

Plant strategy theories: a comment on Craine (2005)

J. PHILIP GRIME

Unit of Comparative Plant Ecology, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

Summary

1 It is suggested that arguments concerning the nature of primary plant strategies could have been resolved more rapidly by reference to older literature relating to the behaviour of solutes in the rhizosphere and by more active programmes of plant trait screening.

2 The critique of CSR theory in Craine (2005) is rejected largely on the basis that it misunderstands the role of fundamental and proximal controls on vegetation composition (*sensu* Welden & Slauson 1986).

3 The ‘way forward’ advocated in Craine (2005) is flawed in its exclusive reliance on competition experiments. Recent progress in community and ecosystem ecology is strongly related to an increasing recognition of the declining importance of competition in unproductive or heavily disturbed environments.

Key-words: plant strategies, trait screening, competition, ultimate and proximal controls.

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Introduction

In an informal and unpublished presentation to the British Ecological Society in 2004, Peter Grubb expressed some dissatisfaction that progress in ecology was often hampered by our failure to reject wrong ideas and faulty interpretations. I agree with this conclusion and suggest that this problem is, in part, a consequence of specialization and fragmentation of ecological research. In the absence of agreed protocols and overarching theory, Ecology with its numerous subdisciplines, can sometimes resemble an amorphous, postmodern hotel or rabbit warren with separate entrances, corridors and rooms that safely accommodate the irreconcilable. The persistence of the differing perspectives of Grime (1974) and Tilman (1982) provides an obvious example of this phenomenon.

In 2005, new voices (Craine 2005; Pierce *et al.* 2005) joined this debate. I welcome this development. In recent years it has become apparent that failure to reinvigorate and resolve the key arguments has become one of the barriers to progress toward a more unified approach to understanding variation in the structure and functioning of plant communities and ecosystems.

In this short paper, no further reference will be made to that of Pierce *et al.* (2005) except to record that it usefully assimilates aspects of molecular ecology into our understanding of the stress–tolerator syndrome and is broadly supportive of the CSR strategy model (Grime

1974). My main purpose here is to comment on the review by Craine (2005). Later, I respond to five specific points raised in his Table 1, but first I wish to raise the question ‘Why has the debate remained unresolved for such a long time?’.

The long debate: two possible explanations

In my opinion there have been two main reasons why the debate has continued for such a long time. First, there has been a persistent failure to utilize existing sources of information on solute behaviour in the rhizosphere and, second, ecologists have only recently begun to assemble large-scale trait data bases for vascular plants.

NEGLECT OF EXISTING RESEARCH FINDINGS

Using the concept of R^* , Tilman (1982) extended to soils and vascular plant communities a theory of coexistence that had been developed for aquatic conditions.

Craine (2005) is correct in his rejection of this application to soils and roots of an approach developed for aquatic algae but his account is historically incomplete. In Bhat & Nye (1973), Nye & Tinker (1977) and Huston & De Angelis (1994) all the elements required for falsification of R^* in the rhizosphere were available. On this basis it is hard to escape the conclusion that the impasse between Grime and Tilman was avoidable from the beginning and was attributable to the compartmentalized structure of ecological research and its publishing

to which reference has been made in the introduction to this paper. Future historians of ecology may be perplexed that at no point in the debate was it requested by reviewers or editors that Tilman should explain the inconsistency between R^* and the established model of rhizosphere physics expounded by Nye & Tinker (1977).

THE SLOW DEVELOPMENT OF PLANT TRAIT DATA BASES

It is more than 25 years since the key traits and trade-offs of CSR theory were proposed (Grime 1977; Chapin 1980). Trait screening is an arduous activity and we should not be too surprised that it has taken a long time to accumulate data on the scale required. However, recent publications (Grime *et al.* 1997; Diaz *et al.* 2004; Wright *et al.* 2004; Grime *et al.* 2006) provide evidence of accelerating progress and the prospect of definitive tests of plant strategy theories.

Specific issues

Although, after long delay, the debate concerning primary plant strategies appears to be moving toward a resolution, some issues remain. It is therefore disappointing that the “five tenets of Grime’s work” identified as “incomplete, inconsistent or incorrect” in Craine (2005) do not refer to these but instead appear to arise from misunderstandings and unfamiliarity with research conducted in my laboratory and elsewhere. In the following responses to the five points in Craine (2005) it has been convenient to combine those addressed to his points (1) and (3).

(1) AND (3) COMPETITION FOR NUTRIENTS ON INFERTILE SOIL

Craine (2005) concedes that in Tilman’s experiment at Cedar Creek, decreasing soil N content reduced above-ground biomass of the fast-grower *Agropyron* six times more than 5 years of competition with the slow-grower *Schizachyrium*. Even in the face of this overwhelming evidence of the relatively small contribution of competition to the debilitation of *Agropyron* growing on infertile soil, Craine argues that competition was more important than nutrient stress in explaining its absence from plots where *Schizachyrium* was also present. This use of ‘important’ abandons the classic distinction of Welden & Slauson (1986) between ultimate and proximal determinants. Even if it could be established without doubt that competition was responsible for the last fatal step in the failure of *Agropyron*, this does not diminish the importance of soil infertility as the dominant factor that has made the final extinction events possible. There is also a considerable amount of experimental evidence that suggests that plants associated with infertile soils remain inferior competitors for nutrients when growing under conditions of low fertility. This conclusion has been drawn from experimental studies of plant growth

and competition under uniformly infertile conditions in the field (Grime & Curtis 1976) and in the laboratory (Mahmoud & Grime 1976). In a particularly relevant experiment measuring the performance of contrasted species in mixture and monoculture across five-step gradients of nutrient supply maintained by frequent replenishment (Campbell *et al.* 1991; Campbell & Grime 1992), the declining importance of competition at low fertility was confirmed. More recently, a similar phenomenon was described in experiments comparing plants from fertile and infertile habitats with respect to growth at various levels of nutrient supply (Grime *et al.* 1997). In microcosm experiments involving highly contrasting supplies of nutrients, plant communities have been allowed to assemble from a pool of candidate species drawn from fertile and infertile habitats. These experiments (Grime *et al.* 1987; Fraser & Grime 1999; Buckland & Grime 2000) have examined the consequences for community assembly of excluding herbivores, carnivores and mycorrhizas. Consistent features of the results of these studies are: (1) the superior ability of plants of fertile soils to capture nutrients at low levels of supply and, under such conditions, to suppress the growth of inherently slow-growing species characteristic of infertile soils; and (2) loss of the advantage of the fast-growers and promotion of slow-growers when generalist herbivores are introduced to the assemblages developing on infertile soil. This provides evidence in direct conflict with the suggestion in Craine (2005) that competition for nutrients plays an important role in structuring plant communities in infertile habitats. The weight of evidence now clearly supports the hypothesis that it is the capacity to retain captured resources, rather than competitive ability itself, that distinguishes the biology of the plant species that occupy infertile soils. This conclusion is also consistent with accumulating experimental evidence of the role of positive interactions (as distinct from competition) between neighbouring individuals in unproductive habitats (Brooker & Callaghan 1998; Callaway *et al.* 2002).

(2) THE ROLE OF DISTURBANCE IN UNPRODUCTIVE VEGETATION

The second criticism is a charge of inconsistency with regard to the importance of disturbance as a determinant of the vegetation on infertile soils. Craine (2005) states that in CSR theory disturbance is assumed not to be important at low nutrient supply, yet at the same time Grime asserts that disturbance is important in removing species from these same habitats. It is again apparent that although Craine (2005) refers to the seminal paper of Welden & Slauson (1986), he does not recognize the elegance and force of their distinction between ultimate and proximal controls on plant communities. The ultimate selective mechanism responsible for the traits of the stress-tolerator, including its defensive characteristics, is the low availability of mineral nutrients. This is because, under the constraint of low nutrient supply, slow-growing plants are severely restricted

in their ability to replace even quite small losses of tissues or individuals. However, this should not be interpreted as evidence that disturbance has provided a dominant selective mechanism during plant evolution on infertile soils. When the vegetation of infertile habitats is destroyed by frequent and severe disturbance, such as heavy trampling, soil erosion or fire, we are immediately reminded how slight (in comparison with the ephemerals of constantly disturbed, productive habitats) has been the evolutionary investment of stress-tolerators in adapting to this factor.

(4) THE ROLE OF NUTRIENT STRESS IN SHADED HABITATS

Craine (2005) states that:

‘Grime now contends that the dynamics of plants in shade is driven by nutrient deficiencies. Yet the hypothesis that the traits of species that dominate shaded habitats and the dynamics of assemblages there are driven by energy/carbon economies cannot be rejected, and may provide a more parsimonious explanation of these patterns.’

It is false to suggest that I reject the importance of energy/carbon economies in shade plants and I refer the reader to Grime (2001; pp. 52–55) for a recent treatment of this subject. However, there is abundant evidence that variation in soil fertility, even on a local scale, can radically alter the types of plant strategy that occupy areas of a woodland floor. This impact of soil fertility has been described as follows:

‘Long-lived, slow-growing herbs are of widespread occurrence throughout the world beneath evergreen and deciduous tree canopies but their abundance declines sharply in circumstances of high soil fertility. In cool temperate regions this phenomenon is particularly obvious during the spring in deciduous woodlands (Al-Mufti *et al.* 1977). On infertile soils this vernal phase is not characterized by major phenological events; the spring period simply coincides with flowering and modest expansions of the biomass of the evergreen stress-tolerators that dominate the herbaceous layer. A very different sequence of events occurs in neighbouring areas of deciduous forest on fertile soils; here the vernal phase commences with an eruption of ephemerals and ephemeroïds and, following closure of the tree canopy, terminates with an abrupt decline and senescence of the herbaceous canopy. This remarkable contrast in the species composition and seasonal dynamics of the herbaceous layer indicates a controlling effect of soil fertility on the strategic composition beneath deciduous forest. Although stress-tolerators of the woodland herb layer are distinguished by physiological traits that confer shade-tolerance, it would appear that tolerance of mineral nutrient stress is fundamental to their ecology. The dependence of these plants upon infertile soils is related to the fact

that where the constraint of mineral nutrient stress is removed the vernal phase becomes a ‘window of opportunity’ exploitable by more productive, mineral nutrient-demanding species.’ Grime (2001, p. 69)

(5) COMPETITION IN SHADE

It is asserted that ‘Grime contends that competition is unimportant in shaded habitats’ and that he is unclear whether plants with shorter canopies that can grow and overlap plants with taller canopies should be considered better competitors for light. Craine (2005) is also concerned that we should adopt a long-term view in which competition should be considered important as understorey plants may have a negative effect on the next generation of taller species.

I have never excluded the possibility of competition for light within dense herb layers or for nutrients where trees and herbs have created a dense network of mycorrhizal roots. I would point out, however, that these two conditions frequently coincide and require quantitative assessment in each situation.

I am pleased to concur with Craine (2005) about the need, where possible, to review the role of competition in relation to the long-term dynamics of woodland:

‘The impact of a dominant plant may be exerted upon neighbours at various stages of their life cycles ... This phenomenon is well illustrated by trees and shrubs, many of which as seedlings are subject to dominance by established perennial herbs but are themselves capable of dominance (often over the self-same herbs) at a later stage of their life-span.’ Grime (2001, p. 180)

Conclusions

The papers by Craine (2005) and Pierce *et al.* (2005) together with the recent reports of large-scale screening of plant traits in local floras appear to signify a shift in emphasis from theoretical to empirical approaches in the search for a functional basis for variation in terrestrial community and ecosystem functioning. This is a promising development particularly where it is associated with parallel comparative studies on the traits of other trophic groups (e.g. Dennis *et al.* 2004).

At the centre of the long dispute between Tilman and Grime has been a difference in our interpretation of the role of resource competition as a vegetation determinant. In a section headed ‘The way forward’, Craine (2005) recommends exploration of a complex array of competition models. I suggest that this approach is contentious in the extent to which, following Tilman (1982, 1988), it continues to place competition exclusively centre-stage in its search for primary plant strategies. The trait data bases currently assembling on a world-wide basis (Grime *et al.* 1997; Diaz *et al.* 2004; Wright *et al.* 2004) point to the necessity for inclusion of resource competition in any functional typology of plants, but it is also evident

that we must recognize that competition declines in importance under the impacts of reduced productivity and/or severe disturbance. Recently, Grime (2001; pp. 67–71) and Caccianiga *et al.* (2006) have sought to explain such persistent emphasis on resource competition as a legacy of approaches derived from agricultural research. As Caccianiga *et al.* (2006, p. 19) explain:

‘The contemporary ecological mindset borrows heavily from agriculture, in which periods unsuitable for growth are disregarded and thus resource acquisition and plant growth are seen as continuous processes ... Life forms in chronically unproductive habitats are primarily defensive adaptations against these perilous episodes, not aggressive adaptations to subtle variations in resource availability and competition during milder periods.’

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