

Commentary

Arsenic and old plants

Terrestrial life, like its marine progenitors, developed around vents in the earth's surface from which spewed a mineral-rich substrate high in a suite of metals and metalloids. To survive in this environment, organisms either had to maintain cytoplasmic homeostasis so that cellular processes could function or have biochemistry that functioned in the presence of what we consider toxicants. Typically, terrestrial and ocean vents release arsenic at much higher concentrations than found on average in the earth's crust, with life evolving in an arsenic rich environment. The most comprehensive picture of the early evolution of land plants comes from the Rhynie Cherts (*c.* 400 million yr old), NE Scotland, which was a subaerial hot-spring environment rich in arsenic (Rice *et al.*, 1995). Could the elevated arsenic in the environment in which fern progenitors evolved be a selection pressure leading to the remarkable phenomenon of arsenic hyperaccumulation in ferns?

Who hyperaccumulates?

Ma *et al.* (2001) first reported arsenic hyperaccumulation in ferns in *Pteris vittata*. *Pityrogramma calomelanos* was rapidly added to this list (Visoottiviset *et al.*, 2002), followed by three more species from the *Pteris* genus (*P. cretica*, *P. longifolia* and *P. umbrosa*), reported in this issue by Zhao *et al.* (pp. 27–31). However, not all ferns hyperaccumulate arsenic, as determined by Zhao *et al.* (2002), and others (Kuehnelt *et al.*, 2000; Visoottiviset *et al.*, 2002). With > 10 000 fern species and their allies to screen, it may be predicted that many more hyperaccumulating ferns will be discovered. Though the number of ferns tested for arsenic hyperaccumulation is small, some patterns are emerging. Fern phylogenies, while complex and evolving, place all five hyperaccumulating ferns in the Pteridaceae family (Fig. 1), within the order Pteridales. The Pteridaceae alone contains > 400 species, with *c.* 10% of all ferns being in the Pteridales.

Ferns are among the most primitive plants (Fig. 2) with molecular (*rbcL* sequences) and morphological characteristics placing the Pteridaceae quite late on in fern evolution (Fig. 1). The Pteridaceae are closely related to other families which, as far as we are aware, do not at present exhibit hyperaccumulation (Fig. 1), but with *c.* 1/1000 of all fern species screened, there is some way to go before the uniqueness of the Pteridaceae with respect to arsenic hyperaccumulation can be assumed. Similarly, the hunt for a nonaccumulating *Pteris* species is on.

The most primitive fern screened to date, *Dicranopteris linearis* in the Gleicheniaceae, does not hyperaccumulate arsenic (Visoottiviset *et al.*, 2002). The most primitive land plants are in the Lycopodophytes (Fig. 2). The only member of the Lycopodophytes investigated to date, a *Selaginella* sp., also did not hyperaccumulate arsenic (Visoottiviset *et al.*, 2002). There are a number of studies on the Equisetaceae, which evolved early on from the Lycopodophytes, which show that although a range of species have high arsenic levels (> 100 mg kg⁻¹ As), none hyperaccumulate arsenic (Wong *et al.*, 1999; Kuehnelt *et al.*, 2000; Hozhina *et al.*, 2001). Caution should be maintained in stating that these members of primitive land flora do not hyperaccumulate arsenic, as all the mentioned studies were from field screening, and issues of the arsenic bioavailability and its heterogeneity need to be addressed.

The hyperaccumulating accessions studied by Ma *et al.* (2001) (*P. vittata*) and Visoottiviset *et al.* (2002) (*Pityrogramma calomelanos*) were from contaminated sites. Zhao *et al.* (2002) also showed that *P. vittata* and the other three *Pteris* species from uncontaminated soils also exhibited hyperaccumulation. Hence, hyperaccumulation is not just a character selected in these species on arsenic contaminated soils, it appears to be constitutive. The constitutive nature of arsenic hyperaccumulation is not unique in this respect as the zinc and cadmium hyperaccumulation in *Arabidopsis halleri* and *Thlaspi caerulescens* is constitutive (Baker & Whiting, 2002). What is unique is that the arsenic hyperaccumulating ferns are extremely widespread, unlike *A. halleri* and *T. caerulescens* which have a limited geographical and ecological distribution.

Evolution of arsenic hyperaccumulation

Land plants that evolved in arsenic rich environments would have required mechanisms for coping with this element, with hyperaccumulation being one strategy. An excluder strategy has been well studied in grasses (Meharg & Hartley-Whitaker, 2002). Tolerance mechanisms may have been lost as plants spread out from hot-springs into nonarsenic contaminated environments, with members of the Pteridaceae for some reason retaining these primeval mechanisms, either as evolutionary baggage or because this trait conferred them with some advantage, arsenic related or not. Alternatively, members of the Pteridaceae evolved hyperaccumulation at a later stage in response to a particular selection pressure, or perhaps they were confined to arsenical habitats until late on in their evolutionary development.

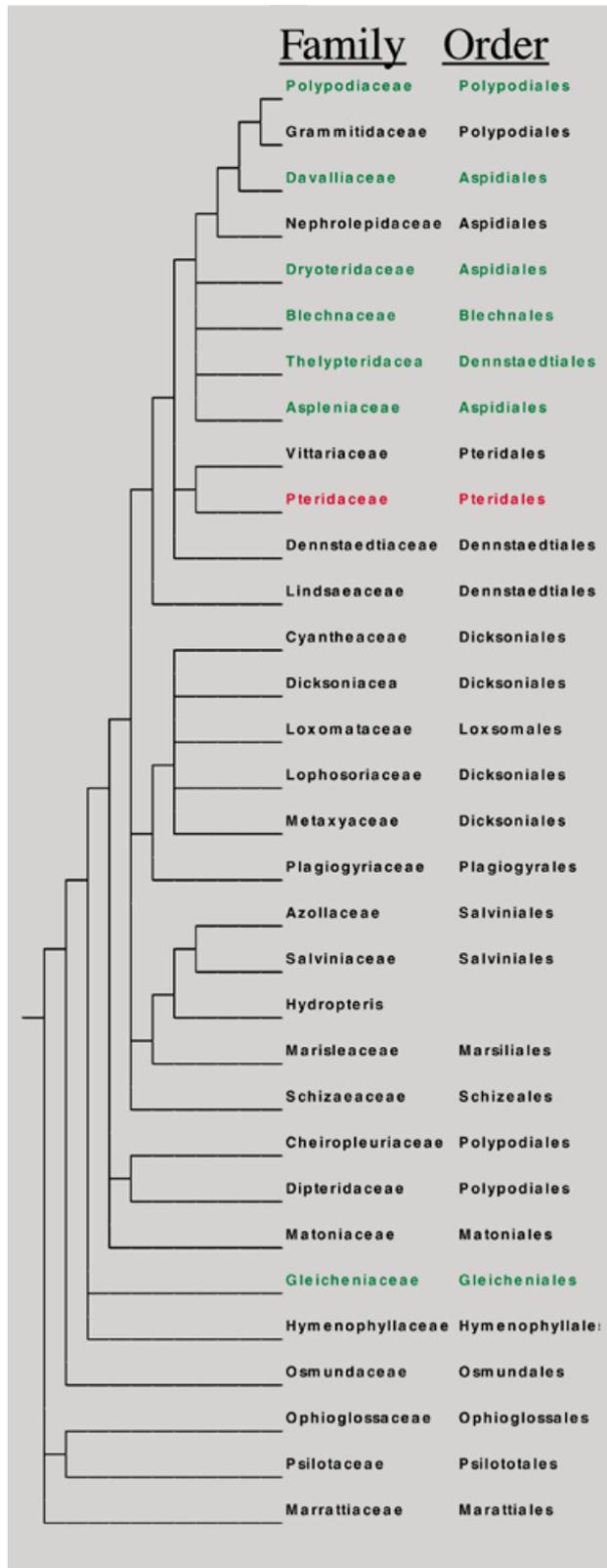


Fig. 1 Evolutionary tree for ferns derived from Pryer *et al.* (1995), with families containing arsenic hyperaccumulating ferns shown in red, and those that have had nonaccumulating ferns identified shown in green. Branch lengths are arbitrary.

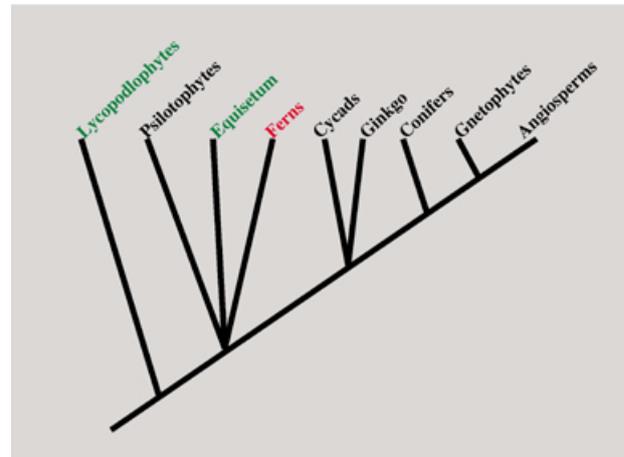


Fig. 2 Evolutionary tree for land flora from Pryer *et al.* (1995), with groups containing arsenic hyperaccumulating species shown in red, and those that have had nonaccumulating species identified shown in green. Branch lengths are arbitrary.

Not all primitive plants may have evolved in arsenic rich environments. We have biased our view of where terrestrial life-forms evolved from the particular conditions that give us the best fossil record of early plant evolution, such as the silica rich extrusions from hot springs which led to the excellent plant preservation in the Rhynie Cherts (Rice *et al.*, 1995).

Perhaps arsenic did not provide the selection pressure that led to arsenic hyperaccumulation. The physiological mechanisms responsible for arsenic hyperaccumulation may have evolved for other reasons, and just happen to confer arsenic hyperaccumulation to the ferns. This is indeed the case for arsenic resistance in angiosperms where resistance is a consequence of having suppressed high-affinity phosphate transport (Meharg *et al.*, 1993; Fitter *et al.*, 1998), as arsenate and phosphate are analogues. Arsenic hyperaccumulation may therefore be a consequence of unusual phosphorus metabolism in ferns, though this seems not to be the case (see below). It is imperative that we understand the physiology of hyperaccumulation to understand the evolutionary basis of this phenomenon.

Mechanisms

Arsenate is the dominant plant available form of arsenic in aerobic environments. Plants will mobilise and take up large quantities of arsenate, if present, in their quest to obtain phosphate. Many ferns grow on peats subject to routine water logging, and the resulting reduced conditions in the production of arsenite from arsenate. It has recently been demonstrated for the first time that arsenite is actively taken up at a high rate by plant roots (rice) (Abedin *et al.*, 2002), probably through aquaporins (Wysocki *et al.*, 2001). Arsenite has a pK_a of 9.2 and is predominantly in an

undissociated form at neutral to acid pHs. In essence, arsenite or arsenate present in the ferns environment would be efficiently accumulated.

Zhao *et al.* (2002) report that there is nothing unusual in the total phosphorus status of arsenic hyperaccumulators. Recent transport studies on *P. vittata* show that there is nothing particularly abnormal about the kinetics of arsenate/phosphate transport, and that arsenite is taken up actively, though at a lower rate than arsenate (Wang *et al.*, 2002). This begs the question: how do arsenic hyperaccumulators mobilise arsenic in such vast quantities from the soil?

The physiological mysteries deepen once inside the plant. Consistently it has been shown that hyperaccumulators store up to 1% arsenic in their shoots, primarily as free arsenite (Ma *et al.*, 2001; Francesconi *et al.*, 2002; Wang *et al.*, 2002). The presence of arsenite is not a surprise in itself as many plants rapidly reduce arsenate to arsenite (Meharg & Hartley-Whitaker, 2002), but the normal model for plant detoxification of arsenic is complexation of As(III) with phytochelatins (PCs) (Meharg & Hartley-Whitaker, 2002). The arsenite (As III) must be compartmentalised in the vacuole, unless the ferns have extraordinary protein biochemistry as As (III) has a high, and therefore disruptive, affinity for –SH groups. The arsenic could be shuttled through the cytoplasm, and indeed translocated from shoot to roots, via As-PC complexes, until deposited in the vacuole. Tonoplast function could be key to solving the mystery of hyperaccumulation. Alternatively, efficient detoxification (through complexation) and translocation to shoot vacuoles is the basis of this phenomenon. It could be that more than one adaptation is required.

In any case, arsenic acting as a phosphorus analogue does not appear to be at the basis of the tolerance these ferns have to arsenic, or their ability to hyperaccumulate arsenic. Potential candidates for arsenite analogues are notable by their absence. It appears that arsenic is the selection pressure that led to arsenic hyperaccumulation. This raises more problems in trying to work out the logic of arsenic hyperaccumulation, given that the phenomenon is found in species not endemic to arsenic contaminated sites.

The ecological advantages conferred by hyperaccumulation, of any metal that exhibits this phenomenon, is still a mystery (Baker & Whiting, 2002). There are no studies published to date examining if these ferns hyperaccumulate arsenic in soils with low arsenic.

Concluding remarks

These are exciting times for those interested in metal(loid) tolerances in plants. It is not every day that a phenomenon such as arsenic hyperaccumulation is revealed. Many questions are raised by arsenic hyperaccumulation of ferns. The growing list of hyperaccumulators may help us to piece

together the evolutionary origin of this phenomenon. Phylogenetic trees point clearly to where we should look for more hyperaccumulating ferns.

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Key words: fern, hyperaccumulation, arsenic, metal-tolerance, evolution.

Categories and CAM – blurring divisions, increasing understanding?

Science needs categories. The bewildering variation in nature's forms and processes would be impossible for the human mind to grasp without division into groups. There are natural subdivisions, as in the concept of a biological 'species' – taxonomy aims at the identification and labelling of discontinuous forms of organisms. Many other divisions, however, define entities along an axis of more or less continuous variation – take functional groups ('pioneer' vs 'late successional' species), phenological plasticity ('shade' vs 'sun' leaves in a tree), morphological features (e.g. leaf size classes) or phytosociological entities for example. Although typological approaches are certainly important in order to work with biological diversity, they may also cause problems for scientific progress when gaining a life of their own. Once we forget about the continuous nature of variation in these cases and think of artificial borders between groups as real, we might miss very important features of nature or ask the wrong questions.

'Could C₃ and CAM be understood as a continuum instead of two distinct groups?'

In this issue, Pierce *et al.* (2002) (pp. 75–83) report on investigations of CAM in bromeliads. In order to study CAM, the dangers of categorization must be borne in mind. Comparison with other epiphytes and mistletoes, illustrate the dangers of artificial borders only too well. It is often emphasised that mistletoes are parasites while true epiphytes are not (Benzing, 1990). Technically, this is correct. Epiphytes are metabolically separated from their host trees, hence they cannot be parasites by definition (but see Ruinen, 1953). In terms of an adequate understanding of a 'tree's perspective' on canopy dwelling plants, however, such a distinction may not be helpful. Arguably (parasitic) mistletoes may have no noticeable negative impact at all on a rain forest tree, while (nonparasitic) water-filled tank bromeliads may cause substantial structural costs or, conversely, increased rates of branch breakage. Hence the 'nonparasitic' commensal may be more detrimental than the 'parasite'.

Although Darwin, almost 150 years ago, introduced variation as a central theme to biology and not as an aberrant deviation from a true type, there is still a lot of emphasis on classes and categories. Bennett (1987) pointed out that researchers perceive variation frequently as a nuisance – this is not only true for continuous variation, but also for variation around an average, which led Bennett to coin the term 'tyranny of the golden mean'.

A brief history of CAM

Nocturnal uptake of CO₂ in succulent plants has been known for almost 200 yr, but it took more than a century for the mechanistic connections between the basic features of CAM (inverse stomatal opening, nocturnal acidification, reciprocal oscillation in carbohydrates) to be understood (Winter & Smith, 1996). Following the subsequent discovery of C₄ plants in the 1960s, the plant kingdom seemed neatly divided into three groups, with plants showing either C₃, C₄, or CAM as their photosynthetic pathway. Recent work has revealed, however, that CAM is much more diverse than formerly thought: there are species with almost no CO₂ uptake in the light, while at the other extreme plants may show C₃-like gas exchange patterns in the light and (some) re-fixation of respiratory CO₂ at night (Cushman, 2001; Dodd *et al.*, 2002). Thus, could C₃ and CAM be understood as a continuum instead of two distinct groups? While the anatomies of C₄ and CAM plants may indeed be rather incompatible (Sage, 2002), the very nature of CAM (CO₂ uptake during night and day in varying proportions) allows plants to be ranked along an axis from exclusively diurnal (C₃) to exclusively nocturnal CO₂ uptake ('extreme' CAM). Even a single leaf may shift between these extremes depending on ontogenetic state or environmental conditions, which may be particularly pronounced in the genus *Clusia* (Lüttge, 1996).

The shades of CAM

A common method to screen a larger sample of plants for the occurrence of CAM takes advantage of the stronger discrimination of Rubisco against the heavy isotope ^{13}C compared with the other carboxylating enzyme, phosphoenolpyruvate carboxylase (Griffiths, 1993). This method has obvious shortcomings: because $\delta^{13}\text{C}$ signatures are not only influenced by the carboxylating enzyme, species merely recycling respiratory CO_2 or showing little nocturnal CO_2 uptake will have C_3 -like $\delta^{13}\text{C}$ signatures and cannot be distinguished from proper C_3 plants (Zotz & Ziegler, 1997). The elegant study of Pierce *et al.* who used gas exchange, stable isotopes ratios and nocturnal acidification as indicators of CAM in 50 bromeliad species, now allows us a first estimate of the number of 'hidden' species: 13% of those species that would be assigned to the C_3 pathway in a traditional screening study show some degree of nocturnal acidification, even under well-watered conditions. Furthermore, they show that among acid-accumulating bromeliad species there is a tight correlation between $\delta^{13}\text{C}$ ratios and the degree of nocturnal carboxylation.

Implications

What are the implications of this study? First, a scaling exercise to the entire Bromeliaceae and other families with CAM members (Smith & Winter, 1996) would probably add hundreds or even thousands of species to the list of CAM plants, a group already assumed to comprise some 16 000 species or 6% of all vascular plants (Winter & Smith, 1996). Some may consider this an inflation of the term CAM plant, and clearly we cannot avoid the question 'what makes a plant a CAM plant?' More interesting than terminology, however, is the underlying biology. As long as we took the bimodal distribution of $\delta^{13}\text{C}$ ratios as a reflection of the existence of two clearly defined groups, a paucity of species with $\delta^{13}\text{C}$ ratios of around -20‰ came as no surprise. When, however, species on both sides of the gap are capable of nocturnal carbon gain, the finding becomes enigmatic. Pierce *et al.* tell us that this gap in $\delta^{13}\text{C}$ ratios represents a contribution of C_4 carboxylation to diel carbon gain of 30–50%. Why should plants be incapable of regulating CAM activity at such a level? And, can we really conclude from a small, yet measurable contribution of nocturnal CO_2 fixation to the overall carbon budget that there is adaptive significance (Gould & Lewontin, 1979)? If we want to understand the possible significance of the shades of CAM, we have to put physiology in an ecological context, we must study these interesting plants directly in the field, and also under realistic circumstances in the laboratory (which in turn is only possible when analysing field conditions). But even then, due to our lack of background information on their biology, similar results

are frequently interpreted in different ways. For example, in a field study with the epiphytic orchid, *Dimerandra emarginata*, Zotz & Tyree (1996) found a slight increase in nocturnal acidification in drought-stressed leaves, but – by contrast to Pierce and coworkers – dismissed its overall significance because of the small amount of carbon fixed at night. Such conflicting conclusions call for a better basis for such judgements. Without such common ground we will certainly not progress in our understanding of the relevance of these shades of CAM. Ideally, we should measure the actual currency in evolutionary terms, that is, fitness, although this is difficult in long-lived organisms such as most CAM plants. In short-lived *Mesembryanthemum crystallinum* the induction of CAM led to increased fruit production (Winter & Ziegler, 1992). What alternatives do we have? Most of the bromeliads that are now identified as species with a certain potential for nocturnal CO_2 fixation (e.g. *Werauhia sanguinolenta* or *Tillandsia cretacea*) are epiphytes. How often are they drought-stressed in their native habitat, and what is the overall contribution of nocturnal acidification to the long-term carbon budget? Unfortunately, even with such information at hand we would still face the problem that physiological performance at the organ level is not necessarily a good predictor for growth and survival of entire plants (Körner, 1991). Hence, we may better analyse the vegetative performance of organisms and then ask questions, such as, do species like *Werauhia sanguinolenta* do better than co-occurring C_3 bromeliads with similar morphology? This is tedious field work, but probably the best way to reach our goal.

Conclusions

There is a continuum between C_3 and CAM plants, and irrespective of terminological questions we face the task of understanding the ecological importance of this plasticity both within and among species. The study by Pierce *et al.* suggests that many more species than previously assumed show some low degree of C_4 carboxylation. The ecological significance of these shades of CAM is a particularly interesting topic for future study.

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Key words: CAM, epiphyte, bromeliad, photosynthesis, carbon fixation.

Books

Competitors, ruderals and stress-tolerators

Plant strategies, vegetation processes, and ecosystem properties

By J. P. Grime. 417 + xxxvii pages. Chichester, Sussex, UK: John Wiley & Sons Ltd, 2001. £80.00 h/b ISBN 0471 49601 4

Grime's book 'Plant strategies and vegetation processes' (Grime, 1979) has started a second life under the title 'Plant strategies, vegetation processes, and ecosystem properties'. The author deliberately retained 'with slight expansion, the original title and resisted the temptation to replace "strategies" with the now fashionable "functional types"'. Plant strategies are the core concept and are consistently dealt with throughout the book. Some sections of the book have hardly changed but the chapters on 'Primary strategies in

the established phase' and 'Succession' have been expanded. Also, a new chapter on 'Trophic structure, productivity, and stability' has been included.

High and low intensities of stress and disturbance are key factors in classifying plant species as competitors, ruderals and stress-tolerators. However, where this classification is elucidated, and unlike the first table in the 1979 edition, no intensity of stress is shown. Stress is replaced by productivity, because stress tolerance is mainly associated with mineral nutrition stress. By indicating that the 2001 table is reproduced from Grime (1974), it seems that earlier ideas return in this latest edition. However, the 1974 paper in *Nature* does not include such a table at all, so it is not clear whether the author changed his mind. Apparently other potential stress factors, such as minimal light stress are considered less important. It is a pity that recent experiments on competition for light (Huisman & Weissing, 1994, 2000) are not taken into account. Huisman's experiments were carried out with plankton species where it is still questionable how they can be translated into terrestrial systems, although recently Huisman tried to do so (Huisman *et al.*, 1999).

Competition for resources other than nutrients introduces Grime's debate with Tilman. Grime mentions the extensive literature that falsifies the notion of tradeoff between competitive ability for above- and below-ground resources. This brings the long argument involving Tilman and Grime, and many others, within sight of a final resolution. 'Our task is designing experiments to determine whether changes in species composition coinciding with the transition from fertile to infertile soils arise from a switch in the mechanisms of competition (Tilman) or are due to the declining importance of competition and to an increased impact of other selection mechanisms such as drought or herbivory (Grime)'. Indeed results of experiments on fertile and infertile soil including the presence and absence of herbivores, reveal the selective pressure of the herbivores on fast growing species. It is unfortunate that a crucial illustration (Fig. 21) is missing the asterisks indicating which species show significant changes in weight associated with herbivory by slugs and aphids. I think it remains to be shown how representative the latter are for other herbivorous species. Apart from the experimental inclusion of herbivores, Grime suggests that an important difference between his view and that of Tilman could be that the latter does not recognize as a recurring strategy the 'competitors'. These fast-growing perennial herbs and trees are lacking in the nitrogen-deficient sandplain at Cedar Creek, Minnesota, USA, but are prominent in the area of Northern England (long history of eutrophication, disturbance and dereliction) studied by Grime. If this is true, a reciprocal transplant experiment of researchers seems an option to progress the debate further.

The chapter on 'Rarefaction and extinction' mainly deals with the functional characteristics of species that are currently in decline and those which are expanding in abundance. The following chapter 'Colonisation and invasion' mainly covers community invasiveness. I feel it would have been more exciting to combine both short chapters, and discuss the strategies of declining species and increasing, colonizing and invading species in the framework of the communities in which changes are taking place.

Competitors, ruderals and stress-tolerators are the dominant functional types of species discussed, and they are often presented in a triangular configuration. A large number of plant traits has been investigated for 43 species in the Integrated Screening Programme (Hendry & Grime, 1993). When a scatter-diagram is constructed by plotting species positions on different axes, it is apparent that groups of species with sets of traits and ecologies consistent with competitor, stress-tolerator, ruderal (CSR) theory occupy characteristic areas within a triangular space. It seems to follow that in succession, for example, arable weed communities and *Calluna vulgaris* moorland can rely on a persistent seed bank. This may hold for the dominant plant species, but taking into account rarefaction and extinction, it is clear that arable field (e.g. *Agrostemma githago*, *Ranunculus arven-*

sis) and moorland communities (e.g. *Gentiana pneumonanthe*, *Pedicularis sylvatica*) harbour species that have a transient or short-term persistent seed bank (Bekker *et al.*, 1998). Such life-history traits may explain the increasing rarity of these species. I also feel that Grime's discussion of dispersal is too easy. Referring to Ridley (1930) and Van der Peijl (1972) depends too much on the morphology of dispersules. Recently Bonn & Poschlod (1998) gave an overview on dispersal of Central European plant species, and showed that predicting dispersal from morphological traits is unreliable. Unfortunately, their book is in German. I suppose Grime agrees that we need a database of many life-history traits for plant species of entire floras in order to gain more knowledge of endangered individual species.

The 'Trophic structure, productivity, and stability' chapter deals with plant strategies and ecosystem properties. Attention is paid to the hypothesis proposed by Oksanen *et al.* (1981) and Fretwell (1987) to link trophic structure and dynamics to productivity. With increasing productivity, carnivores can be supported by the system, and hence can control (top-down) the number of herbivores with a very large compartment of plants as a result. Excluding carnivores experimentally would result in an expanding herbivorous population and subsequent destruction of the vegetation. I think this is not always true. Van de Koppel *et al.* (1996) describe the productivity gradient of a salt-marsh system. Herbivores are present in the form of winter and spring migrating geese and resident hares. Harriers occasionally take a young hare, but ground predators are lacking on this island salt marsh. Despite the lack of carnivores, the plant biomass increases with increasing nutrient availability because the hares and geese are not able to maintain a short sward as the quality of the forage decreases (unfavourable leaf: stem ratio), and they leave the system (bottom-up control). When larger herbivores such as cattle are introduced, the sward gets lower (with higher leaf: stem ratio) and the hares and geese return into the system (Olf *et al.*, 1997). The theoretical framework may need some adjustments with respect to quantity and quality of the forage for herbivores, and with herbivore type.

The synthesis of ecosystems is finally dealt with in a discussion of the idea that species richness and productivity are positively correlated (Naeem *et al.*, 1999). Grime points out that this relation can be both positive and negative, depending in which zone of the 'humped-back' model the research is taking place. The synthesis of ecosystems from seed mixtures varying in richness is criticized. The main point of concern is that many researchers do not take into account the characteristics of the species involved. This inevitably leads to 'a confounding of the two possible explanations for any rise in productivity that is found to be associated with increasing the number of species in the seed mixture. Higher yield might be the result of greater species richness but it is also possible that this effect could be the result of including

particular species of high potential productivity'. The effects of different environmental variables, such as drought and temperature, were experimentally tested in an existing infertile grassland at Buxton, UK and an existing eutrophicated grassland at Wytham, UK. Both grasslands harbour the same number of species but, of course, they differ in species composition. The results show that the community at Wytham was much more responsive to the treatments than that at Buxton. Both communities were species-rich; hence it is unlikely that diversity is a key variable in the response to climate change events.

It is a pleasure to read the new version of Grime's book. Moreover, it is good that it is available again for new generations of students in plant ecology.

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