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Forum

Does photoinhibition avoidance explain divarication in the New Zealand flora?

A recent paper by Howell, Kelly & Turnbull (2002) proposes a new answer to the old question 'why is the divaricate habit so common in the New Zealand flora?' Small-leafed shrubs occur in many regions of the world, but as much as 10% of the New Zealand woody flora has an unusual 'divaricate' growth form, characterised by interlaced wide-angle branches with small widely spaced leaves (Kelly 1994; McQueen 2000). The divaricate habit has long fascinated local ecologists (Cockayne 1912), occurring as it does locally in no fewer than 18 different families (Lloyd 1985). What peculiar feature of New Zealand ecosystems past or present could have conferred a strong selective advantage on this growth form, which is less common elsewhere?

One famous peculiarity of New Zealand's ecological history was the presence of large avian herbivores (mainly Dinornithiform ratites, 'moas' in Maori), which radiated in the absence of mammalian competitors, and became extinct within the last millenium after the arrival of humans and other predators. Building on previous speculation about the possible influence of moas on New Zealand vegetation, Greenwood & Atkinson (1977) argued that the divaricate habit could have evolved as a defence against these herbivores, whose depredations may have posed problems of a rather different nature from those associated with mammalian browsing. The divaricate habit has therefore been termed, perhaps prematurely, a biological effect of moa 'ghosts' (Diamond 1990). A strength of this hypothesis is its congruence with the restriction of the divaricate habit to low-growing shrubs and to the juvenile phase of some taller-growing trees, i.e., to plants growing within reach of large ground-based herbivores. However, large numbers of twigs of divaricate plants have been found in subfossil moa gizzards (Burrows 1980), calling into question the effectiveness of this habit as an antibrowsing defence. It is also probably fair to say that the picturesque nature of the moa hypothesis has always provoked the scepticism of some scientists. The same authors later broadened their hypothesis, suggesting that reduced apparency to visually oriented avian herbivores may also have been an important advantage of the divaricate habit (Atkinson & Greenwood 1989).

Climatic explanations of the divaricate habit were foreshadowed in the early work of Diels (1897) and Cockayne (1912). McGlone & Webb (1981) suggested that the divaricating habit evolved in the Pleistocene as 'an adaptation which enables the plant to resist damage from wind, frost and desiccation, while retaining enough flexibility to exploit a wide range of habitats'. Although experimental work has failed to support some of the mechanisms initially proposed (Kelly & Ogle 1990; Darrow *et al.* 2001), a more recent physiological study (Howell *et al.* 2002) presents experimental evidence for a new climatic explanation: protection from photoinhibition during cold weather. Below I argue that there are at least three difficulties with this new hypothesis and the supporting evidence.

What have Howell *et al.* (2002) shown?

Howell *et al.* (2002) showed that pruning the outer layer of sparsely leafed branches of three divaricate shrub species during winter reduced photosynthetic capacity and photochemical efficiency in the underlying foliage. Affected leaves of two of these species continued to show impaired performance after 3 months, consistent with lasting damage to photosystem II reaction centres, whereas leaves of the third species (*Coprosma propinqua*) recovered fully within this period. Their interpretation is that the primary selective advantage of the divaricate habit is protection of foliage from excessive irradiance during cold conditions, especially on winter mornings.

Adaptation or acclimation?

As Howell *et al.* (2002, p. 237) themselves appear to note in passing, these results leave us in some doubt about cause and effect. It is hard to say to what extent the photoinhibition they observed reflects selective pressures that might have favoured the divaricate habit, and to what extent it resulted from the acclimation of foliage to the semi-shaded environment beneath the outer branches that Howell *et al.* later removed. As both photosynthetic capacity and photodissipative capacity are cued to light environment (Chazdon & Field 1987; Logan *et al.* 1998), sudden increases in ambient irradiance often cause photoinhibition, and sometimes lasting photodamage, in the photosynthetic organs of all manner of non-divaricate plants (Mohammed & Parker 1999; Kitao *et al.* 2000; Hader, Porst & Lebert 2000). The relatively rapid recovery of photosynthetic capacity and photochemical efficiency by *C. propinqua* leaves reminds us that the second of these two possibilities should not be ruled out at this stage. Even the failure of the other two species' leaves to recover within 3 months is not conclusive evidence, as acclimation to a new light environment sometimes is not completely accomplished without the production of new leaves (Mohammed & Parker 1999). Follow-up observations of the plants experimented on by Howell *et al.* could add interesting evidence in this respect.

Plant height

A strength of this new hypothesis is its relevance to the association of many divaricate species with frosty habitats, such as inland basins and valley bottoms, where cold-induced photoinhibition is likely (Ball 1994). However, it is hard to see how this hypothesis can explain the restriction of the divaricate habit largely to plants < 3 m tall. During radiative frosts, ground-level temperatures can drop several degrees below those occurring 10–20 m higher. However, tall plants are likely to be hit by direct sunlight earlier in the morning than short plants, so it is not clear how the risk of photoinhibition will vary with plant height.

Energetics

The low leaf area ratio and heavy self-shading associated with the divaricate habit imply a considerable sacrifice in carbon gain potential, and hence growth rate, under favourable conditions (Greenwood & Atkinson 1977; McGlone & Webb 1981). The adaptive payoffs of divarication must be commensurately important. Plants have developed a variety of morphological traits (e.g. leaf hairs) and biochemical mechanisms (the xanthophyll cycle) that reduce the risk of photoinhibition by regulating the light energy absorbed by leaves, without drastically modifying architecture or sacrificing carbon gain potential (Bisba *et al.* 1997; Adams *et al.* 1992; Björkman & Demmig-Adams 1994). These other mechanisms seem likely to be energetically less expensive than protecting foliage with woody screens, as well as involving lower opportunity costs. Although it is naïve to imagine that evolutionary patterns represent optimal solutions to ecological problems (Gould & Lewontin 1979), we are still left wondering why a problem that is commonly ameliorated in a variety of other ways would have given rise to such a drastic means of photoprotection in so many lineages in the New Zealand flora. While it may eventually be demonstrated that photoprotection is one of the benefits of the divaricate habit, it would be surprising if it were the primary one.

Where to from here?

Many New Zealand divaricates have closely related non-divaricate congeners. Comparative observational studies on sympatric populations of such species pairs, or common garden experiments, have great potential for evaluating the possible climate-related advantages of the divaricate habit, such as that proposed in the photoinhibition hypothesis. However, at present the empirical evidence for this hypothesis is equivocal, and there are also difficulties with the hypothesis itself which must be overcome if photoinhibition avoidance is to deserve currency as the primary selective advantage of the divaricate habit. Howell *et al.* (2002) hint at 'exorcising' moa ghosts, but it must be remembered that exorcism requires a very strong case.

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C. H. LUSK
Departamento de Botánica,
Universidad de Concepción,
Castilla 160-C,
Concepción, Chile

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Photoinhibition, acclimation and New Zealand's divaricate plants: a reply to Lusk

Christopher Lusk raises some interesting points in his Forum article (Lusk 2003). We agree wholeheartedly with him on his most important point: that a resolution of the debate surrounding the convergent evolution of New Zealand's divaricate plants is still some way off, and will require a great deal more active experimental research than currently exists in the literature. Our view is that the debate surrounding explanations of this unusual growth form has been rather heavy on conjecture, but light on experimental tests. The purpose of our paper (Howell, Kelly & Turnbull 2002) was to present initial findings from field experimentation that introduces a potentially new factor (photoinhibition of photosynthesis) into the debate. Although our title was a provocative reference to previous claims on the impacts of moa 'ghosts' (Diamond 1990), we did not wish to imply that our results provided the whole story.

ADAPTATION OR ACCLIMATION?

Lusk's most serious criticism of our findings is that we cannot rule out that the observed photoinhibition is simply a response to the increase in irradiance imposed in the experiment. This is an issue we considered in some detail in our paper. However, we believe that the conditions experienced by our study species are quantitatively quite different from experiments in many previous studies, including those cited by Lusk, where deep-shade leaves of (largely) forest plants are moved to supersaturating irradiances. The experimental leaves in our two most sensitive species initially received ~40% of full sunlight prior to experimental manipulation, which subsequently increased irradiance to full sunlight for a period during the morning. Our experimental manipulation imposed a smaller increase in irradiance, from a higher initial irradiance, than in many studies investigating the dynamics of photosynthetic acclimation in shade-adapted plants (Figure 1). Numerous studies show that photosynthetic acclimation can often compensate for larger increases in PFD in more shade-adapted leaves than our study species (Lovelock, Jebb & Osmond 1994; Mulkey & Pearcy 1992; Newell *et al*. 1993; Ogren & Rosenqvist 1992; Roden, Wiggins & Ball 1997; Thiele, Krause & Winter 1998; Turnbull *et al*. 1993). Finally, although acclimation potential is affected by past light history, even the example cited by Lusk (Mohammed & Parker 1999) showed more complete recovery than two of our three species. His example is a highly shade-tolerant species (*Tsuga canadensis*) transferred from 20% to full sunlight. Even under these circumstances, Mohammed & Parker (1999) found that maximum photochemical efficiency (F_v/F_m) dropped initially but showed substantial capacity for recovery, and was not significantly different from shaded leaves after 26 days. In contrast, leaves in our species were moved from ~40% to full sunlight, and two of the three species still had significantly lower F_v/F_m some 70 days later. In this case, photoinhibition was more severe and longer lasting after a smaller increase in irradiance than in many previous studies. This indicates that photoinhibition may be a particular problem for these species, which is ameliorated by the divaricate habit.

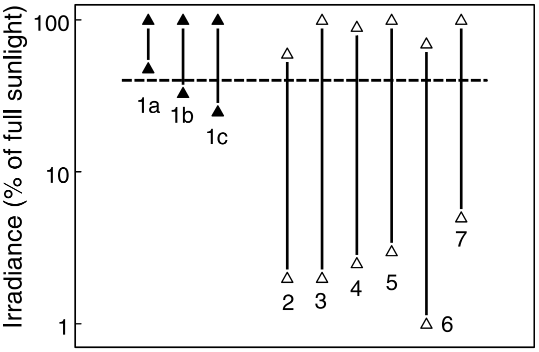

Fig. 1. Relative changes in irradiance (as a percentage of full sunlight) experienced by leaves in a range of experiments undertaken to investigate the dynamics of photosynthetic acclimation of pre-existing leaves to increases in light. 1, Howell *et al.* (2002): (a) *Aristotelia fruticosa*; (b) *Corokia cotoneaster*; (c) *Coprosma propinqua*; 2, Sims & Pearcy (1989); 3, Mulkey & Pearcy (1992); 4, Oquist, Chow & Anderson (1992); 5, Newell *et al.* (1993); 6, Turnbull, Doley & Yates (1993); 7, Kitao *et al.* (2000). Dashed line drawn at 40% full sunlight to indicate approximate irradiance required to saturate photosynthesis.

PLANT HEIGHT

Lusk says 'it is hard to see how this hypothesis [cold-induced photoinhibition] can explain the restriction of the divaricate habit largely to plants <3 m tall'. This is a difficult question to address directly, but the divaricate habit is most strongly developed in open shrublands and hollows, where the plants are prone to exposure to low temperatures as a result of cold air drainage (McGlone & Webb 1981; Wilson & Galloway 1993). There are two important mechanisms whereby shrubs (and tree juveniles) are exposed to greater risks of cold-induced photoinhibition than trees. First, as Lusk notes, during frosts temperatures are significantly lower at ground level than higher up (Leuning & Cremer 1988). This effect contributes to significant differences between grass minimum temperatures and those measured at meteorological screen height (1·4 m), which is much less than the 10–20 m quoted by Lusk (Larcher 1995). Changes in the impacts of frost can be measured over a range of scales, from centimetres (Ball, Hodges & Laughlin 1991; Leuning & Cremer 1988) to metres (Nunez & Bowman 1986) to kilometres (Kelly 1987). Second, continuous stands of forest gain some mutual protection from frosts when compared to exposed plants such as isolated shrubs (Kelly 1987; Nunez & Bowman 1986). For example, *Beilshmiedia tawa*, a common forest dominant in the North Island of New Zealand, was damaged by severe frosts in July 1982. Damage was widespread on forest edges and up to 1 km into the forest where cold air drained down-valley, whereas *B. tawa* trees further into the forest were largely unaffected (Kelly 1987). A significantly higher percentage of trees within 1 km of the edge showed damage (78·0%) than for trees in the forest interior (28·3%, $F_{1,32} = 24{\cdot}5$, $P < 0{\cdot}001$, one-way ANOVA). These factors suggest that that shrubs and tree juveniles growing in open frosty habitats could gain far more from ameliorating photoinhibition than adult trees growing in continuous forest, consistent with the current distribution of the divaricate habit.

ENERGETICS

Lusk states that because divaricate plants have low leaf area ratios and high levels of self-shading, they must be at a considerable disadvantage in growth rates compared to non-divaricate plants. Neither of these assertions is yet supported by the literature. There are no published data concerning biomass allocation in divaricates; however, our current measurements (R.C., D.K. and M.H.T., unpublished results) do indicate that divaricate plants have lower leaf-area ratios than their non-divaricate congenors. The key point of the only published study relating to self-shading (Howell *et al*. 2002) is that this shading is not necessarily a cost, but may even be a benefit. The level of self-shading is relatively low – the majority of leaves at 20–30 cm into the canopy of our three species of shrub receive 20–40% of full sunlight, which is approaching values that could saturate photosynthesis in many species, including our study species. This degree of self-shading does not necessarily imply a sacrifice in terms of carbon gain; this would be true only if >40% sunlight was required to saturate photosynthesis. Our results indicate that, in the study species at least, a degree of self-shading actually maintains photosynthetic capacity at high levels. This implies that divaricate plants may bear no, or little, cost related to self-shading.

THE WAY FORWARD

Interestingly, our view of the way forward coincides closely with that of Lusk, and we are currently conducting common-garden and field studies as he suggests. These are in the form of comparative experimental studies involving divaricate species and their non-divaricate congeners. We are investigating the impact of light environment on plant architecture and growth, in addition to physiological responses to combinations of environmental stresses (cold temperatures or water stress in association with high irradiance). We would like to think that Lusk's call-to-arms places a strong onus on proponents of alternative hypotheses to also develop appropriate tests. We are pleased that tests of the moa-browsing hypothesis are also being made (W. Lee and W. Bond, personal communication). Such tests will require some careful thought, as moa are now extinct.

One difficulty with any evolutionary ecology is that features that arise initially in response to one selective force may later provide advantages largely through pressure from a different selective force, and at any time features may provide benefits simultaneously in several different ways. Debates about why a particular feature arose initially are often fruitless, as the relevant data from the evolutionary past are unobtainable. The only objective way forward in studying the divaricate habit is to quantify the current empirical benefits of this growth form for photosynthesis and/or for reducing ratite browsing. If either one of these hypotheses can provide a large enough selective advantage, the most parsimonious explanation is that one hypothesis can account for the frequency of divaricate plants. Meantime, speculation about what is the 'primary' selective benefit of divarication is premature.

We acknowledge that our work on photoinhibition in divaricate plants leaves many questions unanswered, and is far from a final answer on this topic. However, it is worth pointing out that the data in Howell *et al*. (2002) are the first direct, quantitative tests of divaricate plants that show any significant benefit from the habit. Previous empirical studies on climate (Darrow *et al*. 2001; Kelly & Ogle 1990) and on moa gizzards (Burrows 1989) have failed to show clear support for either the climate hypothesis or the moa hypothesis. To that extent, our work on responses to environmental factors is perhaps the first concrete step in banishing the ghosts of moas, although we fully agree that the house cannot be declared completely free of ghosts just yet.

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M. H. TURNBULL, C. J. HOWELL*,
R. CHRISTIAN and D. KELLY
Department of Plant and Microbial Sciences,
University of Canterbury, Private Bag 4800,
Christchurch, New Zealand
**Additional address: New Zealand Department of*
Conservation, Wellington, New Zealand

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What is functional androdioecy?

Androdioecy denotes the co-occurrence of males and hermaphrodites in a sexually reproducing population. As Darwin (1877) first noted, the breeding system is exceedingly rare, and theoretical studies have shown why this is so (Charlesworth 1984; Charlesworth & Charlesworth 1978; Lloyd 1975). In particular, males can invade a hermaphroditic population only under the restrictive condition that they sire more than twice as many successful offspring as do the hermaphrodites. Moreover, unlike gynodioecy, androdioecy cannot evolve from hermaphroditism as a result of selection for inbreeding avoidance, because selfing immediately makes ovules unavailable for males to fertilize.

Seemingly in agreement with theory, Charlesworth (1984) found that there was no convincing example of the breeding system in nature. Instead, she concluded that populations with morphological male and hermaphrodite individuals, which have often been called androdioecious, were cryptically dioecious, with a 1 : 1 sex ratio and hermaphrodites that function only as females (see also Mayer & Charlesworth 1991). Although functional androdioecy has been confirmed for several species of plants and animals in the past couple of decades (reviewed in Pannell 2002), the breeding system must still be regarded as very rare.

Given this rarity, and because cryptically dioecious species have so often been misconstrued as androdioecious, functional interpretations of putatively androdioecious populations have been understandably cautious. One issue that has been raised concerns the extent to which sex or gender (see below) in androdioecious populations ought to have a genetic basis. Functional males and hermaphrodites co-occur, for example, in populations of the herb *Mercurialis annua* (Durand & Durand 1992; Pannell 1997b). However, because sex in *M. annua* is determined by genetic and environmental factors (Pannell 1997a), several authors have suggested that this species should strictly not be regarded as functionally androdioecious (e.g. Dommée *et al*. 1999; Ishida & Hiura 1998; Webb 1999; Wolf, Rieseberg & Spencer 1997).

The issue is important as it brings into focus the relative weight given to functional (ultimate) *vs* mechanistic (proximal) causes in naming and understanding reproductive strategies. A strong case can be made for favouring the former of these two alternatives. Indeed, sex allocation theory is founded on interpretations of gender that are based on prospective and realized reproductive success through male and female functions, irrespective of how allocation patterns are determined mechanistically (Charnov 1982). A definition of functional androdioecy based on mechanistic rather than purely functional considerations is therefore retrogressive.

This note aims to clarify a functional basis for the definition of androdioecy, with particular reference to the questionable relevance of the sex determination mechanism. A key point is that populations should be regarded as functionally androdioecious only if they comprise two classes of individual: one in which all fitness is gained through male function, the other in which fitness is gained substantially through both male and female functions. How these two strategies are determined mechanistically is of secondary importance. Consistent with the notion of a stable polymorphism, individuals in the male class of an androdioecious population should not differ in average fitness from those in the hermaphroditic class when the population is at equilibrium. I first illustrate the significance of these points by highlighting the apparent similarity, but functional difference, between androdioecy and a particular type of size-dependent sex allocation, where individuals are male when small and hermaphrodite as they grow. I then argue against a definition of androdioecy that gives primacy to the mode of sex determination. While I restrict this note to a discussion of androdioecy, it illustrates the general importance of functional, as opposed to mechanistic, interpretations of gender.

GENDER DIPHASY AND RESOURCE-DEPENDENT SEX ALLOCATION

Small individuals are often found to emphasize their male function, with larger plants being more female (Lloyd & Bawa 1984). Where this size-dependent sex allocation is extreme, gender may fall into two distinct categories, with small plants being fully male and larger plants expressing male and female function. Such cases of gender diphasy, exemplified by *Arisaema dracontium* (Clay 1993), may easily be confused with androdioecy. However, they do not represent a dimorphic strategy, and each individual is expected to make an equal genetic contribution over its lifetime through each of the two sexual functions.

A related issue concerns the importance of distinguishing between gender switching, or 'gender diphasy' (Lloyd & Bawa 1984; Schlessman & Lovett Doust 1988), and functional androdioecy. Presumably because of the heavy reproductive burden of fruit production, hermaphrodites that fruit one year may be incapable of producing fruits the next, and may thus function solely as males for a season. Such populations, surveyed only once, may appear to be androdioecious. The herbaceous alpine perennial *Lloydia serotina*, for instance, was first suspected as being androdioecious (Jones & Gliddon 1999), but subsequent study has shown that individuals possess only a single strategy, with switches in gender from year to year (Manicacci & Despres 2001).

RELEVANCE OF THE MODE OF SEX DETERMINATION

A concern over gender switching may have fuelled the idea that sex or gender in functionally androdioecious populations should be determined genetically. Certainly, populations in which males and functional hermaphrodites differ at one or more sex-determining loci are likely to be good examples of functional androdioecy, particularly as sexual diphasy and gender switching are at once ruled out as an explanation of observed phenotypic variation in any one reproductive season. However, the requirement for androdioecious populations specifically to be genotypically dimorphic is unhelpful because it does not emerge clearly from sex-allocation theory.

The theory of sex allocation attempts to explain the phenotypic mix of allocation strategies found in populations in terms of evolutionarily stable strategies (ESS) (Charnov 1982). This includes the ESS sex ratio in dioecious species (Fisher 1930; Hamilton 1967), the ESS allocation of limited resources to male and female functions in hermaphrodites (Charnov, Maynard Smith & Bull 1976), and the optimum sequence and timing of sex reversals in sequential hermaphrodites in terms of the age and size of individuals (Charnov 1982). Whether sex is environmentally or genetically determined is subsumed under the more general question of whether it is evolutionarily optimal for sex to be determined at the time of conception and zygote formation, or at some later time in development (Charnov & Bull 1977). The timing of allocation decisions in androdioecious populations, and thus whether sex is determined genetically or environmentally, raises interesting questions and may be an important component in explaining the evolution or stability of the breeding system in certain cases. However, understanding the mode and timing of sex determination is logically secondary to the primary task of describing a population's breeding system.

Models of androdioecy have typically been coined in terms of contrasting sexual strategies, with little attention paid to how these strategies are determined (Charlesworth 1984; Charlesworth & Charlesworth 1978; Charnov *et al.* 1976; Lloyd 1975; Maurice & Fleming 1995; but see Vassiliadis *et al.* 2000). Nevertheless, they have at times been discussed in the language of genetics. For example, Lloyd (1975) noted that if 'androdioecy [is] controlled by nuclear genes, the effects [of population parameters] on the equilibrium sex ratio do not depend on the precise mode of inheritance.' It is important to note that this does not presume sex must be determined by nuclear genes. Rather, the reference to genetic control simply emphasizes that if the reproductive strategy in a population were transmitted uniparentally rather than biparentally, the model's predictions of the sex ratio would no longer hold.

Lloyd (1975) did not pursue this issue further, noting only that '[a]ndrodioecy, unlike gynodioecy, cannot be maintained by cytoplasmic inheritance.' His statement here assumes that cytoplasmic genes are maternally inherited. The transmission of cytoplasmic genes through pollen is not unknown (Reboud & Zeyl 1994), and in such cases androdioecy might indeed be maintained by cytoplasmic inheritance, at least in principle. Similarly, segregation distorters linked to a nuclear male-determining gene could conceivably maintain androdioecy (Vassiliadis *et al.* 2000), although no such system has yet been described. In both these cases, Lloyd's sex ratio predictions for androdioecious populations would not apply. However, were such an example to be found in nature, androdioecy would be the appropriate term (just as populations with cytoplasmic inheritance of male sterility are gynodioecious).

It is worth commenting briefly on a distinction that has sometimes been made between 'sex' and 'gender'. In arguing for the primacy of a genetic mode of sex determination in defining androdioecy, Wolf *et al.* (1997) have interpreted Lloyd as suggesting that whereas the sex of a plant is genetically determined, gender 'is determined by the other plants in the population or by the environment'. In fact, Lloyd (e.g. page 258 of Lloyd & Bawa 1984) distinguished between these two terms in a rather different sense that makes no reference to the mechanism of sex determination: 'we […] consider not only the "sex" of a plant in the strict sense of the production and disposition of its gametes, but more broadly its "gender", its maleness or femaleness as a parent of adults of the next generation.' This distinction emphasizes that reproductive success gained through male and female functions depends as much on the relative production of seeds *vs* pollen (a plant's sex or 'phenotypic gender' *sensu* Lloyd 1980), as on the fate of those seeds or pollen grains (its 'functional gender' *sensu* Lloyd 1980). Lloyd (1980, page 107) referred to androdioecy in particular as a gender dimorphism in which 'there are two distinguishable *morphological* classes of plants …' (my italics).

FUNCTIONAL DEFINITION OF ANDRODIOECY

In keeping with the conventions of breeding-system terminology, and in accordance with usage adopted in theoretical discussions, a description of functional androdioecy should be based on the following criteria.

Androdioecious populations should display a clear sexual or gender dimorphism in which there are two distinguishable classes of plants: males, which lack female function; and hermaphrodites which, as a class, make a substantial genetic contribution through both sexual functions.

Populations displaying a uniform gradation in sex allocation from pure maleness through to female-biased hermaphroditism should not be described as androdioecious.

Populations in which morphological hermaphrodites fail to sire seeds through their male function should be viewed as cryptically dioecious rather than androdioecious (Mayer & Charlesworth 1991). Ideally, paternity analysis could confirm the male function of hermaphrodites (Vassiliadis *et al.* 2002).

Populations in which males co-occur with females or morphological hermaphrodites that disperse some pollen but sire only a limited number of progeny might better be viewed as examples of 'leaky dioecy' or subdioecy (Baker & Cox 1984; Lepart & Dommée 1992).

Bimodality in sex expression is a necessary, but insufficient, condition for the definition of androdioecy. This is because functional gender, as defined by Lloyd (1980), characterizes individuals in terms of the *proportion* of their genes that they contribute through their female (or male) function, without reference to their total fitness. This is useful if we wish to determine the extent to which individuals emphasize one sex function over the other in different contexts, for example as a function of age or size. However, for the maintenance of polymorphic strategies, the absolute genetic contributions made by members of each class are important (Sarkissian, Barrett & Harder 2001). At equilibrium in a polymorphic population, we expect individuals within each phenotypic class, on average, to possess equal fitness. Thus an androdioecious population at equilibrium ought to comprise males and hermaphrodites that make, on average, equal genetic contributions to the next generation. A positive correlation between quantitative gender in a population, expressed as prospective femaleness, and total reproductive success, for example, would therefore be inconsistent with functional androdioecy and may rather reflect size-dependent sex allocation.

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J. R. PANNELL
Department of Plant Sciences,
University of Oxford,
Oxford OX1 3RB, UK

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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.

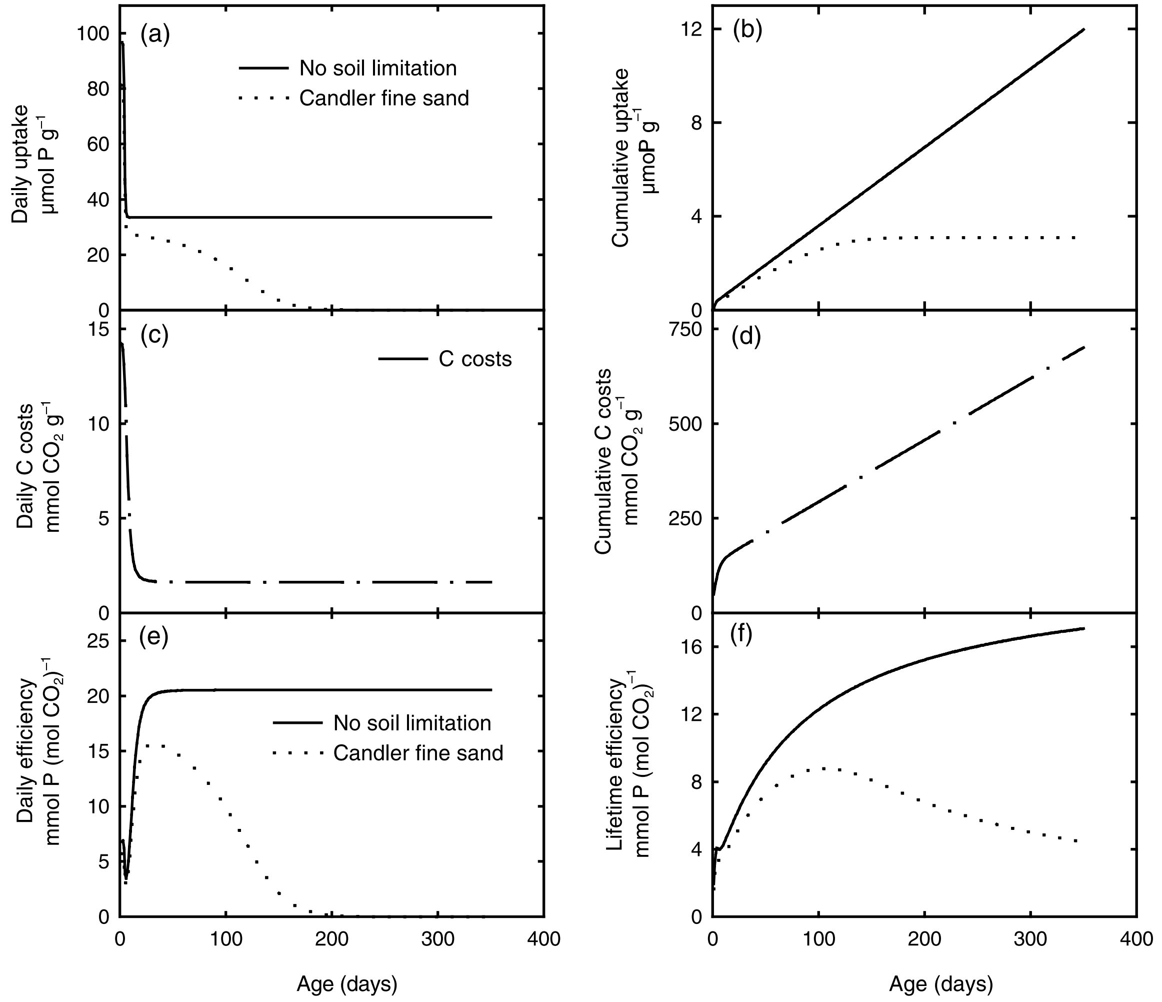

Fig. 1. Daily P uptake (a); lifetime P uptake (b); daily C cost (c); lifetime C cost (d); daily efficiency (e); and lifetime efficiency (f) of citrus roots. Solid line, simulated uptake with no soil depletion; dashed line, uptake with soil P depletion based on soil parameters of Chandler fine sand (see 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 ($4{\cdot}1 \times 10^{-8}$ cm^2 s^{-1} instead of the published value of $4{\cdot}1 \times 10^{-4}$ cm^2 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 & Comerford 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 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

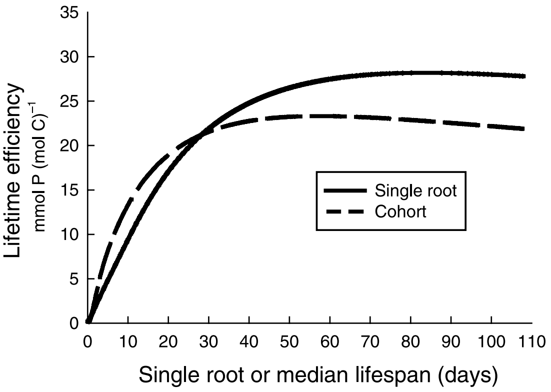

Fig. 2. The lifetime efficiency of a single root as a function of age and the efficiency of cohort of roots as a function of the median lifespan, or $\ln(0.5)/k$, assuming that the distribution of lifespans in the cohort follows first-order kinetics, where the death rate is k times the pool of living roots. This illustration is based on Uptake [mmol P (g root)$^{-1}$ day^{-1}] $= 4400 \times \text{age}/(\text{age}^2 + 7 \times \text{age} + 83)$ and Respiration [mol C (g root)$^{-1}$ day^{-1}] $= 14{\cdot}3 + 12{\cdot}6 \times \text{age}^4/(\text{age}^4 + 2600)$, where age is in days (Bouma *et al.* 2001).

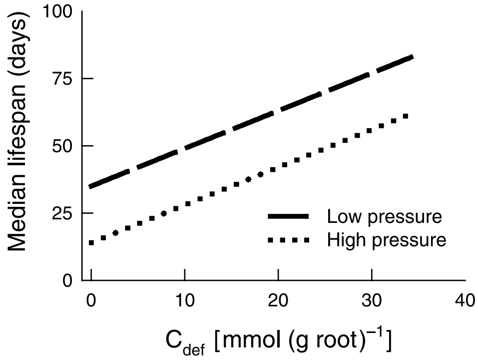

Fig. 3. The assumed relationship between C expended for defence of roots and the resulting half-life of the cohort of roots, for scenarios of higher (High) and lower (Low) pressure from herbivores and pathogens.

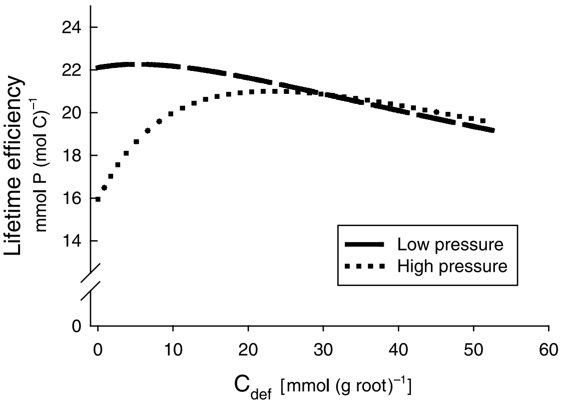

Fig. 4. The efficiency of a cohort of roots as a function of C expended for defence (C_{def}). The efficiency of the cohort is based on respiration and uptake rates of individual roots (Fig. 2) and exponential decay at rates determined by the defensive C investment (Fig. 3).

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 & Gershenzon 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 & Gershenzon 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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R. D. YANAI
College of Environmental Science and Forestry,
State University of New York, 1 Forestry Drive,
Syracuse, NY 13210, USA

D. M. EISSENSTAT
Department of Horticulture, The Pennsylvania State
University, 103 Tyson Building, University Park,
PA 16802-4200, USA

Received 30 November 2001; revised 29 May 2002; accepted 4 June 2002