used equations for P uptake by citrus and respiration by apple (Bouma *et al.* 2001), which have the convenient property of exhibiting an optimal lifespan even when soil depletion is not simulated (Fig. 2). In this illustration, the optimal lifespan for an individual root to maximize E is 86 days. The optimal half-life of the cohort, assuming exponential decay, is shorter (about 60 days) because of the death of young, highly absorptive roots.

The cohort model has an advantage over the single-root model in that the former describes a distribution of root ages, corresponding to observed patterns of root lifespan. It also provides the basis for a theory of plant control over root lifespan under pathogen and

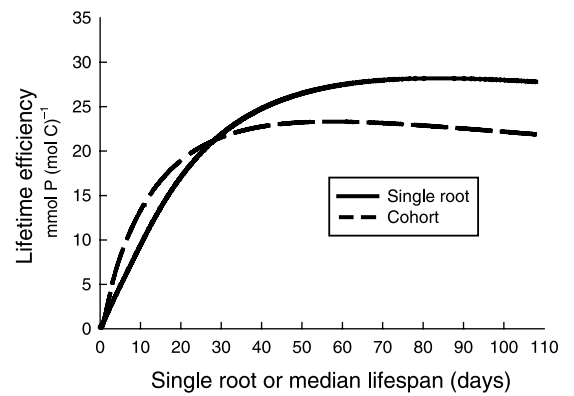


Fig. 2. The lifetime efficiency of a single root as a function of age and the efficiency of cohort of roots as a function of the median lifespan, or $\ln(0.5)/k$, assuming that the distribution of lifespans in the cohort follows first-order kinetics, where the death rate is k times the pool of living roots. This illustration is based on Uptake [$\text{mmol P (g root)}^{-1} \text{ day}^{-1}$] = $4400 \times \text{age}/(\text{age}^2 + 7 \times \text{age} + 83)$ and Respiration [$\text{mol C (g root)}^{-1} \text{ day}^{-1}$] = $14.3 + 12.6 \times \text{age}^4/(\text{age}^4 + 2600)$, where age is in days (Bouma *et al.* 2001).

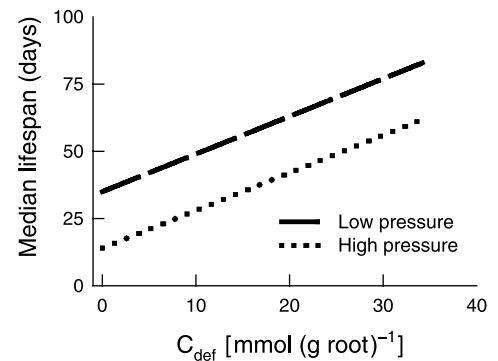


Fig. 3. The assumed relationship between C expended for defence of roots and the resulting half-life of the cohort of roots, for scenarios of higher (High) and lower (Low) pressure from herbivores and pathogens.

herbivore pressure. The risk of root death, or k in the exponential model, can be treated as a combination of external pressures, such as pathogens and herbivores, and root defence, which has its costs and benefits to the plant. Although the benefits of a C investment in root defences have yet to be quantified, it is clear that substantial increases in root longevity can be achieved by allocation to defence (Kosola, Eissenstat & Graham 1995; Weste 1986).

In the absence of data, we chose a linear relationship between the cost of defence, C_{def} , and the median lifespan of the cohort (Fig. 3). We assumed shorter lifespans in the case of higher pressures, for the same investment in C_{def} . Given these assumed costs and benefits, we can predict the optimal allocation to defence as that which maximizes cohort efficiency (Fig. 4). Clearly, the allocation to defence that optimizes cohort efficiency is greater under higher herbivore and pathogen pressure. The cohort efficiency is always higher

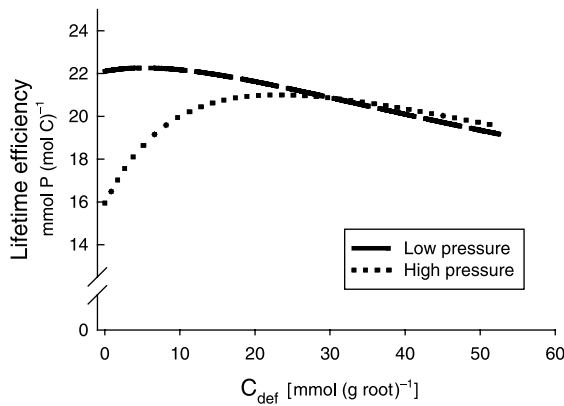


Fig. 4. The efficiency of a cohort of roots as a function of C expended for defence (C_{def}). The efficiency of the cohort is based on respiration and uptake rates of individual roots (Fig. 2) and exponential decay at rates determined by the defensive C investment (Fig. 3).

under low pressure, unless the plant allocates unreasonable (supraoptimal) C to defence. The efficiency of the cohort at the optimal C_{def} (Fig. 4) is less than in the case without herbivory (Fig. 2), as is the optimal median lifespan at this C_{def} (Fig. 3). These predictions are strictly qualitative, as the parameter values are not based on any observations. The assumed relationships seem entirely reasonable, but they should be determined experimentally.

It is not difficult to find evidence for the importance of root herbivory and parasitism (Kosola *et al.* 1995; Maron 1998; Wells *et al.* 2002a), which suggests that root death is not completely under the control of the plant (Fisher, Eissenstat & Lynch 2002). Root mortality may be indirectly controlled by the production of root defences such as condensed tannins associated with root browning (Wells & Eissenstat 2001; Wells *et al.* 2002a); phytoecdysteroids (plant-produced insect moulting hormones; Schmelz *et al.* 1998); and furanocoumarins (Zangerl & Berenbaum 1998). The cost of these defences, however, is not easily estimated.

Costs of chemical defence have been studied in leaves (Lerdau & Gershenson 1997). As in roots, there is a trade-off between allocating C to produce resource-gathering tissues and defending those tissues (e.g. Bryant *et al.* 1983; Coley *et al.* 1985). Even in leaves, however, it is not easy to assess the costs of construction, storage, transport, and maintenance of a defence compound (Lerdau & Gershenson 1997). It may be helpful to distinguish immobile compounds (such as lignin, suberins and condensed tannins, which require only construction) from mobile defences that require more maintenance. It may also be necessary to control for root age and environmental conditions, as defences may be induced over time by herbivore feeding or pathogen infection. Apple roots, for example, turn brown from condensed tannins at different rates depending on abiotic conditions such as soil moisture and temperature, and biotic conditions such as insect feeding (Wells *et al.* 2002a).

We hypothesize that different orders of roots will vary in their patterns of defence, as they do in function and longevity (Wells & Eissenstat 2001). As a root only 1 mm in diameter may have several orders of finer roots depending on it for transport, there is greater value in defending this root than the finer-order roots. Obtaining a sufficient mass of roots (>1 g) to conduct a typical proximate analysis of the various families of chemical compounds will be very challenging for roots of the finest order, particularly if controlled for root age. To explain why some roots should be defended and others abandoned in favour of new root deployment may ultimately require acknowledging the dependency of root orders, as well as using a cohort approach to defining the optimal median lifespan of roots.

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