

## Competitive hierarchies in herbaceous plant communities

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Using data from eight published competition experiments with diallel designs, and a new method of analyzing such data, we present evidence that competition among herbaceous plants has two general properties: pairwise interactions are predominantly asymmetric, and competitive hierarchies exist, i.e. competitive networks are primarily transitive. This empirical evidence is compared with what is known about the mechanisms of plant competition. Finally we present an hypothesis to explain some of the variability in the degree to which competitive networks display asymmetry and transitivity, and explore some of the consequences of this in terms of developing a predictive theory of plant competition.

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### Introduction

In developing a predictive theory of competition in plant communities, we require some measurable state variables of such systems which will allow us to extrapolate from the particular to the general. The recent reviews by Connell (1983) and Schoener (1983) on the prevalence of competition however, show that most of our current knowledge about competition is a collection of special cases with limited generality. The vast number of species and habitats in nature argues against such a phenomenological approach and suggests that we need measures of how groups of species in communities interact (Keddy 1989).

One growing body of information on plant interactions comes from studies which have measured pairwise interactions among many pairs of species simultaneously (Caputa 1948, Williams 1962, Harper 1965, Goldsmith 1978, Wilson and Keddy 1986, Mitchley and Grubb 1986). These experimentally derived competition matrices may contain important information about the nature of plant interactions. We therefore explored such matrices for two properties: (1) the degree of asymmetry (non-reciprocity) of pairwise interactions, and (2) the degree to which species are arranged in competitive hierarchies (transitive networks). This fol-

lows on work by Buss (1980 and references therein) in the context of bryozoan communities.

We first define "asymmetric" and "transitive" properties of competition matrices and introduce some simple inferential statistics to test for pattern in them. Using these statistics, we analyze the data on eight published competitive diallels involving herbaceous species from wetland, sea-cliff, chalk grassland, weed, pasture and crop communities. Possible mechanisms of plant competition that might account for the observed pattern of transitive asymmetric competitive networks are discussed. The last section of this paper discusses the implications of these results for studies of co-existence and suggests paths for developing predictive theories of plant competition.

### Defining and measuring transitive asymmetric competition

Most published measurements of pairwise competition between plants have been based on a de Wit replacement series (de Wit 1960), in which the yield of a species in mixture is compared with its yield in monoculture. Although such an experimental design has recently been criticized (Firbank and Watkinson 1985, Connolly 1986) we will define transitivity and asymmetry relative

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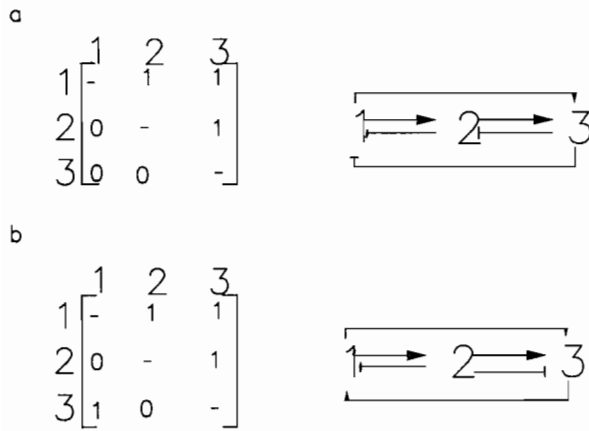


Fig. 1. (a) A binary matrix which contains a transitive path of length two, and its corresponding digraph. (b) A binary matrix which contains an intransitive path of length two, and its corresponding digraph.

to such an experimental design, since we want to use published evidence, although other (perhaps better) designs are possible.

Let  $Y_{ii}$  be the yield of an average individual (ramet) of species  $i$  grown in monoculture and  $Y_{ij}$  be the yield of an average individual of species  $i$  when grown in mixture with species  $j$ . A common measure of competitive ability of species  $i$  relative to species  $j$  is its relative yield per plant:

$$RYP_{ij} = Y_{ij}/Y_{ii}.$$

A  $RYP_{ij}$  value greater than unity means that species  $i$  grows better in mixture with species  $j$  than it does in monoculture. If  $n$  species are grown in all pairwise combinations then an  $n \times n$  matrix of RYP values is obtained. It is useful to construct a binary matrix  $A$  in the following way:

$$a_{ij} = \begin{cases} 1 & \text{if } RYP_{ij} > 1 \\ 0 & \text{if } RYP_{ij} < 1 \end{cases}$$

Here, an RYP value of exactly unity is treated as a limiting case. This matrix  $A$  can be used to construct a digraph (directed graph) with each species at a vertex and an arrow ( $I \rightarrow J$ ) going from species  $i$  to species  $j$  if  $a_{ij} = 1$  and a broken line ( $I - J$ ) if  $a_{ij} = 0$ . Fig. 1 shows two such binary matrices and their corresponding graphs.

#### Asymmetry

Pairwise asymmetric competition exists when  $a_{ij} = 1$  (i.e.  $RYP_{ij} > 1$ ) and  $a_{ji} = 0$  (i.e.  $RYP_{ji} < 1$ ). Jacquard (1968) called this form of interaction "antagonisme" and Silander and Antonovics (1982) called it a "devia-

tion from reciprocity", but our term is used here because it is probably more familiar to most readers. Biologically, this means that species  $i$  grows better in mixture with species  $j$  than it does in monoculture but species  $j$  grows worse in mixture with species  $i$  than it does in monoculture. Therefore, species  $i$  will eventually exclude species  $j$ . Note that such measures as RYP are phenomenological rather than mechanistic; they provide information on the outcome of an interaction but not of the underlying causes.

#### Transitivity

The definition of asymmetric competition given above considers only pairwise interactions. Normally however, plants can potentially interact with many different species, giving rise to a competitive network. To extend the concept of asymmetric competition to this more general case, we introduce the notions of transitivity and of path length. Here, we use the definition of path length employed in graph theory, i.e. the number of edges in the graph. The length of a path is therefore one less than the number of species included within it. Fig. 1a represents a transitive path of length two. The path begins with species 1, passes through species 2 and ends at species 3. The path is transitive because knowledge that species 1 competitively excludes species 2, and that species 2 competitively excludes species 3, implies that species 1 also competitively excludes species 3. Thus, the species can be ranked in a hierarchy from species 1, which is capable of excluding other species, to species 3, which is capable of excluding neither of the other two species. Note that there are also three transitive paths of length one, corresponding to the three cases of pairwise interactions. In Fig. 1b there is also a path of length two but this time the path is intransitive, since although species 1 excludes species 2, and species 2 excludes species 3, species 1 does not exclude species 3. From such a definition it follows that pairwise asymmetric competition is simply a transitive path of length one.

To test for transitivity we need to determine whether this binary matrix differs from an appropriate null model (Harvey et al. 1983). We are specifically interested in the number of subsets of species possessing hierarchical structure relative to the number expected by chance. The Appendix presents details of measuring transitivity and testing for significant departures from a null model.

#### Empirical evidence

Few published studies have compared competitive abilities amongst a large group of species which have the potential to interact in the field. Six such studies, involving eight competitive diallel experiments, will be analyzed in this section to determine the degree to which they display transitive, asymmetric competition.

Tab. 1. The total number of transitive paths of various lengths (L) in the binary matrices of eight published competitive diallel experiments. Symbols: the total possible number of transitive paths of various lengths in each matrix (T(L)), the binomial probability of "success" (p), the number expected ( $\mu$ ), the number observed (m(L)), and the probability of at least m(L) transitive paths occurring under the null hypothesis. S is the number of species (or varieties) in the matrix, and  $\theta$  is the frequency of 1's in the binary matrix.

L	T(L)	p	$\mu$	m(L)	probability ( $\geq m(L)$ )
Wilson and Keddy (1986): S = 7, $\theta = 26/42$					
1	21	$4.8 \times 10^{-1}$	4.95	16	$6.6 \times 10^{-3}$
2	35	$2.6 \times 10^{-2}$	0.46	16	$1.3 \times 10^{-16}$
3	35	$6.2 \times 10^{-3}$	0.11	7	$2.0 \times 10^{-9}$
4	21	$1.5 \times 10^{-3}$	0.02	1	$3.0 \times 10^{-2}$
Mitchley and Grubb (1986): S = 6, $\theta = 19/30$					
1	15	$4.6 \times 10^{-1}$	3.48	11	$3.3 \times 10^{-2}$
2	20	$2.6 \times 10^{-2}$	0.25	5	$1.1 \times 10^{-4}$
3	15	$5.8 \times 10^{-3}$	0.04	1	$8.4 \times 10^{-2}$
Goldsmith (1978): S = 13, $\theta = 86/156$					
1*	78	$5.0 \times 10^{-1}$	19.29	56	$< 5.0 \times 10^{-7}$
2**	286	$3.0 \times 10^{-2}$	4.33	90	$< 5.0 \times 10^{-7}$
3**	715	$7.4 \times 10^{-3}$	2.68	98	$< 5.0 \times 10^{-7}$
4**	1287	$1.9 \times 10^{-3}$	1.19	60	$< 5.0 \times 10^{-7}$
5**	1716	$4.6 \times 10^{-4}$	0.39	19	$< 5.0 \times 10^{-7}$
6**	1716	$1.1 \times 10^{-4}$	0.10	2	$1.6 \times 10^{-4}$
Caputa (1948), year 1944: S = 9, $\theta = 34/72$					
1	36	$5.0 \times 10^{-1}$	18.0	32	$8.9 \times 10^{-7}$
2	84	$3.1 \times 10^{-2}$	2.60	50	$4.5 \times 10^{-53}$
3	126	$7.7 \times 10^{-3}$	0.97	47	$2.9 \times 10^{-64}$
4	126	$1.9 \times 10^{-3}$	0.24	26	$1.3 \times 10^{-43}$
5	84	$4.8 \times 10^{-4}$	0.04	8	$1.2 \times 10^{-15}$
6	36	$1.2 \times 10^{-4}$	0.00	1	$4.3 \times 10^{-3}$
Caputa (1948), year 1945: S = 9, $\theta = 39/72$					
1	36	$5.0 \times 10^{-1}$	18.0	27	$1.7 \times 10^{-3}$
2	84	$3.1 \times 10^{-2}$	2.57	31	$2.2 \times 10^{-24}$
3	126	$7.6 \times 10^{-3}$	0.96	17	$2.0 \times 10^{-15}$
4	126	$1.9 \times 10^{-3}$	0.24	3	$1.8 \times 10^{-3}$
Caputa (1948), year 1946: S = 9, $\theta = 31/72$					
1	36	$4.9 \times 10^{-1}$	17.65	27	$1.4 \times 10^{-3}$
2	84	$2.9 \times 10^{-2}$	2.48	26	$1.1 \times 10^{-18}$
3	126	$7.2 \times 10^{-3}$	0.91	18	$3.9 \times 10^{-17}$
4	126	$1.8 \times 10^{-3}$	0.22	7	$3.9 \times 10^{-8}$
5	84	$4.3 \times 10^{-4}$	0.04	1	$3.6 \times 10^{-2}$
Williams (1962): S = 7, $\theta = 24/42$					
1	21	$4.9 \times 10^{-1}$	10.29	16	$1.0 \times 10^{-2}$
2	35	$2.9 \times 10^{-2}$	1.03	16	$1.9 \times 10^{-14}$
3	35	$7.2 \times 10^{-3}$	0.25	5	$5.2 \times 10^{-6}$
Harper (1965), low density: S = 6, $\theta = 17/30$					
1	15	$4.9 \times 10^{-1}$	7.37	11	$5.2 \times 10^{-2}$
2	20	$3.0 \times 10^{-2}$	0.59	6	$1.8 \times 10^{-5}$
Harper (1965), high density: S = 6, $\theta = 17/30$					
1	15	$4.9 \times 10^{-1}$	7.37	7.0	$6.7 \times 10^{-1}$
2	20	$3.0 \times 10^{-2}$	0.59	2.0	$1.2 \times 10^{-1}$

\*: Using a normal approximation, rounded to six digits.

\*\* : Using a Poisson approximation, rounded to six digits.

The results are summarized in Tab. 1. The binary matrices derived from these data can be calculated from the definitions in the previous section, or are available from the second author.

The first data set comes from Wilson and Keddy (1986, Tab. 1). Seven species of herbaceous wetland plants were grown in all pairwise combinations in pots in the field. The competitive abilities of these species were expressed as the ratio of the yield of each species in mixture to its yield in monoculture. These seven species occur naturally along shoreline exposure gradients in eastern Canada with similar rank abundances. The competitive network was predominantly transitive, involving up to five species. Sixteen out of a possible twenty one pairwise interactions were asymmetric.

The second data set comes from Mitchley and Grubb (1986: Tab. 10, part b), in which the relative yield (mixture:monoculture) of six co-occurring plant species from chalk grassland was measured, again in all pairwise combinations. There were many more transitive paths than expected under the null hypothesis, for those paths involving up to three of the six species. Eleven out of a possible fifteen pairwise interactions were asymmetric.

Goldsmith (1978: Tab. 1) grew thirteen populations of seacliff plants in all pairwise combinations. There were seven different species and a number of different ecotypes within species. Again, there were many more transitive paths than expected under the null hypothesis, for paths involving up to seven species, and fifty out of a possible seventy eight pairwise interactions were asymmetric.

Caputa (1948) carried out three competitive diallels, one for each of three successive years, involving nine species common to permanent pastures in Europe. The data for these three diallels were reproduced by Jacquard (1968: Tabs v, vi, vii). In all three years there were highly significant asymmetric interactions, with transitive paths involving up to six of the nine species. Those interactions that were not asymmetric tended to involve species capable of fixing nitrogen (Jacquard 1968). Jacquard ranked species according to their ability to reduce the growth of other species ("aggressivité"), and their ability to resist depression in their own growth is due to the effects of others ("résistance à l'agression") and found that such rankings were relatively stable between years and that there was a tight negative correlation between these two attributes ( $r = -0.945$ ). This is similar to Goldberg and Fleetwood's (1987) recent ideas on "response" and "effect", although they have proposed that these aspects of competitive ability need not be strongly correlated.

Williams (1962) published an analysis of variance on data from an (uncited) mechanical diallel performed by R. M. Moore and J. D. Williams, involving seven species of Australian weeds; unfortunately, the species names were not provided. Using Tab. 2 of Williams (1962), we find that competition was predominantly

asymmetric and transitive, with transitive paths involving up to four species.

Finally, Harper (1965: Figs 12, 13) published data on two mechanical diallels involving six varieties of *Linum usitatissimum* (three of flax and three of linseed) at two different planting densities. In this data set the relative yield of seed, rather than of biomass, was used. In these two diallels, there was much less evidence of asymmetry. At the lower planting density there may have been some asymmetry ( $p = 0.052$ ), and there was transitivity in loops involving three species, but at the higher planting density there was neither asymmetry nor transitivity.

In five out of six studies, involving wetland, sea-cliff, chalk-grassland, weed and pasture herbaceous species, there was the same strong pattern: competitive networks were primarily asymmetric and transitive. The exception found in Harper's (1965) data set will be discussed later. Note however, that in none of the studies were the matrices composed entirely of transitive paths.

### Consideration of mechanism

Although the phenomenon of asymmetric transitive competitive networks appears to be present in the data sets analyzed above, the mechanisms generating these patterns remains obscure. In this section we suggest a tentative mechanism, while recognizing that some contrary evidence exists.

If two plants are growing sufficiently close to each other and one overtops the other, there may be two immediate consequences. First, the taller plant will intercept some of the incoming light, allowing further growth. Simultaneously, the absorbed photons will no longer be available to the shorter plant, thereby inhibiting its growth. Since light availability and quality decreases exponentially with distance below the top of the canopy (see, for example, Fitter and Hay 1983), even small initial differences in height should have major effects on the relative growth of each, and therefore on the outcome of competitive interactions. This was shown theoretically by Ford and Diggle (1981) and experimentally by Weiner (1986) and Weiner and Thomas (1986).

Of course, light is not the only resource for which plants can compete. Mineral nutrients and water are also necessary for growth, and in artificial experimental designs in which competition for light is prevented (e.g., Donald 1958, Aspinall 1960 and studies reviewed in Wilson 1988), competitive interactions still occur. Weiner (1986) provides evidence suggesting that when *only* roots compete, competition can be symmetric. However, under natural conditions, the effects of root and shoot competition can not usually be partitioned as causal factors, and the partitioning of variances in such designs is misleading (Levins and Lewontin 1974). This is because plant competition is profoundly local in na-

ture and, with some exceptions (in semi-deserts, for example), plants whose root systems are sufficiently intermingled to compete will also have canopies close enough to affect one another. Roots and shoots are an integrated unit and reduced growth in either component results in reduced growth in both. Thus, treatments such as shading or defoliation can curtail root growth and mineral uptake within 24 h (Caldwell et al. 1987). In experiments involving a shrub (*Artemisia tridentata*) and two species of bunch grasses (*Agropyron spicatum* and *Agropyron desertorum*), when the grasses were clipped, the shrub took up more radiolabeled phosphorus than when the grasses were not clipped (Caldwell et al. 1987). Thus, a reduction in above ground tissues resulted in a reduction in the ability to compete for mineral nutrients.

Wilson (1988) reviewed 17 studies in which root, shoot, and total (i.e. both root and shoot) competition were measured and concluded that statistical interactions between root and shoot competition rarely occurred; in other words, the total competitive effect was a linear combination of separate root and shoot interactions. This could lead to symmetric interactions and prevent transitive networks from forming if there was a tradeoff between root and shoot competitive abilities leading to one species being the superior competitor for below ground resources and the other a superior competitor for light. This tradeoff occurred only in a minority (17/49) of the published studies that Wilson (1988: Tab. 5) reviewed. In addition, it is not known if any of these cases were statistically significant. The relevance of this to natural plant communities is unclear since all of Wilson's (1988) examples are of agricultural species and varieties, but if those species were grown in all pairwise combinations the resulting competition matrices would likely display transitivity due to the correlation of abilities for root and shoot competition.

The way in which plants compete for resources suggests that an initial advantage in one plant over another results in a positive feedback and culminates in an asymmetric outcome (Harper 1977). As well, the mechanisms of plant competition appear to be related to variables implicated in plant size: height, leaf area or canopy form in competition for light, and root density, length or rooting depth in competition for water or nutrients (Gaudet and Keddy 1988). These points have important implications for plant communities, and are mirrored in the literature of bryozoan competition, where size differences can be used to predict competitive outcomes (Buss 1980).

### Predicting plant competitive abilities

In completely transitive networks the outcome of competitive interactions (in the absence of subsequent disturbance) is easy to predict: all but the competitive dominant will be excluded. In completely intransitive networks the outcome is not obvious, and a detailed

knowledge of the exact functional form of the interactions, as well as the initial conditions, is necessary to determine the outcome. Therefore, the results of the analyses of the diallels, showing that herbaceous species can often be ranked in a competitive hierarchy, and the above arguments concerning how plants acquire essential resources, suggest that it should be possible to predict the outcome of competitive interactions, rather than simply describe the outcome post facto. In general, those attributes of a plant that allow it to suppress the growth of neighbors, and those traits that influence how sensitive a plant will be to suboptimal levels of resources caused by the presence of neighbors, should be good predictor variables. Curiously, little effort has been expended in determining how such traits might be used to predict the outcome of competitive interactions. Of those few studies that have attempted this, many have used species which were already morphologically similar (e.g. Sakai 1961, Clatworthy and Harper 1962, Assemet et al. 1981).

Although it is possible to list a large number of attributes which may influence competitive abilities, it is reasonable to ask: are there a small subset of traits of predominant importance which allows good predictive ability in most situations? Once these primary traits have been identified, then exceptions to the general trend will lead us to more subtle differences. In what follows, we show how one easily measured attribute, plant height, can account for a significant portion of the variance in competitive abilities. We do this, not to argue that height is the only important plant trait, but to demonstrate the potential of such an approach.

Clements (1933) summarized the results of hundreds of transplant and removal experiments in prairie vegetation (e.g., Clements et al. 1929) and concluded that, in general, "the taller grasses enjoyed a decisive advantage over the shorter". Mitchley and Grubb (1986), whose data set was analyzed above, showed a significant correlation between position in the dominance hierarchy and mean turf height in monocultures, and noted that "the plants with the tallest leaves were the most effective in interference". Goldsmith's (1978) data, also analyzed above, showed that the larger species generally suppressed the smaller ones.

Gaudet and Keddy (in press) have screened 44 wetland species for competitive ability against two indicator species (*Lythrum salicaria* and *Penthorum sedoides*) using an modified additive design. Regression analysis revealed that the average dry weight biomass of the test species when grown singly could predict 64% of the variation in competitive depression of the two indicator species. The slopes of the two regressions were not statistically different, suggesting that biomass might be a general predictor. Inclusion of other size-related variables (height, canopy diameter, leaf shape and canopy area) accounted for 74% of the variation.

We are aware of only one study in which the morphological basis of competitive ability was determined by

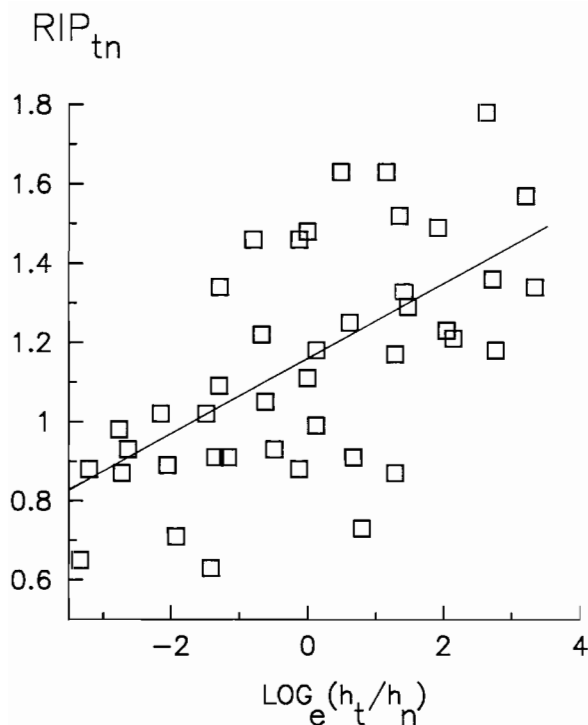


Fig. 2. The relationship between competitive ability ( $RIP_{tn}$ ) of a target species vs its neighbor and the logarithm of the ratio between its height and the height of its neighbor.  $r = 0.61$ .

experimental manipulations rather than through inference from correlation. Benjamin (1984) performed a series of experiments with carrot plants in which the height of foliage relative to neighbors was controlled by gently bending the petiole towards the ground and pinning it. He found that "lowering the petiole angle of carrot leaves greatly reduced the ability of plants to compete against untreated neighbors, but did not affect growth when all plants were treated similarly". Thus, it was differences in height that determined competitive outcomes.

To assess the usefulness of height as a variable for predicting the outcome of competition experiments, we performed a multiple regression in which the response variable was competitive ability (relative increase per plant,  $RIP$ ) obtained from Tab. 1 of Wilson and Keddy (1986), and the predictor variables were the height of photosynthetic tissues of the competing species.  $RIP$  is the ratio of the average yield per target plant in mixture with the neighbor, to the average yield per target plant in monoculture, both corrected for the starting mass of the target plant; details of the experiment can be found in Wilson and Keddy (1986). The average heights per species were averages over ten randomly chosen ramets per species, growing on the shore of Axe Lake, Ontario (the site of the field experiment) on 22 August, 1985 (kindly provided by S. Wilson). Fig. 2 shows the rela-

tionship between competitive ability and the difference in height between the plants. The regression is highly significant ( $F_{1,40} = 24.08$ ,  $p < 0.0005$ ). Competitive ability increased with increasing height differences between the target and the neighbor. Despite the fact that the experiment lasted only three and a half months, and that the differences in size between the species were not large, 37% of the variation in competitive ability was explained by this single plant attribute ( $r = 0.61$ ).

This points out an important aspect of asymmetric competition. The ability to predict competitive outcomes decreases as the competing plants become more similar. Thus, contrary to the competitive exclusion principle, similarity may promote coexistence while differences result in predictable, transitive, asymmetric competition resulting in the exclusion of the smaller species. Similar species could coexist precisely because interspecific competition is approximately equal to intraspecific competition, thereby weakening differential interspecific interactions, which might otherwise lead to exclusion (Goldberg and Werner 1983, Aarssen 1983, 1985, Ågren and Fagerström 1984, Keddy 1989). Minor environmental fluctuations might allow nearly equivalent species to persist indefinitely, or to result in indeterminate outcomes caused by largely stochastic factors.

In this context, it is interesting to note that the data set that showed the least asymmetry and the most intransitivity (Harper 1965) was comprised of different varieties of the same species. This suggests the following hypothesis: the degree to which a competitive network displays transitive asymmetric competition should be related to the degree of similarity of the morphologies and physiologies of the component species. The degree of transitivity might be measured by the difference between observed and expected numbers of paths of different lengths. The degree of similarity must remain unoperational until we know which plant traits best correlate with competitive ability, but an initial attempt might include such variables as height, total biomass or other attributes implicated in the occupancy of space. If this hypothesis is shown to be true, there may well be systematic variation in the degree of asymmetry and transitivity in competitive networks during secondary succession.

#### Reversals of rank order

It is not yet known whether reversals of rank order in competitive abilities are common, and, if so, how sensitive such reversals are to changes in the environment. Certainly, the hypothesis put forward above suggests that some communities will be more hierarchical than others. The data provided by Harper (1965) show that reversals did occur in his group of morphologically similar varieties of the same species, and Jacquard (1968) mentions that, although the competitive hierarchy was relatively stable between years, there were some in-

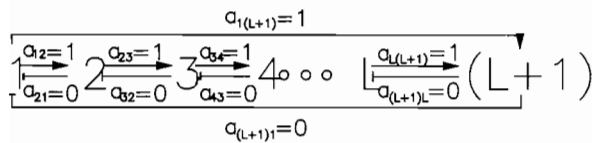


Fig. 3. Shown is a transitive path of length  $L$  going from species 1 (the competitive dominant) to species  $M$  (the competitive subordinate). For this to occur, there must be  $(L + 1)$  elements of the binary matrix equal to 1 and  $(L + 1)$  elements equal to 0.

stances of reversals between species. There are currently two viewpoints in the literature about how competitive abilities change with different resource levels. Grime (1979) argues that in stressful sites (i.e. sites with low productivity), competitors are not excluded by the “stress tolerators” that normally occupy such sites, but by an inability to tolerate the physical conditions of the environment. In contrast, Tilman (1982) contends that those species which occupy stressful sites do so by excluding those species that would be better competitors at more fertile sites. Rank reversals would be more common in the latter than in the former but if such rank order reversals vary systematically with plant morphology and environmental conditions, as hypothesized by Tilman (1982), then competitive outcomes in multispecies assemblages might still be predictable. It is clear that such differences in opinion about how competition changes along gradients is fundamental to our understanding of plant community structure and also well suited to experimental study.

In conclusion, we propose that asymmetric transitive competitive networks are common in herbaceous plant communities. There are two important consequences of this: first, it provides a conceptual framework which allows us to move towards a predictive approach to plant competition, and second, it provides a set of useful and testable assumptions which can be objectively resolved by experimental studies.

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## Appendix

To determine whether an empirically derived competitive matrix is unusual, and therefore whether we should place any importance on the structure it possesses, we must compare it with a matrix which we know to possess no unusual structure. In other words, we require a null model.

If there was a systematic tendency for either asymmetric or symmetric competition to occur, then the probability that  $a_{ij} = 1$  would not be independent of the

probability that  $a_{ji} = 0$ . Since the presence of these types of interactions is precisely the hypothesis that we want to test, the appropriate null hypothesis is that the state of  $a_{ij}$  (0 or 1) is independent of the state of  $a_{ji}$ , for all  $i, j$ , such that  $i \neq j$ .

Discounting the diagonal elements of a binary matrix  $A$ , which are not used in the determination of paths, there are  $N = S(S-1)$  elements, where  $S$  is the number of species which compose the matrix. The best estimate of the probability that  $a_{ij} = 1$ , denoted by  $\theta$ , is

$$\theta = \sum_i \sum_j a_{ij}/N; \quad (1)$$

for all  $i, j$ , such that  $i \neq j$ .

Since there are a total of

$$T(L) = \binom{S}{L+1} \quad (2)$$

possible paths of length  $L$  in an  $S \times S$  binary matrix, there are

$$\binom{T(L)}{X} \quad (3)$$

ways of choosing  $X$  paths of length  $L$ . Under the null hypothesis, the probability of obtaining at least  $m(L)$  paths of length  $L$  in such a matrix is

$$\sum_{x=m(L)}^{T(L)} \binom{T(L)}{x} p^x q^{(T(L)-x)} \quad (4)$$

This, of course, is a binomial distribution with a probability of “success”,  $p$ , ( $q = 1-p$ ) equal to

$$\begin{cases} p = 2 \cdot \theta \cdot (1-\theta) & \text{if } L=1, \text{ i.e. pairwise asymmetry} \\ p = 2 \cdot (\theta(1-\theta))^{(L+1)} & \text{if } L > 1 \end{cases} \quad (5)$$

and with a mean and variance equal to

$$\begin{aligned} \mu(L) &= T(L) \cdot p \\ \sigma^2(L) &= T(L) \cdot p \cdot q. \end{aligned} \quad (6)$$

To see this, consider Fig. 3. For such a path to exist, we require that  $(L + 1)$  elements equal 1 ( $a_{12}, a_{23}, \dots, a_{(L)(L+1)}, a_{1(L+1)}$ ) and that  $(L - 1)$  elements equal 0 ( $a_{21}, a_{32}, \dots, a_{(L+1)L}, a_{(L+1)1}$ ). Thus, the probability of obtaining this particular path is  $(\theta(1-\theta))^{(L+1)}$ . However, given the sequence of species  $(1, 2, \dots, L)$ , a transitive path can exist in two directions, from species 1 to  $L$  or from species  $L$  to 1. Therefore, the probability that this sequence of species would show a transitive path of length  $L$  is  $2 \cdot (\theta(1-\theta))^{(L+1)}$ .

For small matrices the probabilities can be obtained from tables of the binomial distribution. For larger matrices, one can refer to the normal distribution if the variance is at least 3, or the Poisson distribution, if the probability of "success" is less than 0.1 and the mean is less than 5 (Sokal and Rohlf 1981).

A FORTRAN 77 program to determine the number of transitive paths of lengths up to 12, and the probability of the observed number of paths occurring under the null hypothesis, is available from the second author.

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