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A clarification of the debate between Grime and Tilman

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Introduction

Attempts to understand plant-community structure have led to various theories about the forces leading to these patterns (Pickett, 1976; Connell, 1978; Grime, 1979; Huston, 1979; Tilman, 1985, 1988; Keddy, 1990). Particularly controversial has been the role of plant traits in competitive success (Grace, 1990). Grime's theory of life histories (Grime, 1979) is one attempt to explain the range of plant traits found in various community types. In this theory Grime has invoked the processes of disturbance, stress, and competition as opposing forces selecting for contrasting syndromes of characteristics. Another attempt at understanding community structure has been Tilman's resource-based theory of competition (Tilman, 1977). This theory has recently been extended to explain suites of traits associated with old-field succession and gradients in soil fertility and disturbance (Tilman, 1985, 1988).

Considerable debate has developed concerning the validity of the theories proposed by Grime and Tilman (Thompson, 1987; Tilman, 1987, 1989; Grime, 1988; Thompson & Grime, 1988). A great number of issues have been discussed during this exchange relating to both the functions performed by various plant traits and the nature of the environment. During these discussions, there has been no apparent resolution of issues. In this paper I wish to examine the debate about the nature of competitive interactions and to discuss the role that definitions have played in this part of the controversy. Also, I attempt to eliminate the semantic confusion surrounding the definition of 'competition' and compare these theories on equal grounds. Finally, I provide a brief discussion of the remaining issues to be resolved.

Grime's theory

Grime's theory is based on the recognition of three major syndromes of life-history traits, 'Ruderal', 'Stress-tolerator', and 'Competitor'. The 'Ruderal' syndrome is characterized by high reproductive effort and high growth rates, and is predicted to occur in disturbed, productive habitats. The 'Stress-tolerant' syndrome is characterized by low reproductive effort and low growth rates, and is predicted to occur in undisturbed, unproductive (stressful) habitats as well as among the subordinate plants in late successional, productive habitats where the resources per individual are low (Grime, 1987). The 'Competitor' syndrome is characterized by low reproductive effort and high growth rate, and is predicted to occur in undisturbed, productive habitats (exclusive of the late successional phases which are deemed to be biotically stressful). While this theory is primarily concerned with life histories, an integral part is its assumptions/predictions about the relationship between plant traits and competitive success.

Tilman's theory

Tilman's theory is based on a mechanistic approach to predicting competitive success as a function of the concentration of limiting resources. In its simplest form, Tilman's theory is based on an analytical model consisting of a pair of equations that describe the dynamics of populations as a function of resource concentration and the concentration of resource as a function of supply rate and uptake rate (Tilman, 1982). In this original model populations are summarized by average density and the behaviour of individual plants is not incorporated. By incorporating additional assumptions, Tilman has extended this theory to explain competition for multiple resources, and patterns of species diversity.

Recently, Tilman (1988) has developed a numerical model of cohorts of individual plants based on more biologically explicit assumptions about resource capture as a function of plant traits. Simulations have been used to further examine

resource competition, the traits of species expected along fertility and disturbance gradients, and the relationship between plant traits and succession.

Points of dispute

It is clear that these two bodies of theory have developed from different perspectives and with different objectives. However, there are a number of overlapping elements that lead to apparently contradictory predictions. Among the major contradictions are the following:

- 1 Competitive superiority will result from high resource uptake capacities (Grime) vs competitive superiority will result from having the lowest equilibrium resource requirement (Tilman).
- 2 A species will have a positive correlation among its abilities to compete for different resources (Grime) vs a species will have a negative correlation (trade-off) among its abilities to compete for different resources (Tilman). A corollary is that species can be classified as good competitors in some absolute sense (Grime) vs species' competitive ability is conditional depending on the environmental conditions (Tilman).
- 3 Competition is less intense in unproductive habitats (Grime) vs competition in unproductive habitats may be just as intense as it is in productive habitats (Tilman).
- 4 Competitors dominate during mid-succession (Grime) vs competition determines dominance during all phases of succession (Tilman).

While the above four points do not represent an exhaustive list, they do include some of the most highly debated issues.

Semantics and the meaning of 'competition'

Recent discussions of these theories have pointed out that Grime and Tilman use different definitions of competition and competitive success (Goldberg, 1990; Grace, 1990). Of fundamental importance is that Grime defines competition in terms of the capacity for resource *capture* and goes on to state that it is only part of the mechanism whereby a plant may suppress the fitness of a neighbour. Tilman, in contrast, defines competitive success as the ability to draw resources to a low level and to tolerate those low levels (also defined as the ability to have a low equilibrium resource requirement). As an operational definition, in both the model results and most field studies, Tilman *measures* competitive success as

the ability to *dominate* in a habitat. Thus, both Tilman's theoretical and operational definitions contain many elements including both resource uptake and tolerance abilities. It is insightful to recognize that their definitions represent the extremes of the range of definitions used for the term competition with Grime's definition being very narrow and Tilman's being very broad. It should be no surprise that their predictions are at odds.

Translation of disputed points

When their contrasting definitions are considered it can be seen that the four points of dispute (above) are partly semantic. It is possible to clarify matters somewhat by recognizing that Grime's 'competitor' syndrome can be described as a 'resource capture specialist' (alternatively, 'capitalist' *sensu* Grime, 1989). The concept of 'resource capture specialist' is a plant well equipped to capture resources when in abundant supply. According to Grime (1989) this syndrome is one characterized by active foraging for resources and high metabolic costs. With this substitution of terms in mind, it is possible to reexamine the above-disputed points.

- 1 *Dominance when habitat is fertile (and not recently disturbed) will result from a high resource capture capacity (Grime) vs dominance when resources are reduced to equilibrium levels will result from being able to utilize and tolerate lower resource concentrations (Tilman)*

When examined in this fashion it can be seen that Grime and Tilman are not in direct conflict. Grime explicitly assumes a trade-off between tolerance and capture capacity for a resource and would agree that eventual success will be determined largely by tolerance characteristics. While not requiring it, Tilman's theory often assumes a trade-off between maximum growth capacity and the tolerance of low resource levels. Because of this trade-off, dominance when resources are abundant would be associated with a high resource capture capacity while dominance at low resource levels would be associated with tolerance traits. Thus, the above predictions by Grime and Tilman are largely consistent even if disagreement remains about the exact nature of underlying processes.

- 2 *A species will have a positive correlation among its abilities to take up different resources*

(Grime) vs a species will have a negative correlation among its abilities to tolerate (and compete) at low levels of different resources (Tilman)

This issue has been discussed to some extent by Goldberg (1990) who concluded that these were both possible since resource capture and tolerance are separate attributes. As with (1) above, Grime and Tilman are again discussing different phenomena. However, in this case, either statement is empirically falsifiable and the validity of either is currently undetermined.

In evaluating these predictions it would seem as though the context of comparison is very important. Within a life form, a trade-off between stress tolerance and resource capture could result in a positive correlation amongst resource capture capacities for several resources. However, comparisons across life forms, especially trees vs herbs, can be confusing in this context. What life-stage of the tree is to be compared with the herb? Over what time-span are they to be compared? One gets the impression, again, that Grime and Tilman are developing their predictions with different comparisons in mind. However, the apparently global nature of their generalizations makes it likely that both supporting and refuting comparisons can be found. If these statements are subjected to 'risky' tests (i.e. refuted by any exceptions; Loehle, 1987), both can likely be falsified as global statements and must, therefore, be restricted to a narrower set of contrasts. Such 'bounding' of the model predictions will be necessary in order to clarify matters.

3 Resource capture capacity will be less important in unproductive habitats (Grime) vs competition may be just as intense in unproductive as in productive habitats (Tilman)

As for various points above, it is again the case that Grime and Tilman are not discussing the same thing. For this translation of Grime's prediction, it is reasonable to expect that unproductive habitats will favour the ability to tolerate low resource supply rates rather than high resource capture capacities. A recent elaboration of Tilman's model for nutrient competition has led to the same prediction. Substantial empirical evidence suggests that this is generally true (e.g. Chapin, 1980; Berendse & Elberse, 1990).

When considering predictions about the intensity of competition, we must deal with several complicating issues. First, Weldon & Slauason (1986) have recently pointed out the need to

distinguish the *importance* of competition from the *intensity* of competition. The *intensity* of competition refers to the degree to which a plant population is reduced by the presence of neighbours. In contrast, the *importance* of competition refers to the relative reduction of a plant population by competition compared to the reduction due to other forces such as herbivory or unfavourable abiotic conditions (stress). In that paper, Weldon & Slauason illustrated numerous cases of confusion resulting from a failure to recognize this distinction. Any discussion of either intensity or importance of competition that does not make clear this distinction must be considered carefully because of the potential for confusion. For example, within the context of Grime's theory, statements about the *intensity* of competition should be considered carefully since his system is one that is explicitly based on trade-offs in the relative *importance* of selective forces.

Tilman's prediction that the intensity of competition is constant regardless of habitat productivity is based on a carrying capacity mentality. If two habitats are both near carrying capacity then there is a sense in which the intensity of competition would be equivalent (it is maximal in both cases). However, since Tilman's model deals only with competition, it is unavoidable that his model will always find competition to be both maximally intense and important. Further, it is important to note that because Tilman's definition of competition includes so many processes, neither disturbance nor abiotic stress act to reduce the importance of competition (Grace, 1990).

A further complication regarding discussions of the intensity of competition comes from the fact that it is possible to consider the intensity of competition per gram of competitor, per plant, or for the total community. The interpretation is quite different for these three different forms of expression. Further, within the context of the above 'carrying capacity perspective', it is possible to consider that intensity should be proportionally against the capacity of the environment. Further work is clearly required (especially a clarification of predictions) if we are to resolve issues about the intensity and importance of competition.

Comparison of the two theories on the effect of habitat productivity also reveals a conflict associated with the concept of 'stress' ('the external constraints which limit the rate of dry matter production of all or part of the vegetation' — Grime, 1979). For Grime, stress is viewed as a force

that selects for tolerance. Tilman does not recognize stress as a valid concept (D. Tilman, personal communication) and considers habitat productivity to be a less ambiguous term for the same thing. Both authors discuss gradients in habitat productivity as if it makes no difference whether they are gradients in fertility (resource supply rate) or non-resource factors (e.g. soil salinity). It is likely that this distinction is important when considering the trade-offs amongst plant traits and I believe that the failure to make this distinction has contributed to the confusion (Grace, 1990; J.B. Grace, unpublished observations).

In summary, for point 3, Grime's prediction that unproductive habitats will select for tolerance traits would seem both consistent with Tilman's predictions and likely valid. Statements about the intensity of competition require clarification before an unambiguous evaluation can be made.

4 'Resource capture specialists' dominate in mid-successional communities (Grime) vs competition determines dominance during all phases of succession (Tilman)

Once again, Grime's and Tilman's predictions are not directly comparable. This translation of Grime's statement would seem to be verifiable and, in general, is consistent with recent findings by Tilman and others (Tilman & Wedin, 1991). Tilman's prediction, however, depends upon succession being a 'shifting equilibrium' where the dominant species at any point in time is the superior competitor for the particular conditions (ratios of resources) at that stage of succession. Tilman & Wedin (1991) recently reported results for Minnesota old-fields indicating the early phase of succession to be determined by colonizing ability and not competitive ability (the Colonization-Competition hypothesis) while later stages were determined by competitive ability (the Resource-Ratio hypothesis). These results indicate that Tilman's general prediction may be false for the earliest stages of succession.

The discussion of this point of debate brings up an additional point of disagreement between Tilman's perspective and that of Grime and others. This point of disagreement has to do with the role of equilibrium processes (and equilibrium models) in community dynamics (particularly succession). Aside from Tilman (1985), most authors currently seem to consider succession as a non-equilibrium process (e.g. Pickett, 1976). However, it is not necessarily true that the answer must be either one or the other option. Theoretical

and empirical analyses by J.S. Clark (personal communication) have led to the conclusion that forest succession involves a mixture of processes partially consistent with both Grime's life-history viewpoint (non-equilibrium) and Tilman's resource-ratio viewpoint (equilibrium). As in other debates, considerable disagreement exists as to the role of equilibrium processes. Before this can be resolved it will be necessary to *specify* what constitutes evidence for or against equilibrium effects. At present, debates about 'equilibrium' are rather sterile and it is likely more profitable to confine ourselves to a discussion of the role of various plant traits or specific processes in determining community structure.

Towards theory maturation

Since the above discussion emphasizes the confusion caused by definition problems, it is fair to ask, 'Why weren't the differences in definitions obvious in the first place?' The answer to this question provides a valuable lesson for many areas of ecology. The reason that the differences were not obvious is that the definitions were misunderstood, a common characteristic of newly developed theories (Loehle, 1987). What counts when making predictions are the *operational* definitions, i.e. how competitive ability and success are to be evaluated. In effect, the operational definition is determined by experimental methodology. If dominance in mixture is used to declare competitive success (Tilman, 1988) then the operational definition for competitive success is dominance. Grime, on the other hand, has been primarily concerned with classification of life histories and competitive success has been defined as success by 'competitors' (i.e. success by capture specialists). Many of the other controversies in the study of plant competition are difficult to resolve because of the reliance on contrasting methodologies for evaluating competitive success. In essence, these different methodologies represent different operational definitions and lead to unresolved debate. Future work needs to refine the existing theories. Part of this maturation process will be to clarify the interpretation of both terminology and methodology. Only with such clarification will it be possible to resolve the debate about the role of competition in communities.

Conclusions

Differences in the definitions used by Grime and Tilman have contributed significantly to the debate about the validity of their theories. When

these differences are clarified it can be seen that these theories are less conflicting than previously thought. For their two theories, there actually exists a general agreement about the roles of resource capture capacity and tolerance to low resource levels in determining community structure.

The primary differences between theories are of perspective and emphasis. These differences are especially reflected in their contrasting predictions about the nature of trade-offs amongst traits. Grime's theory is one that considers a broad range of traits including reproductive effort, dispersal characteristics, and other attributes affecting the colonization process. Tilman's theory, in contrast, focuses on resource use traits and is less explicit in considering trade-offs associated with colonization ability.

The conflict between these two theories can serve as a case history of how general theories must be refined and clarified before they can be fully evaluated. Contrasting perspectives and starting points have combined with differences in terminology to exaggerate the actual contradictions between theories. Elimination of differences in terminology alone permits us to focus on the real differences. Further, the analysis presented here also points out the need to specify the realm in which a statement is to apply ('bounding the theory'). Predictions about whether correlations amongst traits are positive or negative are highly sensitive to the plants (and life stages) that are compared.

Both theories have captured considerable attention over the past decade and have greatly stimulated the field of plant ecology. The process of theory maturation will require a refinement of the theory as well as the application of tests if further progress is to be made.

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