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COMPETITION AND COMPLEX INTERACTIONS AMONG SPECIES: COMMUNITY STRUCTURE IN AN EARLY OLD-FIELD PLANT COMMUNITY

By

Thomas Edward Miller

A DISSERTATION

Submitted to Michigan State University
in partial fulfillment of the requirements
for the degree of

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and
Department of Zoology

1985

"Sum hic et potam cervisiam"

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ABSTRACT

COMPETITION AND COMPLEX INTERACTIONS AMONG SPECIES: COMMUNITY STRUCTURE IN AN EARLY OLD-FIELD PLANT COMMUNITY

By

Thomas Edward Miller

Experimental studies of interactions among five plant species in a first-year old field in southwestern Michigan were conducted to determine the relative importance of direct (intraspecific, interspecific) and complex (indirect, higher-order) interactions in determining the community structure. The five species were grown in all possible one-, two-, four-, and five- species combinations across a range of densities. There was a consistent hierarchy of competitive ability among the five species. _Ambrosia artemisiifolia_ had the greatest competitive effect on other species and demonstrated the least competitive response to the presence of other species. _Ambrosia_ was followed in the hierarchy by _Agropyron repens_ > _Plantago lanceolata_ > _Lepidium campestre_ = _Trifolium repens_ = _Chenopodium album_. This hierarchy was established by midsummer and was consistent in both years of the study and in all different species mixtures.

Most species had a non-linear response to increases in the abundance of competitors, with the competitive effect of adding competitors gradually approaching zero. The results also suggest that there was a general per-amount equivalence of competitive effects among the species. There were no differences among associate species in the competitive effects on a single focal species at any particular yield (biomass/m^2).

A method was developed to predict the separate direct, indirect, and higher-order components of the total effect of one species on another in the full community. The direct effects were always detrimental and often quite large. The indirect effects were very small or zero, and facilitative, acting against the direct effects. The higher-order effects were important for the competitively subordinate species; the competitive effect of a dominant species on a subordinate species was always a function of both the yield of the dominant species and the yield of still other species in the community.

Thus, the plant community studied is structured by hierarchical, asymmetric competitive effects. The growth of the dominant species, *Ambrosia,* is restricted by strong intraspecific effects. The species of intermediate competitive ability, *Agropyron*, is restricted by both intra- and interspecific effects. The competitively subordinate species, *Plantago*, *Lepidium*, *Trifolium*, and *Chenopodium*, are restricted by interspecific and higher-order effects.

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Chapter 1

INTRODUCTION

Each species in a multispecies community is affected by many different forces, through interactions with other species in the community and with the abiotic environment. The goal of community ecology is to understand this complex set of interactions affecting each species in the community; that is, to understand what determines the "structure" of the community. Community structure is the pattern of spatial and temporal abundance of species in a community as well as the pattern of resource allocation among the species (Cody and Diamond 1975).

Attempting to understand how all the various interactions between different species and between species and their resources affect or define the community structure has proven to be very difficult. Because of this, the field of community ecology has been perceived as being poorly focused (MacFadyen 1975, Smith 1975, McIntosh 1976, 1980a) or, more kindly put, a field "still in its infancy" (Pianka 1983). Much of the difficulty is caused by the fact that there is no standard protocol for investigating communities (Inger and Colwell 1977). Investigators have attempted many different and often disparate ways of understanding community dynamics and structure. This has caused confusion when different studies are compared.

There have been two primary causes of division in community ecology: the level of organization at which to begin understanding community structure (reductionism vs. holism) and the choice of aggregate variables or "currencies" to use (energy or whole organisms). The currency question actually separates ecology into two relatively nonoverlapping fields, ecosystem ecology and population-based community ecology. Ecosystem ecology views communities in terms of their trophic organization and the movement of energy or materials through the ecosystem (see Odum 1983). In general, ecosystem ecology stresses a holistic approach, addressing questions at the community or trophic level. A common theme running through this work is that the community has emergent characteristics, and that one cannot investigate communities as being the "sum of their parts" (Lane et al. 1975, Innis 1976, O'Neill 1976, Patten 1976). A more recent offshoot of ecosystem studies, systems ecology, takes an ultra-reductionist view that communities can be viewed as highly complex systems of interlocking cause-effect pathways (Watt 1966, Patten 1982, Odum 1983). The operational basis for systems ecology includes the use of sophisticated computer simulation modeling of complex systems (Watt 1966).

Ecosystem approaches have been very useful for understanding the processing and flow of energy and associated nutrients through communities. However, because this approach views individual organisms only as filters through which energy or materials must pass, it largely ignores the diversity and characteristics of component species. This severely limits the ecosystem approach when addressing questions or drawing on knowledge at the organismal and population level.

Population-based approaches to community structure use populations and individual organisms as the currencies of study and again, there are both holist and reductionist approaches. The holistic approaches use patterns of species number and abundance to infer causality about the forces structuring communities. For example, species rank - species abundance relationships have been noted to resemble particular statistical distributions (Motomura 1932, Fisher et al. 1943, Preston 1948, MacArthur 1957). The different forms of this relationship (log normal, broken-stick, etc.) have strong implications about the mechanisms of species interactions operating in each community (see Hutchinson 1977). Another holistic approach that has been somewhat successful in describing community patterns is island biogeography (MacArthur and Wilson 1963, 1967). This theory predicts the numbers of species on local "islands" based on the expected rate of species migration to the island and species extinction rates and has been a useful conceptual framework for investigating patterns of species diversity (see Simberloff and Wilson 1970, Brown 1978, Gilbert 1980).

The population-based holistic approach has been useful in suggesting what underlying mechanisms may be important in structuring communities. These holistic approaches are generally nonexperimental, but are often useful for developing hypotheses by finding correlations between patterns and probable mechanisms. Tests of the mechanisms often require an experimental reductionist approach. However, like ecosystem ecology, this approach often assumes that communities have hidden emergent properties or are too complex to understand by "building-up" from the interrelationships between individuals or populations (McIntosh 1980a, 1980b, Brown 1981, Simberloff 1982). Because of this, such studies still fail to directly address questions about the abundance and characteristics of individuals or species.

Population-based reductionist approaches assume that whole communities must in some way be a sum of their parts and so that complex dynamics can be predicted with a thorough knowledge of the dynamics of the contained populations and abiotic influences. The advantage of this approach is that the currencies of study are the individuals of each species. So, this general approach can be used to address questions that deal with the biological characteristics of individuals, such as in evolution, genetics, behavior, etc.

The difficulty of the reductionist approach is that the numerous inter- and intraspecific forces simultaneously operating in a multispecies community can yield a very tangled plexus of species interactions. It has become apparent not only that there are many forces operating directly between individuals or populations in a mixed community, but that there are often interactions between these forces. This complexity has been long perceived to be the major obstacle of this type of approach (Haeckel 1891), an obstacle that some ecologists feel to be impossible to overcome (Lane et al. 1975, Brown 1981).

The different types of forces that potentially limit the success of an individual species may either be single forces acting directly on the population or they may involve an interaction of two or more forces. These forces may also be biotic or abiotic; however, in this dissertation I will generally only discuss biotic forces. The direct forces, including competition, predation, and facilitation, I will define as simple effects. The effects caused by interactions between these simple effects have been given many different names in the literature but have been most commonly called indirect effects or higher-order interactions. I will define the interactions between simple forces as complex effects.

There are four distinct ways in which an associate species can affect the growth of a focal or subject species, based on whether they include simple or complex effects and whether or not they include an intraspecific effect (see Figure 1.1). Each of these effects can be defined by a unique mathematical term that quantifies the effect of an associate on a focal species and it may a power or exponential term. No attempt should be made to ascribe any biological cause or mechanism to each type of effect, because different biological mechanisms may be described by very similar mathematical terms.

Simple Effects

1. Simple Intraspecific - any effect of individuals on the performance of conspecifics (Figure 1.1a). Mathematically this is incorporated as a term that defines the effect of the abundance of a focal species 1 (N_1), and only species 1, on the success of species 1 (e.g. cN_1^p, where c and p are constants).
2. Simple Interspecific - the separate effects of associate species in an mixture on a focal species (Figure 1.1b). Mathematically, this is a term defining the effect of the abundance of an associate, species 2 (N_2), and only species 2, on the success of the focal species 1 (e.g. cN_2^p).

Complex Effects

3. Complex Intraspecific - the net result of the abundance of an associate species on the intraspecific effect of a focal species on itself. Complex intraspecific effects can be due to two different "pathways": the abundance of the associate species can affect the abundance of the focal species (a simple interspecific effect in combination with a simple intraspecific effect; Figure 1.1c) or the associate species can affect the way in which the

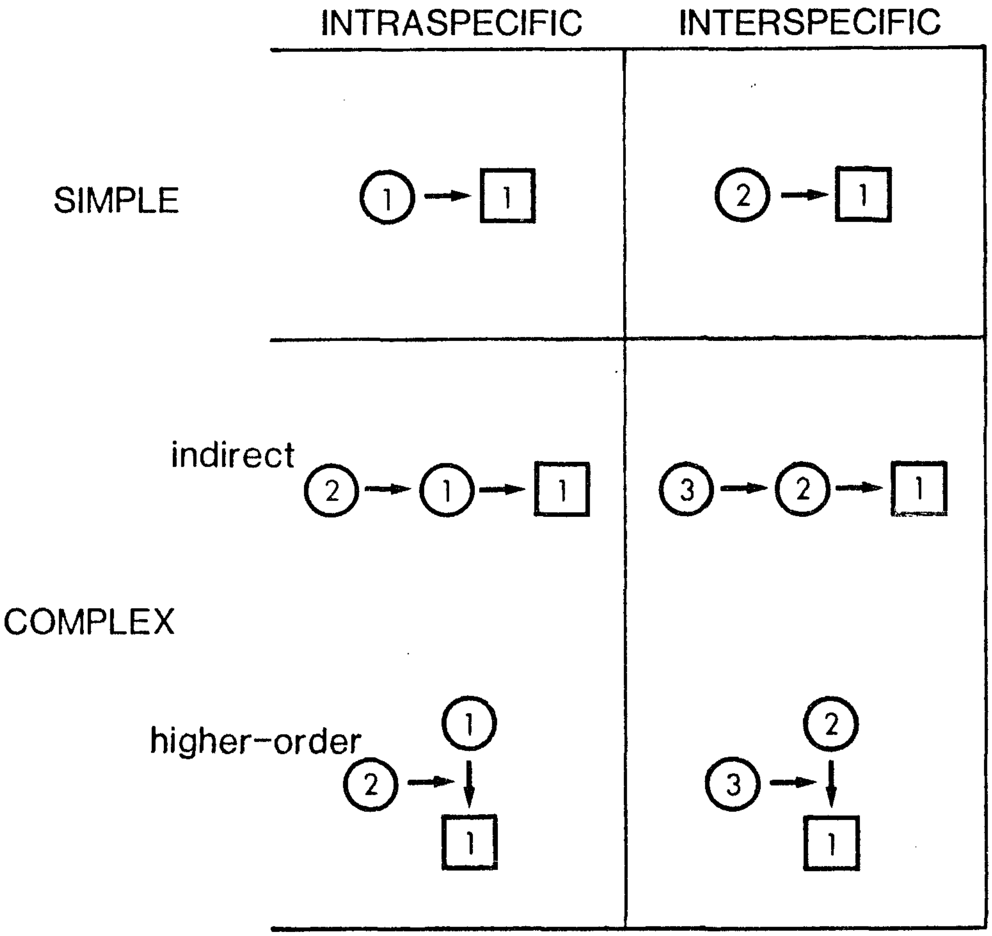


Figure 1.1. The different types of species interactions that can potentially restrict the growth of a species. The circles represent the species producting the effect (associate species); the squares represent the species receiving the net effect (focal species). The arrows indicate the direction of the effect, pointing from the associate species to the focal species

focal species affects itself without directly affecting the abundance of the focal species (Figure 1.1e). Neither of these effects have been generally discussed previously, but both can be represented mathematically by a term which includes the abundance of the associate species and the abundance of the focal species (e.g. the effect of $c(N_1N_2)^p$ on the success of species 1).

4. Complex Interspecific - the net result of the abundance of an associate species on the interspecific effect of a second associate species on a focal species. Complex interspecific effects can come about through at least two different pathways. (a) The abundance of the first associate species (N_3) can affect the abundance of the second associate (N_2), thereby changing the magnitude of the simple interspecific effect of the second associate species on the focal species (Figure 1.1d). Generally this has been referred to as an <u>indirect effect</u> of the first associate species (N_3) on the focal species (N_1). (b) Alternatively, the abundance of the first associate species (N_3) can affect the mechanism of interaction between the second associate species and the focal species: this has been referred to as a <u>higher-order interaction</u> (Figure 1.1f). Either way, the effect can be mathematically represented by a term which includes the abundance of both associate species (e.g. effect of $c(N_2N_3)^p$ on the success of species 1, N_1)

While the simple effects of competition, predation, and facilitation have been well studied, very little is known about the importance of complex effects in community structure. One approach to understanding complex effects has been to view simple interactions as loops representing cause-effect pathways between species or connecting a species with itself (see Levins 1975). A complex effect is represented by the combined effect of two or more connected loops. Using this representation, two simple arguments suggest that, in general, complex effects should be important. First, if two loops having a species in common are both strong (e.g. the effect of species A on species B and the effect of species B on species C), then it seems that the effect of the first loop must be known to determine the importance the second loop. That is, there will be a strong indirect effect of species A on species C. Secondly, while there can only be a single direct loop between species, there can be a very large number of potential complex loops.

The total number of possible complex loops is an exponential function of the number of species in the community. Even if on average the complex loops are not as strong as the direct loops, it would seem that the sum of their effect may be quite strong. In part for these reasons, it has recently been suggested by several ecologists that complex effects may be both important and common (Lawlor 1979, Abrams 1983, Schaffer 1981, Bender et al. 1984).

The general purpose of this dissertation is to investigate the presence and importance of complex effects in a natural multispecies system. A weedy plant community was selected for study because (1) the species under consideration all grow relatively rapidly, leading to rapid dynamics of interaction, (2) it was known from pilot studies that the simple interactions in the community can be quite strong, and (3) pilot studies had also shown that the simple interactions between species were all competitive, which restricts all of the complex effects to interactions between competitive effects. These characteristics suggest that this community would be a good system in which to investigate the effects of complex interactions.

Specifically, this dissertation consists of a field experiment designed to (1) quantify the effect of competition in a first-year old-field plant community, (2) quantify the potential simple competitive and complex effects in the community using monocultures and two-species mixtures, and (3) determine the presence and relative importance of complex species interactions among a group of five competitors in a natural community. These three objectives are presented in chapters 3, 4, and 5, respectively.

Previous Studies on Complex Effects

Several theoretical studies have suggested that complex effects may be very important in communities. Abrams (1980a, 1983) has noted that non-linearities in intraspecific terms will require that there also be interspecific higher-order interactions. Several other authors have pointed out that it is reasonable to expect to find complex effects in biological systems (Smith-Gill and Gill 1978, Ayala et al. 1973). Most theoretical studies on indirect effects have assumed stable, equilibrium communities and completely linear, additive species effects (i.e. no higher-order effects; Levine 1976, Lawlor 1979, Schaffer 1981). Nevertheless, given these restrictive assumptions, these studies have indicated that indirect interactions may be very strong relative to simple intra- and interspecific forces and that serious errors may occur from not considering the indirect higher-order processes in communities (see also Bender et al. 1984).

Most of the experimental work on complex interactions has focused on the role of predation in controlling species diversity. One effect found in many communities is the effect of a "keystone" predator which feeds on competitively dominant prey, and thus allows the persistence of other prey that might otherwise be competitively excluded (Paine 1966, Harper 1969, Paine and Vadas 1969, Dayton 1971, Menge 1976, Lubchenco 1978, Lubchenco and Menge 1978, Estes et al. 1978, Duggins 1980, Jara and Moreno 1984). This is an interspecific indirect effect of the predator on the subordinate prey. Another effect is "vaulting" where a predator allows the existence of a second predator by preventing a competitively dominant prey species from excluding the prey species of the second predator (Dodson 1970, Vandermeer 1980, Kerfoot and deMott 1983). Predators have also been suggested as being the intermediate species in interspecific indirect effects between prey species ("apparent competition", Holt 1977).

Complex interactions in communities without predation have been little studied. In plant communities, the simple intra- and interspecific effects are generally competitive and so the complex effects would result from interactions between competitive forces. If there is no herbivory, this has some very interesting implications because the simplest indirect interactions should be facilitative, acting against the simple competitive interactions. This facilitation is the outcome of two negative (competitive) interactions acting in sequence. If these facilitative indirect interactions are strong, then we need to change our view that the interactions in communities of competitors are solely antagonistic.

There have only been a handful of experimental studies which have attempted to determine if complex effects within a trophic level, i.e. between competitors without predation, can be predicted using a knowledge of the simple intra- and interspecific interactions. Probably the first attempt was the work done with protozoans by Vandermeer (1969). His work provides a good example of the difficulties and controversies involved in this type of experiment. Vandermeer cultured each of four species of protozoans alone and in all possible pairs to estimate growth rates using the logistic equation and linear Lotka-Volterra competition equations. He used the parameter values obtained to predict the success of each species in four species mixtures. By comparing these predictions with actual results from mixtures, he concluded that the linear equations that did not include complex terms were sufficient to predict the result of multispecies interactions. His conclusion should not have been unexpected. The actual four-species competition resulted in the extinction of two of the species. The behavior of the two-species mixture can be described by linear equations because the final two-species mixture has a low potential for complex intraspecific interactions and no potential for complex interspecific interactions. There has been some controversy over the interpretation of his results (Brenchley 1979, 1981, Thomas and Pomerantz 1981, Vandermeer 1981). The conclusion of this controversy is that only simple effects were necessary to predict the final outcome of the four-species competition (Thomas and Pomerantz 1981), but that there is some indication from the data that higher-order interactions were important in determining the species abundances before extinctions occurred (Brenchley 1981).

A similar experiment was performed by Richmond et al. (1975) using Drosophila species to "search for emergent competitive phenomena". They constructed laboratory cultures of one, two, and three species in all possible combinations and also found no evidence of direct or indirect higher-order interactions. Their analysis and interpretation suffer from a flaw similar to that in Vandermeer's work: the three-species experiments always resulted in the extinction of at least one species. So the correct interpretation of their work is that it is not necessary to include complex interactions to determine the final competition-induced extinction, but it does not exclude the possibility that complex interactions may have been very important in determining the time to extinction or the final species abundances.

Two early experimental studies claimed to find evidence of higher-order interactions in multispecies systems. Neill (1974) calculated linear competition coefficients from laboratory experiments using various mixtures of four species of algae. He was able to demonstrate that the coefficient between any pair of species changed depending upon the identity of other species present, which he interpreted as being the effect of complex interactions. Wilbur (1972) experimentally manipulated the densities of three species of salamanders in pond enclosures. He found that the various measures of competitive effect were all dependent on the presence and densities of still other species which he also interpreted as evidence for higher-order interactions. However, both Neill and Wilbur used an analysis which assumed that the intraspecific effects were linear with species density (Pomerantz 1981). It is not possible to discern whether their results were caused by higher-order effects or just nonlinear intraspecific effects or both (see also comments on stability of the matrices used in Neill's analysis, Pomerantz 1981).

Seifert and Seifert (1976, 1979) used multiple linear regression analysis to quantify species interactions in insect communities found in Heliconia flowers. The regression method yielded equations that predicted the abundance of each of four species, using the abundances of the remaining species as independent variables. The studies suggested that the competitive interactions between species generally had very little impact on species abundances. In the second study, Seifert and Seifert (1979) also attempted a very simple test to determine the importance of any type of complex interaction by testing the significance of including a single higher-order term ($N_1N_2N_3$) in the regression analysis. The term was significant in one out of the four possible cases. However, in both studies, the predicted equilibrium densities for each species were quite different from those densities actually found in undisturbed flowers. This indicates that the proposed models were not sufficient to explain the species dynamics, because either the communities tested were not at equilibrium or the models failed to incorporate the effects of other important factors (e.g. predation or complex effects).

Davidson (1980) quantified species interactions among several species of harvester ants. She used the resource overlaps of sizes and types of seeds used by the ants as estimates of competition coefficients (simple interspecific effects) and constructed an estimated community matrix for six species of ants. By using matrix inversion, she obtained a second matrix whose entities gamma_{ij} gave a measure of the total (simple interspecific + complex interspecific) effect of species j on species i (see Levine 1976, Lawlor 1979 for discussions of this method). Davidson used the gamma matrix to successfully predict the positive and negative correlations in abundances between the ant species. To use this method, she had to make the poor assumption that resource-overlap was a good measure of potential direct competitive effects (see Culver 1973, Seifert and Seifert 1976, Abrams 1980b, Aarrson 1983). Also, the Levine matrix inversion method makes certain untested assumptions about the form of the higher-order effects (see Lawlor 1979). However, it is difficult to criticize a successful use of the method. Davidson was able to correctly predict the abundances of various species of ants using the matrix method. Because the initial community matrix (containing estimated direct effects) was very different from the inverted matrix (containing total effects), the Davidson study also suggests that this community structure is strongly influenced by complex effects. Unfortunately, Davidson did not discuss or investigate these differences and so it remains unknown what type of complex effects may have been involved.

Another experiment providing experimental evidence for higher-order effects is the work of Case and Bender (1981). The authors present a method for investigating the presence of higher-order effects and provide an example of the method using laboratory mixtures of three species of hydra. They found significant higher-order effects in three out of six possible cases. Their method only detects the presence of complex higher-order effects; it may not be useful in determining what species are involved or in quantifying the importance of the complex effects.

Competition and Complex Interactions in Plant Communities

A great deal is known about effects of density in monocultures and in certain types of two-species cultures from a vast number of agricultural studies (see Harper 1977). However, almost nothing is known about the actual mechanisms of interaction between individual plants, very little is known about species interactions in natural plant communities, and virtually nothing is known about complex interactions in either the greenhouse or field.

All plants have very similar resource needs, each individual requiring light, water, and a limited number of crucial nutrients. The uptake and use of these resources occurs at the molecular level, making it very difficult to quantify. There are strong interactions among these resources; for example, the uptake rates of most soil nutrients are affected by the soil moisture level. While there are many studies that measure individual responses to different resource levels (see Harper 1977), I can find only three studies that measure how individual species affect local resource availability (Williams 1963, Fonteyn and Mahall 1978, Foster et al. 1980). Even these types of studies provide only circumstantial evidence for a particular mechanism of interaction by correlating a level of resource availability with a particular species response. Clearly, we need to know more about the actual mechanisms of interaction between plants (see also Tilman 1982), which will probably require more of a physiological approach to individual interactions. Meanwhile, we can still address other questions dealing with the results of interactions in natural communities and the mode of interaction (e.g. intraspecific, interspecific, simple, complex, etc.).

Many competition experiments using two species have been performed and it is tempting to extend knowledge of competitive interactions obtained from these studies to multispecies systems. These studies have been very useful in demonstrating the potential for competitive interactions by exploring density effects (intraspecific interactions) and interspecific interactions in the simplest types of communities. However, these two-species studies do not include most of the complex effects that may be operating in multispecies systems. Also, most one- and two-species studies were done under artificial environmental conditions and often at densities that are very different from those found in natural environments (see reviews in Trenbath 1974, Harper 1977). To explore the importance of complex effects, the experiments must be performed in multispecies assemblages and, ideally, in natural communities.

Competition in natural plant communities has been investigated several different ways, each of which reveal different types of information. First, the complete removal of neighbors about an individual of a focal species allows a comparison of the growth of individuals in the full community with growth when completely isolated. It provides an estimate of the total effect of all competitors, both con- and heterospecific, on the growth of individuals (e.g. Putwain and Harper 1970, Raynal and Bazzaz 1975). But total removal experiments do not measure how much of the competitive reduction in the focal species is caused by each of the different associate species. A second type of experiment involves the removal of all species except the focal species, which may be maintained at different densities and thus provide information about the intensity of intraspecific interactions. A third type of experiment involves the removal of a subset of the species in the community and measuring the subsequent response of remaining individuals or populations (e.g. Sagar and Harper 1961, Pinder 1975, Gross 1980, Hils and Vankat 1982). These experiments are very difficult to interpret because they do not reveal which species of the removed group are most strongly interacting with the focal species and because changes in unidentified complex interactions can affect the response of the focal species. A fourth type of experiment measures the response of individuals or populations to the removal (or addition) of a single species, defined as "press" experiments by Bender et al. (1984). Press experiments provide a measure of the total interspecific effect (simple interspecific + complex intra- and interspecific effects) of the removed or added species on each of the remaining focal species. Examples of the use of press experiments include understanding the role of dominant species in communities by measuring the response of the remaining species to the removal of the dominant (e.g. Friedman, et al. 1977, Abdul-Fatih and Bazzaz 1979) and determining the factors limiting colonization success of species (Werner 1977). A more interesting use of this experimental technique is to perform a series of experiments removing each species of the community singly (Fowler 1981, Silander and Antonovics 1982). The results provide a measure of the total intensity of interaction between each pair of species in the community; again, measuring total effects does not allow a separation of effects into simple interspecific and complex components (see Bender et al. 1984).

None of the above methods alone has the potential to investigate both the simple and the various complex species interactions potentially important in natural communities. Each method quantifies one or some combination of the four types of interactions (simple intra- and interspecific and complex intra- and interspecific) but no method provides a measure of either of the complex interactions individually. This suggests that a study must incorporate several different experimental methods and use a comparison of the results to quantify the different types of interactions.

I have found only three plant community studies that have used this multipartite approach to understand community structure. Haizel and Harper (1973) investigated the interactions between two weed species, white mustard and wild oats, and the effects of these weeds on the crop barley. By growing the three species in various combinations, the authors determined that the effects of the two weeds on the crop were not additive and suggested that "synergistic" effects occurred between the two weed species. They found situations in which the mixture of two competitors produced less of a reduction of a focal species than the sum of their independent actions (mustard and wild oats on barley). They also found combinations of competitors that produced more of a reduction in the success of a focal species than the sum of their independent effects (barley and wild oats on mustard). Both of these results appear to be caused by complex effects; however, the researchers were unable to separate the effects further into indirect or higher-order interactions.

Fowler (1982) used greenhouse studies to investigate competitive interactions between five herbaceous species that she had previously investigated in natural communities (Fowler and Antonovics 1981, Fowler 1981). She grew each species alone and in all the possible pairs and three-species mixtures. She used the data from the mono- and bi-cultures to generate two different predictions of the success of each species in the three species mixtures. The first prediction used deWit competition equations (deWit 1960, Bauemer and de Wit 1968) which predict the success of the focal species as a function of the density of each species in the mixture and an implicit interspecific higher-order interaction term. The second prediction used a simple proportional model of species interaction developed by Fowler that predicted the success of the focal species as a function of only the densities of the component species of the mixture (no complex term). Both models provided a good estimate of the success of each species in mixtures, with both predictions explaining approximately 90% of the actual observed variance of focal species success. The author did not investigate the cases in which the two models yielded very different predictions nor did she discuss the implications of having two alternate models yield similar results.

Ismail (1983) investigated interference between _Lolium perenne_, _Dactylis glomerata_, and _Plantago lanceolata_ using pure and mixed stands of the three species at two different total densities. The data from all mixtures was described adequately by de Wit equations, which include an implicit direct higher-order term. No attempt was made to investigate indirect pathways or to separately measure higher-order effects from the simple effects.

What are the deficiencies of previous studies that investigated complex interactions among competitors? Of all the animal and plant studies, only four have sufficiently tested for the influence of complex effects among competitors (Haizel and Harper 1973, Davidson 1980, Case and Bender 1981, Fowler 1982). Out of these four studies, three found evidence for some form of complex effects, and the fourth (Fowler 1982) gave ambiguous results. None of these studies has separately measured complex indirect or higher-order effects between competitors (although five of the studies reviewed earlier interpreted their results as being evidence for indirect effects). And while the number and possible importance of indirect loops increases with species number, only one of these studies included more than three species in mixtures. Finally, only one of the four studies was conducted in a natural community (Davidson) and this study was non-experimental.

I conclude that community ecology has neglected a potentially very important group of interactive forces that probably do occur in multispecies communities. This neglect is primarily due to the extreme difficulty in obtaining conclusive experimental evidence of complex interactions in communities. I suggest that complex effects may be the primary cause of so-called "emergent properties" in communities and that we must understand their importance to understand community structure.

Thesis Organization

This thesis investigates the simple and complex interactions that occur among species found in a first-year old-field plant community. This first chapter has provided an introduction to the general problems and questions, definitions of critical terms, and a review of the pertinent literature. Chapter 2 provides descriptions of the species and the general field methods used in the two years of the study. In Chapter 3, the potential for direct, simple competitive interactions are given from the results of two years of field experiments involving all the possible monocultures and two-species mixtures. In Chapter 4, the nature of the simple competitive interactions between species is presented using monocultures and two-species mixtures maintained at a range of densities of the component species. The experiments were designed to study the effects of increasing competition from both conspecifics and other species on the growth of individuals. Chapter 5 presents the results of all the possible four-species mixtures and the five species mixtures from both years of the study. The data are used to construct a model that describes the mean success of individuals of each species as a function of the total combined yield of all other species in the community. This model is then used to estimate the direct, indirect, and higher-order interactions occurring between the species in the five-species community. Chapter 6 summarizes the conclusions of the preceeding chapters and discusses their implications for further study on the roles of simple and complex pathways of interaction in structuring plant communities.

Chapter 2

EXPERIMENTAL METHODS

Field Site

The plant community studied was in a recently plowed area of Bailey Yard, located at the W. K. Kellogg Biological Station in Kalamazoo County, Michigan. Bailey Yard has been used for the last 12+ years for ecological research and, previous to that, was used as a small garden plot and calf pen. Portions of the field are plowed on an annual, biennial, or quadrennial basis to maintain early successional species arrays. The soil is a sandy Kalamazoo loam that is relatively acid (pH - 5.9, % organic matter - 1.6, total N - .09 % dry wt., PO_4 - 14.8 ppm, K - 135.5 ppm). The portion of the field used in this study has been sprayed with the herbicide Round-Up in 1979, two years before the study began.

Plant Community

The community contains over thirty plant species, most of which contributed less than 1% to the total autumn biomass in the field. The large majority of these species are weedy annuals and short-lived perennials; however, the seedlings of occasional invading tree species are also found. A list of the most common species for the years 1981-1983 is given in Table 2.1.

Six species made up over 90% of the biomass during the period of the study. In each of the two years of the study, the interactions among five of these major species were investigated. Three species each made

TABLE 2.1. Species abundances in Bailey Yard for the years 1981-1983. Species densities and yields were measured in September of all three years. Yield in g/m^2 is above ground dry weight, where samples were dried at 65^o for 72 hours before weighing. Species densities and mean biomass were not determined for the rhizomatous grasses *Agropyron repens* and *Bromus inermis*.

	1981			1982			1983		
Species	Mean Wt.	g/m^2	#/m^2	Mean Wt.	g/m^2	#/m^2	Mean Wt.	g/m^2	#/m^2
Ambrosia artemisiifolia L.	1.03 g	80.28	77.2	1.53	137.17	89.8	1.60	140.55	88.0
Agropyron repens (L.) Beauv.	--	66.38	--	--	36.85	--	--	50.10	--
Plantago lanceolata L.	0.64	24.31	38.2	0.87	32.07	36.9	0.45	11.79	26.0
Chenopodium album L.	0.07	15.68	223.6	0.06	2.56	45.3	0.07	8.80	126.0
Trifolium repens L.	0.12	8.41	67.6	0.16	18.64	113.3	0.06	2.36	38.0
Lepidium campestre (L.) R. Br.	0.13	2.03	15.9	0.05	1.96	40.4	0.08	1.38	15.4
Achillea millifolium L.	1.52	1.21	0.8	0.03	0.04	1.3	.003	.006	2.0
Bromus inermis Leyss.	--	14.46	--	--	8.85	--	--	8.41	--
Daucus carota L.	0.28	2.86	10.3	0.19	4.93	26.2	0.17	2.04	12.0
Oxalis stricta L.	0.04	1.76	46.2	0.02	0.60	28.0	0.04	2.56	58.0
Panicum capillare L.	0.04	1.37	39.0	0.07	2.27	32.9	0.05	1.42	28.4
Polygonum convolvulus L.	0.15	1.28	8.8	0.05	0.25	5.3	0.08	0.16	2.0
Potentilla recta L.	0.03	1.37	51.7	0.03	3.69	120.9	0.02	3.94	176.0
Trifolium hybridum L.	0.41	8.71	21.4	0.19	1.74	9.3	0.20	1.31	6.5

up over 10% of the total biomass consistently each year (Ambrosia artemisiifolia, Agropyron repens, and Plantago lanceolata) while a fourth (Chenopodium album) was one of the most abundant species (numbers/m^2) in all three years abundances were monitored. The choice of the fifth species was different for the two years of the experimental portion of the study due to variation in the abundances of minor species in the field (1st year - Lepidium campestre, 2nd year - Trifolium repens). Ambrosia and Chenopodium are spring annuals, Lepidium is a winter annual, and Agropyron, Plantago, and Trifolium are perennials. Brief descriptions of each of these six species follow.

Ambrosia artemisiifolia L. (Compositae), common ragweed, was the biomass dominant in Bailey Yard in all three years of the study (Table 2.1). It is an annual often found in agricultural fields, open disturbed habitats, and along roadsides in Eastern North America (Bassett and Crompton 1975). Ambrosia is the only one of the six species investigated that is native to America. It is an upright herb often 1-1.5 m high with a short tap root. Individuals emerge from seed in late April, exhibit very rapid growth through May and June, and initiate flower buds in July. The species is wind pollinated and the male flowers produce copious amounts of yellow pollen. Female flowers produce a single rather large seed (3.5mm X 2.5mm), while individual plants produce anywhere from 2,000 to 60,000+ seeds per plant in August and September (Dickerson and Sweet 1971). The species reproduces only by seeds, which are generally dispersed near the adult (within 1m radius). The only importance of this species to humans appears to be detrimental. It is the major cause of hayfever in the eastern North America and areas of Europe as well as being a major crop weed.

Agropyron repens (L.) Beauv. (Poaceae), quackgrass, was the second most abundant species, in terms of biomass/m^2, in the study site (Table 2.1). It is a tenacious, spreading perennial grass, and a very common agricultural weed in North America. Quackgrass is native to Europe but is now circumpolar in distribution (Werner and Rioux 1977). It is commonly found in fallow land such as Bailey Yard, often in very dense stands that exclude the establishment of herbaceous dicotyledonous species (Werner 1977). Agropyron generally produces few seeds, reproducing primarily by vegetative cloning through rhizomes (Werner and Rioux 1977). In fact it was the only species in this study that emerged in the spring from rhizomes rather than completely from seed. The rhizomes initiate growth early in the spring, generally before the emergence of other species' seedlings. Agropyron repens can rapidly tie up soil nutrients and competes strongly with crops. However, it is also occasionally used as a forage or hay species.

Plantago lanceolata L. (Plantaginaceae), narrow-leaved plantain, was the third most abundant species in the Bailey Yard, making up 10-12% of the total biomass of the community in each of the three years of the study (Table 2.1). Plantago is a prostrate perennial found in pastures, lawns, abandoned fields, and along roadsides. It also is native to Europe but now circumpolar in distribution; some consider it to be one of the most common noncultivated species in the world (Cavers et al. 1980). Seedlings emerge in late April and adults consist of up to 100+ basal lanceolate leaves, each 3-40 cm long, forming a flat rosette. The first-year individuals observed in this study generally flowered if they reached a critical size of about .190 g. Plants may produce up to 50+ scapes with densely flowered spikes, usually in late

July or August. *Plantago* is gynodioecious and wind pollinated. Individuals can produce up to 10,000 seeds, though first-year individuals are generally not this productive. Seed dispersal is usually local (within 1 m of parent); however, dispersal by animals and as a contaminant of crop seed is well known (Cavers et al. 1980). This species is considered to be detrimental to agriculture, particularly in pastures and established legumes; however, it is also quite palatable to livestock and is often used as a pioneer species to stabilize soils.

Chenopodium album L. (Chenopodiaceae), lambsquarters, was one of the most numerous species in Bailey Yard in terms of numbers/m^2, but it did not contribute much to the total biomass of the community (Table 2.1). It is an erect annual which is a very common agricultural weed in all temperate areas of the world. The origin of *Chenopodium* is not known. It is considered to be a anthropophilic species found growing in association with other weeds in any open disturbed habitats (Bassett and Crompton 1978). Seedlings emerge in late April or May, had a rapid growth phase through June, initiate buds in July, and flower in August and September. *Chenopodium* produces perfect flowers and is self-compatible and wind pollinated. Individuals can potentially produce up to 100,000 seeds (Stevens 1932). Seed dispersal is usually local (within 1 m of parent), but the seeds are often dispersed by agricultural practices and remain viable for more than 40 years (Toole and Brown 1946). *Chenopodium album* is a problem weed in many crops, particularly in potato, sugar beet, corn, carrot, and soybean (Bassett and Crumpton 1978). It is also toxic to livestock due to concentrations of oxalic acid.

Lepidium campestre (L.) R. Br. (Brassicaceae), field cress, is an annual or occasional biennial common to winter-wheat, newly fallowed fields, and roadsides. The abundance of L. campestre in Bailey Yard fluctuated a great deal during the three years of the study (Table 2.1), never contributing more than 5% to the total biomass of the community. Like most North American weeds, it is native to Europe but has spread with certain agricultural species to now occur in most areas of temperate North America (Gleason and Cronquist 1963). Most seedlings emerge in April or early May and produce prostrate rosettes of basal oblanceolate leaves, 10-15 cm in length. When it flowers, individuals produce an upright stem, up to 60 cm in height, bearing flowers on dense racemes (Buchholtz et al. 1960). Seed dispersal appears to be local, but Lepidium seeds are known to comprise one of the major impurities of winter wheat. In my study plots no plants flowered, though rare individuals elsewhere in the field did flower and set seed, especially in the older, unplowed areas where two-year old individuals were present.

Trifolium repens L. (Fabaceae), white clover, is a low creeping perennial commonly planted in pastures and lawns. It also fluctuated in abundance and importance during the three years of the study (Table 2.1). While native to Europe, this species is now commonly found in North America, particularly in fallow fields and along roadsides (Gleason and Cronquist 1963). Seedlings emerge in late April and early May and, if they reach a sufficient size, flower in July or August. This is the only study species that attracts insect pollinators. Individuals on the study site were very reduced in size and only rarely flowered. In other areas of the field, individuals of Trifolium were much larger and appeared to be older.

General Approach

The analysis of species interactions requires observing the success of each species as a function of the abundance of each of the other species in various species mixtures. There are several special problems and assumptions with this type of approach. First, what is species success and how can it be measured? Ideally, success should be related to the reproductive fitness of individuals, i.e. the ability of individuals to contribute to future generations. However, in this study, I have only followed individuals of short-lived species for single growing seasons. It would be impossible to determine the ability of these individuals to contribute to future generations because of my inability to follow the fate of seeds in the seedbank. Instead, I have used individual plant biomass and survivorship to quantify the response of each species to the abundance of competitors. Obviously, plants must survive to adults to be able to successfully reproduce. Use of plant biomass assumes that larger plants ultimately produce more successful offspring than smaller plants. This assumption is supported by many studies that demonstrate that seed set is a straightforward function of plant biomass (see Harper 1977).

Second, what is a realistic measure of the abundance of competitors in each mixture? Many studies of species interactions, particularly studies on animal populations, used density of individuals as the abundance measure best related to the competitive effect of each species on itself and other. Plants demonstrate extremely plastic growth, with individuals of the same species in the same environment frequently being several orders of magnitude different in size. Thus, density may not accurately reflect the potential competitive effect of a population. In plants, biomass production of individuals is directly related to the uptake rate of the resource that limits growth. So, it has been suggested that the biomass or yield (dry weight biomass/m^2) of populations may be a better variable than density to use in measuring the effect or response of species in competition (Goldberg and Werner 1983, Spitters 1983a). In this study, I will generally use yield (dry weight biomass/m^2) as the measure of the abundance of competitor species.

The third problem is that most plant communities exhibit seasonal growth patterns, with annual plant communities such as the one used in this study being extreme examples. In April, Bailey Yard is a completely bare field, with the plant biomass all contained in either seeds or below-ground rhizomes (for Agropyron). The biomass of individuals in the community increases throughout the season until September. The data analyzed and discussed in this study are from estimated plant weights from midsummer and actual plant weights from plants harvested in September. So, to understand the interaction between any pair of species, I am correlating the final biomass of an associate species with the growth of individuals of a focal species that has accumulated over the whole season. This assumes that the competitive effect of the associate species is reflected by its final (or midsummer) biomass.

Field Experimental Design

Similar experimental designs were used in both 1982 and 1983, but several new treatments were included in 1983 and the two years differed in the number and size of replicates and in how the removals of Agropyron were performed. The basic design was the same in the two years and consisted of different combinations of five species, including each species alone, all possible paired combinations, all the four species combinations, the five species control, and the natural community control. The minor species were removed from all plots. The different treatments used in each year of the study are listed in Table 2.2. Only the design and general field methods are presented in this chapter; the methods of analysis are described in Chapters 3-5.

Field Design 1982 (Year 1) - In November of 1981, approximately 1/4 hectare of Bailey Yard was plowed to a depth of 20 cm. The same area was smoothed in March 1982 using a York rake. Sixty-nine 2 x 2 m quadrats were established in a level section of this area. Each quadrat was randomly assigned a single treatment and each treatment was replicated three times.

Removals of plants were performed by hand beginning in late April as spring growth began. Seedlings were removed by gently pulling up individuals. This removed the root, preventing regrowth, and did not significantly disturb the soil surface. The rhizomatous grasses (Agropyron repens and Bromus inermis) could not be removed this way due to potential extensive soil disturbance. These grasses were removed by continuous clipping at the soil surface throughout the growing season. Most culms did not resprout after two or three clippings. The quadrats were maintained throughout the summer to prevent re-invasion by undesired species.

On July 25, 10 plants of each species from the middle 1 m^2 of each quadrat were measured to estimate treatment effects. From previous

TABLE 2.2 Experimental design for experiments of 1982 and 1983 showing the species present in each treatment. + indicates the presence of the species in the treatment. (G = *Agropyron repens*, A = *Ambrosia artemisiifolia*, P = *Plantago lanceolata*, C = *Chenopodium album*, L = *Lepidium campestre*, T = *Trifolium repens*). Replicates are 1m x 1m plots in 1982 and .6m x .6m plots in 1983.

Treatment code	Species Present						Number of Replicates	
	G	A	P	C	L	T	1982	1983
G	+						3	15
A		+					2	18
P			+				3	18
C				+			2	18
L					+		2	--
T						+	--	18
GA	+	+					2	15
GP	+		+				2	15
GC	+			+			3	15
GL	+				+		2	--
GT	+					+	--	15
AP		+	+				3	15
AC		+		+			2	15
AL		+			+		2	--
AT		+				+	--	15
PC			+	+			3	15
PL			+		+		3	--
PT			+			+	--	15
CL				+	+		2	--
CT				+		+	--	15
GLP	+			+	+		2	--
GCP	+		+		+		2	--
GAC	+	+	+				3	--
-G		+	+	+	+(82)	+(83)	2	5
-A	+		+	+	+(82)	+(83)	2	5
-P	+	+		+	+(82)	+(83)	2	5
-C	+	+	+		+(82)	+(83)	3	5
-L(82)	+	+	+		+		3	--
-T(83)	+	+	+	+			--	5
Control	+	+	+	+	+(82)	+(83)	2	5

experience, different values were chosen for different species: for Ambrosia artemesiifolia and Chenopodium album height and length of longest leaf were measured, for Plantago lanceolata and Lepidium campestre number of leaves and length of longest leaf were measured. No satisfactory non-destructive measure of Agropyron repens abundance could be determined and so there are no mid-summer estimates for treatment effects of this species. At the same time, thirty individuals of each species from nearby non-experimental areas were also measured as above. The above-ground parts of these plants were then harvested, dried at 65^{o} for 72 hours, and weighed to obtain individual dry weights. Multiple regression analysis was used to determine morphology-biomass regressions (Table 2.3). The equations obtained were used to estimate the biomass of individuals in the experimental quadrats.

Autumn harvesting took place during the period from September 28 to October 10. Each individual plant from within the center 1 m^2 (leaving a border of .5 m) of each quadrat was clipped at ground level, pressed, and dried for 72 hr. at $65^{o}C$. Each individual plant was then weighed for above ground biomass. Subsamples of roots of ten individuals of each species in each quadrat were also harvested, washed thoroughly in tap water, pressed, dried, and weighed. The reproductive state of each individual was also noted.

By midsummer, when vegetation was developed, it became obvious that vegetation in the north end of the study area was quite different than the rest. This area had not been plowed in the four years previous to the autumn of 1981, whereas the majority of the study area had been plowed for each of the four years previous to initiation of the study. Plants in this area tended to be larger and included several perennial

Table 2.3. Equations used to estimate the biomass of individuals of each species using morphological measures. The equations were determined using regression analysis of thirty individuals of each species harvesting near the experimental plots in July of both years. 111 = length of longest leaf, 11b = length of longest branch.

	Regression Equation	R^2
Year 1, 1982		
Ambrosia	log(weight) = -1.237 + .019(height)	.84
Plantago	log(weight) = -0.975 + .163(stem diameter)	.89
Lepidium	log(weight) = -1.278 + .047(# leaves)	.85
Chenopodium	log(weight) = -1.387 + .026(height)	.89
Year 2, 1983		
Ambrosia	log(weight) = -1.260 + .020(height) + .068(111)	.88
Plantago	log(weight) = -1.111 + .035(# leaves) + .028(111)	.70
Trifolium	log(weight) = -1.711 + .200(# branches) + .039(11b)	.75
Chenopodium	log(weight) = -2.353 + .433(111)	.90

species not found in the rest of the study area (including *Solidago canadensis* from a previous experiment). Because of these apparent differences, all plots located in this north end area were excluded from the analysis. This resulted in only two of the original three replicates being available for many of the different treatments for Year 1.

Field Design 1983 - Bailey Field in 1983 was prepared as in 1982. Care was taken to place all quadrats within an area of the field that had a single plowing history. The design was also changed to increase both the number of different types of treatments and to increase the number of replicate quadrats for each treatment (Table 2.2). Two-hundred and eighty 1.3 x 1.3 m plots were established in early April 1983, grouped into five blocks. Within blocks, each treatment was randomly assigned to a single plot. Again, removal treatments of plants were performed beginning in late April. Seedlings were removed by hand as before. To eliminate the large amount of work involved with clipping the rhizomatous grasses, the contact herbicide 'Round-up' (the isopropylamine salt of glyphosate) was applied to individual plants. A weak (3%) solution of Round-up was applied to each individual culm of grass by hand using a sponge. This treatment was performed both in early May and in early June and quite effectively removed all of the undesired rhizomatous grasses. It appeared to have no effect on other individuals on the plots. The plots were monitored and weeded where necessary for the rest of the summer to prevent re-invasion.

Species survivorship was also followed in Year 2 for all of the study species but *Agropyron*. Following the initial weeding, the density of individuals for each of the component species was determined from the center .5m x .5m of each plot. Most, if not all, of the individuals of the study species had emerged by this time and were still in the cotyledon or first leaf stage. The density of individuals was again determined when the plants were harvested in September. The values were used to determine the survivorship probability of each species in each plot.

During July 11-15, 5 plants of each species from the middle .5 x .5 m of each quadrat were measured to estimate treatment effects. The same measures and techniques to estimate biomass used in 1982 were repeated (Table 2.3). Biomass estimates for Trifolium repens were determined by measuring the number of main branches and the length of the longest branch. Reproductive state was also noted for all individuals measured of each species.

From September 25 to October 5, all individuals from within the center .6 x .6 m^2 (leaving a border of .35 m) were clipped at ground level, pressed, dried, and weighed as described for 1982 above.

Chapter 3

COMPETITIVE EFFECTS AND RESPONSES OF SPECIES

To begin to understand the role of competition in structuring this community, it was necessary to determine the potential for competition interactions between each pair of species in the community. Interactions between species have two distinct components, effect and response. Comparisons of competitive effect involve contrasting the reduction of growth in a single focal species when in the presence of different associate species. Comparisons of competitive response contrast the reduction of growth in several focal species when each is in the presence of a single common associate species. The competitive effect and response of a species determine the competitive ability of the species; for example, a species could have a high competitive ability by having some combination of a large competitive effect on other species and a low competitive response to the presence of these species.

It would be best to measure the competitive effects and responses of species while in the full community; however, it is impractical because of the complex interspecific interactions in mixtures of more than two species that could confound the results. So, each possible pair of species has been extracted out of the full multispecies community to investigate their interactions. It must be kept in mind that the conditions in two-species mixtures may not always reflect conditions in the full community.

Combining all possible pairs of species in competition experiments is similar to the diallel competition studies most commonly performed in agronomy. Diallel experiments have been used to investigate the competitive effects and responses between different cultivars of crop species or the effects of weeds on crops (e.g. Welbank 1963, Norrington-Davies 1967, Tripathi 1968, Trenbath 1977). This method has also been performed to a much more limited extent using species in natural assemblages (Williams 1962, Jaquard and Caputa 1970, Fowler 1982). The results obtained using this method can only cautiously be extended to understanding interactions in multispecies communities. First, as mentioned above, isolating a pair of species from the full community changes the environment in which the two species are normally interacting. Second, although this method provides a measure of the population level interactions between each pair of species at a single density and at a particular total yield (biomass/m^2), it is not known whether the results can be extended to other densities or total yields. These restrictions are discussed further in Chapter 4.

Methods

Five major species from a first-year old-field community were grown alone and in two-species combinations in two consecutive years, 1982 and 1983. The performance of individuals of each species were analyzed as a function of the species with which they were growing. Two different measures of performance were used, above-ground biomass of individuals (Years 1 and 2) and percent survivorship in each plot (Year 2). The general field methods are given in Chapter 2 and will only be summarized here.

Year 1 (1982) - The natural, unmanipulated density of each species is similar to the diallel competition studies most commonly performed in agronomy. Diallel experiments have been used to investigate the competitive effects and responses between different cultivars of crop species or the effects of weeds on crops (e.g. Welbank 1963, Norrington-Davies 1967, Tripathi 1968, Trenbath 1977). This method has also been performed to a much more limited extent using species in natural assemblages (Williams 1962, Jaquard and Caputa 1970, Fowler 1982). The results obtained using this method can only cautiously be extended to understanding interactions in multispecies communities. First, as mentioned above, isolating a pair of species from the full community changes the environment in which the two species are normally interacting. Second, although this method provides a measure of the population level interactions between each pair of species at a single density and at a particular total yield (biomass/m^2), it is not known whether the results can be extended to other densities or total yields. These restrictions are discussed further in Chapter 4.

Methods

Five major species from a first-year old-field community were grown alone and in two-species combinations in two consecutive years, 1982 and 1983. The performance of individuals of each species were analyzed as a function of the species with which they were growing. Two different measures of performance were used, above-ground biomass of individuals (Years 1 and 2) and percent survivorship in each plot (Year 2). The general field methods are given in Chapter 2 and will only be summarized here.

Year 1 (1982) - The natural, unmanipulated density of each species was used in all monoculture and two-species experiments (see Table 2.1 for ambient species densities). The natural variation in densities between plots was generally quite small; random variations in density will contribute to the error variance in the analysis. Fifteen different treatments were used including all five monocultures and all possible combinations of two species of interest. Treatments were established by removing the unwanted species through weeding and clipping. Each treatment was replicated either 2 or 3 times (see Chapter 2, Table 2.2). The weights of individuals in each plot of all species but Agropyron were estimated in midsummer (July 25) using regressions between plant size (length of longest leaf, height, or number of leaves) and plant weight which were determined for plants in nearby plots. At the end of September, the above ground portions of all plants in all plots were harvested, dried, and weighed.

Both the estimated weights from the midsummer data and the plant weights determined from the autumn harvest were log-transformed following analysis of the weight distributions (Downing 1979). The individual plant weights were used to test the hypothesis that there were no significant differences in weight between the five treatments for each species (in monocultures and with each of four associates. A nested analysis of variance was used to analyze the data, with individual plant weights in each plot nested within treatment type. Due to the loss of some replicates (see Chapter 2) and the natural variations in densities, an unbalanced design was used in the analysis of variance and an all-pairs analysis was not attempted.

Year 2 (1983) - The experimental design in Year 2 was very similar to that in Year 1. Again, the natural, unmanipulated densities of each species were used in fifteen treatments, including all monocultures and two-species combinations. A random block design was used to locate individual plots in the field, using five blocked replicates of each treatment. In Year 2, Lepidium campestre was replaced by Trifolium repens in the experimental design. The densities of each species were determined in both in mid-May and at the September harvest, allowing an estimate of plant survivorship over that period. The mean densities of the other four species were slightly different from those used in Year 1, due to year-to-year variation in emergence rates (Table 2.1). As in Year 1, individuals of all each species but Agropyron were measured at midsummer (July 11-15) to estimate the treatment effects using regressions of plant size vs. plant weight which were determined from nearby plots. Plants were harvested for above-ground biomass in late September, then dried and weighed as in Year 1.

Before statistical analysis, an arcsine transformation was performed on the percent survival of each species in each plot. The untransformed weights of individuals from each plot were used to generate mean individual plant weights for each species in each replicate plot. Plants which died before the end of the summer were included as individuals having zero weight in the fall analysis. This has little impact on the results, as most of the species had very low mortality, and individuals that died were quite small. The mean plant weights from each of the five replicate plots of each treatment were log-transformed following an analysis of the distributions (Downing 1979). Following transformation of the data, differences between treatments in survivorship, midsummer weight, and final weight were analyzed using the Welsch all-pairs analysis (Sokal and Rohlf 1981).

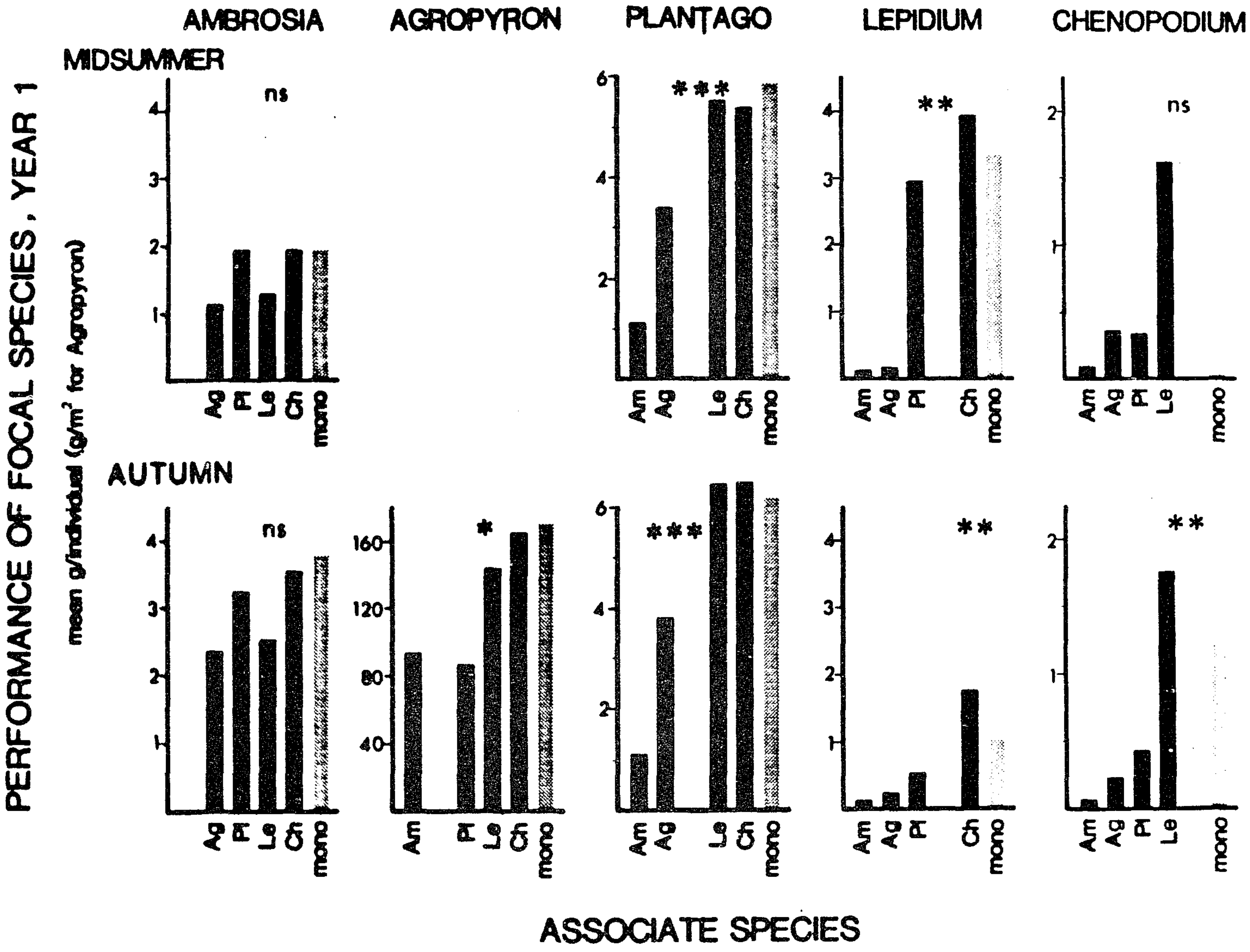
RESULTS

Year 1: The growth of the five species when grown in monocultures and two-species plots exhibited very different patterns, both in their response to the presence of other species and in their effect on the growth of other species (Figure 3.1). However, the data from midsummer is remarkably similar to that from the autumn. Ambrosia demonstrated no significant response when grown with other species, growing as well with an associate species as it does in monoculture. Agropyron harvested in the autumn was significantly suppressed when grown with different associate species. In monoculture, Agropyron reached a yield (dry weight biomass/m^2) of 169 g/m^2, while Agropyron never achieved over 60% of this yield when grown with Ambrosia or Plantago (93 and 86 g/m^2, respectively). Plantago was also suppressed when grown with other species, particularly when grown with Ambrosia and Agropyron. By the autumn harvest, the presence of Ambrosia had reduced Plantago to less than 20% of its growth in monoculture (with Ambrosia - 1.16 g/individual, monoculture - 6.19 g/individual). Chenopodium and Lepidium had no effect on Plantago. The growth of Lepidium was very strongly suppressed by the presence of Ambrosia and Agropyron and was also somewhat suppressed by the presence of Plantago.

In probably the most extreme example of competitive suppression, the presence of Ambrosia reduced the growth of Lepidium to less than 4% of its growth in monoculture (with Ambrosia .12 g/individual, monoculture - 3.21 g/individual). Chenopodium was also affected by the presence of other species, being strongly suppressed by the presence of Ambrosia, Agropyron, or Plantago. Neither Lepidium or Chenopodium

Figure 3.1. The mean growth of individuals of each species in the midsummer and autumn of Year 1 when grown in monocultures and all possible two-species mixtures. Each set of histograms represents the performance of a single focal species (across top) when grown with all possible associates (across x-axis). Each bar represents the mean growth of that focal species when in monoculture or a two-species mixture. The asterisks provide the results of an analysis of variance to determine if any differences exist between the five treatments on each axis (* - P<.05, ** - P<.01, ns - no significant differences found).

Figure 3.1


AMBROSIA
AGROPYRON
PLANTAGO
LEPIDIUM
CHENOPODIUM
MIDSUMMER
AUTUMN
PERFORMANCE OF FOCAL SPECIES, YEAR 1
mean g/individual (g/m² for Agropyron)
ns
***
**
ns
ns
*
***
**
**
1
2
3
4
2
4
6
40
80
120
160
Am
Ag
Pl
Le
Ch
mono
ASSOCIATE SPECIES

appeared to have any effect on one another.

Year 2: The most extreme effect of competition would result in the death of the affected species. There was little or no mortality in Ambrosia, Plantago, and Chenopodium when these species were grown either in monoculture or in mixtures (Table 3.1). Trifolium did exhibit a significant reduction in survival when grown with Ambrosia or Agropyron (74% and 59% survival, respectively). I was unable to determine survivorship of the only grass species, Agropyron, because of my inability to determine precise densities. However, no visible senescence of individual shoots was ever observed for this species until the fall.

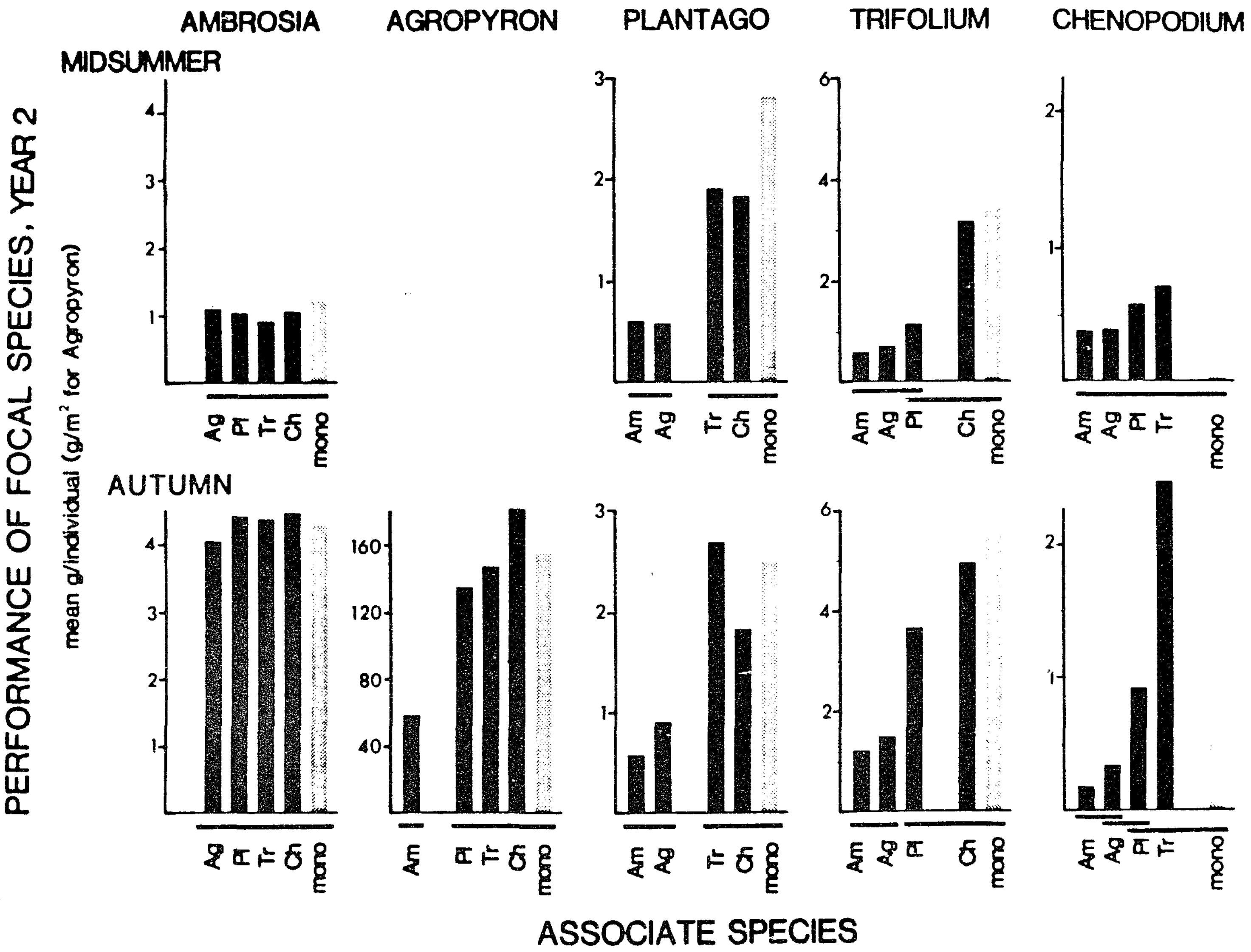
The mean growth of individuals of the five species from Year 2 again shows very different patterns of competitive effect and response by the various species (Figure 3.2). The pattern exhibited by any particular species was consistent between midsummer and autumn. As in Year 1, the growth of Ambrosia was not affected by the presence of any other species. Whether individuals of Ambrosia grew in monocultures or with other species, they always averaged approximately 1.0 g/individual at midsummer and slightly over 4.0 g/individual at the autumn harvest. The growth of Agropyron was only affected by the presence of Ambrosia, which reduced the yield of Agropyron from 155.6 g/m^2 in monoculture to 57.6 g/m^2. At both midsummer and autumn, Ambrosia and Agropyron were the only species to affect the growth of Plantago. The presence of either of these species reduced the growth of individuals of Plantago from over 2.5 g/individual to approximately .5 g/individual. Trifolium, the species which was used in place of Lepidium in Year 2, was also strongly suppressed by the presence of Ambrosia and Agropyron. By the

Table 3.1 Percent survival of focal individuals when grown in combination with different associate species in Year 2. Values in the same row but followed different letters are significantly different ($p<.05$, Welsch Step-up Test). A dash indicates that the mortality could not be determined for that situation.

Focal	Associate Species					none
Species	Ambr.	Agro.	Plan.	Trif.	Chen.	(monoculture)
Ambrosia	-	1.00a	1.00a	1.00a	1.00a	1.00a
Agropyron	-	-	-	-	-	-
Plantago	1.00a	1.00a	-	1.00a	1.00a	1.00a
Trifolium	.74ab	.59a	.93bc	-	.97bc	1.00c
Chenopodium	1.00a	1.00a	.97a	.89a	-	1.00a

Figure 3.2. The mean growth of individuals of each species in the midsummer and autumn of Year 2 when grown in monocultures and all possible two-species mixtures. Each set of histograms represents the performance of a single focal species (across top) when grown with all possible associates (across x-axis). Each bar represents the mean growth of that focal species when in monoculture or a two-species mixture. Below the bars on each axis are the results of all-pairs analysis for the effect of different associate species on growth of the focal species. Species and monoculture treatments underlined by the same line do not differ significantly ($p<.05$, Welsh step-up test).

Figure 3.2


AMBROSIA
AGROPYRON
PLANTAGO
TRIFOLIUM
CHENOPODIUM
MIDSUMMER
AUTUMN
PERFORMANCE OF FOCAL SPECIES, YEAR 2
mean g/individual (g/m^2 for Agropyron)
1
2
3
4
6
40
80
120
160
Ag
Pl
Tr
Ch
Am
mono
ASSOCIATE SPECIES

autumn, the presence of these two species had reduced the growth of Trifolium from .55 g/individual in monocultures to .12 g/individual with Ambrosia and .15 g/individual with Agropyron. Chenopodium exhibited no significant effect of the presence of other species at midsummer. However, in the autumn, Ambrosia, Agropyron, and Plantago demonstrated significant competitive effects on the growth of Chenopodium, with Ambrosia demonstrating the greatest effect, reducing the growth of Chenopodium to less than 9% of its growth in monoculture (with Ambrosia - .18 g/individual, monoculture 2.13 g/individual).

For both years, the data indicate that there were very strong and consistent differences in the competitive effects of the six associate species on focal species. Ambrosia always had the greatest competitive effect on each of the focal species and Chenopodium and Lepidium (Year 1) or Chenopodium and Trifolium (Year 2) had the least effect, if any, on the different focal species.

Competitive responses, as indicated by growth, also exhibited a very consistent pattern. Again, there were large differences in the sensitivity of the various focal species to competitive effects. Ambrosia was never affected by the presence of any of the possible associate species while the populations of Chenopodium and Lepidium (Year 1) or Chenopodium and Trifolium (Year 2) were very strongly affected by the presence of almost any other species. This hierarchy of response is very consistent and is the exact opposite of the hierarchy of effect.

These data indicate that the potential for competition in the full community is very great, as the presence of an associate species may reduce the growth of a focal species by greater that 90%. There are also some insightful patterns in the "competitive ability" of the various competitive species. If competitive ability is defined as being some combination of having a large competitive effect on other species but being little affected by the presence of potential competitors, a very consistent ranking of ability in these species is observed:

Ambrosia > *Agropyron* > *Plantago* > *Chenopodium* = *Lepidium* or *Trifolium*

Note that this hierarchy matches the ranking of biomass/m^2 for these species in the full community. It is important to remember that this pattern is caused by population effects and does not necessarily reflect the per individual or per amount competitive ability of each species (see Goldberg and Werner 1983). Nevertheless, competitive ability does seem to be a transitive property of these populations.

DISCUSSION

Differences in the competitive effects and responses of populations

Several conclusions can be drawn about the nature of the competitive interactions found in this plant community. (1) The consistent hierarchy of competitive effects demonstrates that there is little specificity of species interactions; that is, *Ambrosia* affects all other species strongly, not just some of them. (2) This hierarchy also shows that most pairwise interactions are asymmetric. There are usually definite 'winners and losers' in competitive interactions. (3) The hierarchy and the lack of specificity of interactions suggest that all of these species are limited by and competing for the same resource or resources.

The asymmetric interspecific interactions suggest something about the way plants obtain limiting resources. The fact that the population of Ambrosia has a greater competitive ability than the other species in this community suggests that the Ambrosia population has a greater access to or a greater uptake rate of limiting resources. Due to their nature, some plant resources would seem to bring about a more symmetric or evenly balanced competition between individuals while others would be less likely to do so. For example, when light is the limiting resource, individuals have an "ordered" access to the resource (e.g. Watkinson, et al. 1983). The tallest plant may use the resource freely, unimpeded by other plants, the second tallest plant may use the light which filters through to it unimpeded by those beneath, and so forth. In this simple scenario, the ordered access to light will lead to completely asymmetric interactions between individuals. On the other hand, competition for moisture may lead to a more equable access to the resource if the roots of the different species are intermingled. The consistent competitive hierarchy found in this study with the necessary asymmetric interactions suggests that there may be some sort of ordered access to the limiting resource or resources.

The hierarchy of competitive ability also suggests that resources are not partitioned in this community; that is, there is no evidence that the species are specializing to use different resources or classes of resources. Much of the previous work in theoretical and animal community structure proposed that individual species must have exclusive use of some resources to be able to persist in the community (e.g. May 1973; for plants - Van den Bergh and Braakehekke 1978, Silvertown 1982).

Thus, species should occupy different 'niches', the niche being the set of all biotic and abiotic factors controlling the distribution and abundance of a species. Several authors have argued that this niche diversification hypothesis is not applicable to plant communities because of the very limited potential for partitioning when there is a small number of non-discreet, shared resources (Schaffer and Leigh 1976, Silander 1976, Harper 1977, Connell 1978, Huston 1979, Newman 1982, Goldberg and Werner 1983). Others have quite correctly argued that plants may partition many aspects of the biotic or abiotic environment other than light, moisture and nutrients, such as different microsites or phenologies (Grubb 1977). In fact, as early successional species, nearly all of the plants in this community might be considered to be occupying "disturbance niches". The consistent hierarchy of competitive ability found in this study suggests that resources affecting the growth of established seedlings are not being partitioned, though it does not address the possibility that other niche dimensions are being partitioned.

Consistent hierarchies of the competitive abilities of different species have been found in other studies (Pemadasa and Lovell 1974, Pemadasa 1976, Handel 1978, Fowler 1982), but there is at least one well documented exception. Williams (1962) performed additive competition experiments between all possible pairs of seven species of plants and the data have since been reanalyzed several times (McGilchrist 1965, Durrant 1965, Norrington-Davies 1967, Breese and Hill 1973). Trenbath (1977) reviewed the odd history of this study and published, for the first time, the identities of the species used in the study. Of all the previous analyses, only Breese and Hill noted that one of the species demonstrated a very different competitive effect on the others, though it had a similar competitive response. This species was a nitrogen fixing legume, Trifolium subterraneum, which appeared to have a much reduced competitive effect on the other species. It may be that this species was providing nitrogen for both itself and its neighbors. Such specific species interactions would disrupt any hierarchy of competitive ability.

Variation Within a Season

The plants in this community coexist for a period of some five months, but they probably do not interact at all times during this period. Immediately after germination, most individuals are small and occupy very little space, making it unlikely that they affect or respond to their neighbors. At other times during the season, some resources are in great abundance, such as during periods when rain is abundant. Again, in these periods it seems unlikely that competition is occurring for a temporarily very abundant resource, although competition for other resources, such as light, may still be occurring. Only two census dates were used in both years of this experiments (midsummer and autumn), but these dates can be used to compare the importance of competition before and after the midsummer dates (cf. Figures 3.1, 3.2).

Two questions can be addressed for each of the species in the community about variation within a season: are there differences in growth of individuals and are there differences in species interactions before and after the midsummer census? In both Year 1 and Year 2, Ambrosia continued to grow throughout the summer, with approximately half of the growth in monocultures and mixtures for both years occurring after midsummer. Plantago and Chenopodium exhibited little or no growth after midsummer; mean plant size in monocultures and mixtures exhibited no change between the midsummer and autumn. This also indicates that the patterns of the competitive effects of other species on Plantago and Chenopodium are established before midsummer. Individuals of Lepidum, in Year 1, appeared to actually become smaller during the period from midsummer to when the plants were harvested in the autumn. Trifolium, in Year 2, appeared to almost double in size from midsummer to the autumn in monocultures and in the mixtures. However, the pattern of competitive affects of other species on Trifolium was established before midsummer and did not change at the autumn harvest.

So, while there are differences evident in the timing of growth among the five species investigated, the hierarchy and pattern of species interactions were nearly unchanged between the two sampling periods in both years. The data suggests that the competitive interactions between most species were firmly established before the midsummer dates. This is not too surprising since the time between May and late June is a period of rapid growth for all of the species and it might be expected that during this period resources would be most limiting.

Variation Between Two Successive Seasons

This data also enables us to investigate species interactions and growth in two different years. The densities of Ambrosia, Plantago, and Chenopodium were very similar in the two years of the study (Table 2.1) and so differences between the two years are not attributable to differences in density. I did not determine if the density of Agropyron tillers changed between the two years.

The mean sizes of individuals of Ambrosia and Chenopodium were greater in Year 2 than in Year 1. Individuals in monocultures of Ambrosia exhibited 13% more growth in Year 2 than in Year 1 while Chenopodium exhibited 75% more growth. However, individuals of Plantago in Year 2 exhibited 60% less growth than in Year 1. It is difficult to explain this pattern in the results. The experiments were performed in two consecutive years in the same field after the same soil preparation. A possible explanation for the differences in growth might be that the pattern of rainfall was quite different in the two seasons (Table 3.2). In Year 1, precipitation was fairly continuous throughout May, June, and July, with an extremely dry September. In Year 2, there was very little precipitation, particularly in June and July, but there was an abundance of rain in September when most of the plants were already senescing. The very dry period in June and July Year 2 coincides with the period of intense growth for Plantago, which may have limited the growth of this species in that year. However, the extremely wet month of September in Year 2 may have delayed the senescence of Ambrosia, Agropyron, and Chenopodium. Senescing plants often drop leaves as seeds are being filled and hardened, which reduces their harvested weight.

The most interesting result is that there is no qualitative difference between the patterns of species competitive ability between the two years, despite the differences in mean plant size. The competitive hierarchy appears to be consistent both with and between years. Thus, even though in Year 2 individuals of Chenopodium were very much larger and individuals of Plantago were very much smaller than in Year 1, the relative competitive abilities of these species remained basically unchanged.

Table 3.2 Precipitation by month at the Kellogg Biological Station for the years 1982 and 1983.

MONTH	Year 1 1982	Year 2 1983	Average 1967-81
April	4.75 cm	12.78	10.78
May	10.19	13.82	8.46
June	10.54	4.85	11.73
July	10.82	7.26	15.91
August	5.51	7.32	9.54
September	3.53	11.00	9.04

Chapter 4

THE DYNAMICS OF PLANT POPULATION INTERACTIONS

The experiments discussed in Chapter 3 demonstrated that the five species used in each year had very different competitive abilities. However, the conclusions drawn applied only at the single (ambient) densities at which each species was held. To further explore the competitive abilities of these species, experiments in 1983 (Year 2) were designed to vary the densities of monocultures and two-species mixtures. The purpose was to measure the per-amount competitive effects and responses of each species over a range of abundances. The experiments allowed an analysis of the potential importance of simple intraspecific, simple interspecific, and complex intraspecific effects in regulating the growth of each species.

The basic approach used in this chapter is to quantify the success of individuals of each species as a function of the abundance of competitors. I will first investigate growth in monocultures, then two-species mixtures with the density of one species held constant, and finally, two-species mixtures with varying densities of both species. The monocultures can quantify potential intraspecific effects, the two-species mixtures with the density of one species held constant can be used to estimate interspecific effects, while the two-species mixtures with varying densities of both species investigate the simultaneous action of intraspecific, interspecific, and potential complex intraspecific effects. The results from each section will be discussed using simple mathematical representations of the results.

Several different models of plant interactions have previously been used to describe growth in two-species mixtures (see reviews in Harper 1977, Trenbath 1977). The best known is the model of de Wit (1960,1961), based on Raoults' gas laws, which predicts the relative yields of two species grown in replacement series experiments. A replacement series is a substitutive experimental design in which the total density of individuals is kept constant while the proportions of the two species are varied from 1:0 to 0:1. This model has been extensively used to study two-species dynamics (Harper 1977, Trenbath 1977) and has been successfully extended to three species in at least three studies (Baeumer and de Wit 1968, Fowler 1982, Ismail 1983). However, the model has serious limitations when applied to natural communities. The major difficulties are that the results of the model are dependent on the total density of individuals (Harper and Clatworthy 1963, Marshall and Jain 1969, Wu and Jain 1979) and that it is difficult to determine the biological meaning of the parameters of the model (DeBenedictis 1977, Inouye and Schaffer 1981, Goldberg and Werner 1983, Spitters 1983a).

Watkinson (1981) and Spitters (1983a) both proposed a two-species model based on the reciprocal yield law. The reciprocal yield law is a description of the growth of individuals in monocultures as a function of their density and has been used in both agriculture and ecology (see Willey and Heath 1969, Harper 1977). The two-species version of the reciprocal yield law has been used successfully to describe the results of intercropping experiments (Spitters 1983a, 1983b). It has one large advantage over the de Wit model in that the model is not dependent upon a single total density of individual plants. However, as with the de

Wit model, the terms often do not have any simple biological meaning resulting in the the actual species dynamics being obscured by the form of the model.

The approach taken in this study is to compare the ability of a variety of simple models to explain the variance in the data. This method makes no assumptions about the mechanism of interaction, but should show how the per-amount effects of competition change with the density of competitors.

1. Intraspecific Effects

In 1983, I investigated the intraspecific effects using data from single-species plots over a range of densities. The general methods will only be summarized here; a detailed description of the methods is in Chapter 2.

Monoculture plots for all five species were obtained by removal of all but the desired species from each plot and were initiated in early May using hand-removals and continued throughout the summer using a contact herbicide. Three different treatments were used for each species in an attempt to generate a wide range of densities, with five replicates of each treatment arranged in a random block design. The three density treatments consisted of (1) approximately half-density plots, achieved by randomly removing half of the individuals on the plot using a coin toss to decide the fate of each individual; (2) full (natural) density plots which remained unmanipulated; and (3) high density plots which were seeded with the desired species in early April. Unfortunately, the seedings were only successful for *Chenopodium* and *Plantago*. The seeds planted in high density plots for the other species failed to germinate and these plots only contained naturally occurring individuals. No significant effects of the treatment blocks were found, and so four extra monoculture plots for each species were included in the analysis for all of the species but Agropyron. These plots had been part of a separate experiment and were randomly located in the same area as the other fifteen plots used for each species. All plants within the center .6m x .6m of each plot were harvested at the end of September, oven dried, and weighed.

The effects of density on the mean individual performance show that all five species have a significant negative response to an increasing density of conspecifics, indicating that there was competition for some limiting resource (Figure 4.1, Table 4.1). The shape of the response curves are very different, depending upon the species involved and the range of densities achieved in the monocultures.

The relationship between the mean performance of individuals and increasing density of Ambrosia was significantly negative. The best description of the relationship was given by the reciprocal yield equation (Table 4.1); however, the shape of the relationship was strongly influenced by the presence of a single plot at a very low density which contained very large plants.

The negative relationship between the growth of Agropyron and density was barely significant if compared to a linear model and no other model provided a better description. This reflects a problem in field techniques when working with a perennial rhizomatous grass (see Chapter 2). Agropyron maintains active growth throughout the year, putting up new culms by extending underground rhizomes. It is very difficult to determine the actual density or biomass of individuals

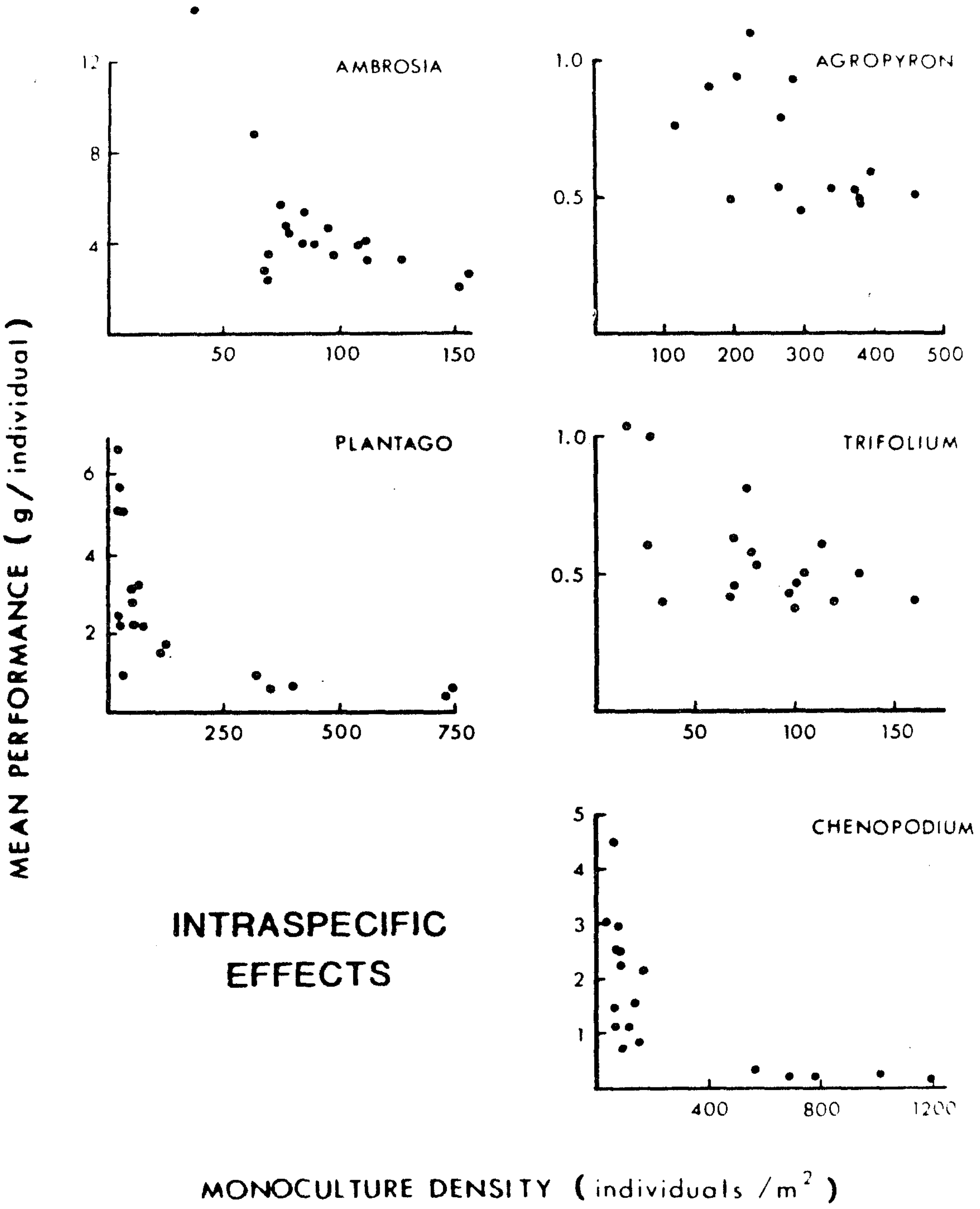


Figure 4.1. The intraspecific effects of density on the growth of individuals of five species grown in monocultures in Year 2.

Table 4.1. The amount of variance explained (R^2) by three equations describing plant performance in monocultures as a function of density. The linear equation describes the mean weight of the focal species as a linear function of the monoculture density; the reciprocal yield equation describes the reciprocal of the mean weight of the focal species as a linear function of the monoculture density; the log-log equation described the logarithm of the mean weight of the focal species as a linear function of the logarithm of the monoculture density. (* - Significant, $P<.05$, ** - Significant, $P<.01$)

Species	Linear	Reciprocal Yield	log-log
Ambrosia	$.36^{**}$	$.74^{**}$	$.47^{**}$
Agropyron	$.32^{*}$	$.29^{*}$	$.30^{*}$
Plantago	$.38^{**}$	$.58^{**}$	$.75^{**}$
Trifolium	$.34^{*}$	$.45^{**}$	$.42^{**}$
Chenopodium	$.46^{**}$	$.63^{**}$	$.85^{**}$

because of these underground connections. In this portion of the analysis, I have estimated densities and plant biomass by treating culms as individual plants, but this overestimates the actual density and underestimates the weight of individuals. Without knowing the initial density, I could not determine whether the low correlation between Agropyron density and weight is due to the problems in estimating the density of this species or whether it is evidence that density-dependent processes are less important in regulating this species.

Plantago demonstrated a highly significant effect of increasing density that resembles a negative rectangular hyperbola (Figure 4.1). The response curve is best described by a log mean weight - log density relationship (Table 4.1). Five of the plots demonstrated very high densities of individuals as a result of seeding, and these plots contribute a great deal to the non-linear shape of the curve. The high density plots contained a heavy cover of stunted individuals which were very tightly packed together. One of these high density plots contained the only vertebrate (other than humans!) observed on the plots; an individual Ambystoma tigrinum which appeared to have taken cover in moist soil found under the heavy growth.

Individuals of Trifolium were also suppressed at high densities, with the non-linear relationship between mean weight and density best described by the reciprocal yield equation. I expect that if I had been able to increase the density of Trifolium to a greater extent that a more curvilinear relationship would have been found. However, processes other than density also appeared to regulate the growth of Trifolium. Even several of the plots maintained at a very low density demonstrated very poor growth of individuals (Figure 4.1).

The growth of Chenopodium was strongly suppressed at high densities, with the overall pattern best described by a log weight - log density relationship. Like Plantago, the highly non-linear response to increasing density was in large part due to the five plots which were seeded to obtain extreme high densities. In this case, seedling establishment was higher than anticipated, with no plots being established at intermediate densities from 180 to 560 individuals/m^2.

In sum, the species for which seeding increased the densities exhibited highly significant, non-linear relationships between mean plant weight and density. I do not know if similar relationships might have been found for the other species if I had been able to increase the densities to high enough levels. However, all five of the species can potentially affect their own growth: some evidence of density-dependent growth was noted for all of the species used.

2. Interspecific effects

It is very difficult to quantify interspecific effects independent of intraspecific effects also usually present in the systems. One method is to use a target-neighbor experimental design which eliminates intraspecific effects (Goldberg and Werner 1983). However, target neighbor designs require a large number of replicates which would have been extremely difficult for experiments which have many treatments. Instead of eliminating the intraspecific effect, I have attempted to hold it constant by maintaining the density of the focal species at a single value and then measuring the effect of varying the density of the associate species (additive design, Harper 1977). This design was used to investigate the effects of varying the densities of each of the four possible associates on each of the five focal species.

To achieve a range of densities, three treatments were used for each pair of species, with each treatment replicated five times in plots arranged in a random block design (see Table 2.2). The treatments consisted of both species at their natural, unmanipulated densities, the first species at the natural density and the second species at half-natural density, and the first species at half-natural density and the second species at the full natural density. Half-densities were obtained by randomly removing half of the individuals on each plot, using a coin toss to determine the fate of each individual. Because individual plots have a variable number of individuals to begin with, this method results in a range of densities for each species in the plots, from less than half-natural average density to over full natural average density. All other species were removed from these plots by hand-weeding and application of a contact herbicide. All plants in each plot were harvested at the end of September, oven dried, and weighed, as described in Chapter 2.

To hold the intraspecific effects constant for each focal-associate combination, only the ten plots which contained focal species densities closest to the natural density found in control plots were used (natural densities of species are given in Table 2.1). These plots were used to determine the effect of associate species yield (dry weight biomass/m^2) on the mean success of individuals of the focal species. This design controls rather than eliminates variance in the intraspecific effects; the variance in intraspecific effects is included in the error variance of the regressions.

As was demonstrated in Chapter 3, there were differences in both the responses of different species to the presence of a single associate species and in the effects of different associate species on a given focal species (Figure 4.2, Table 4.2). As with the intraspecific effects, increasing the abundance of competitors appears to have a negative effect on the weight of focal individuals, but the effect was statistically significant in only four of the twenty possible combinations (Table 4.2).

The growth of individuals of Ambrosia was not significantly affected by the yield of any of the associate species. This agrees with the previous study (Chapter 3) which had demonstrated that, at a given density, Ambrosia was not affected by the presence of any of the other species. The presence of Ambrosia does appear to suppress the growth of the focal species as much or more than any other associate species. However, the suppression is a threshold or asymptotic effect in that, over the range of yields investigated, any increase in yield does not produce an increase in the already large effect. Agropyron is the only species that appears to be unaffected by any yield of Ambrosia, which also agrees with the analysis in Chapter 3.

Agropyron was also not significantly affected by changes in the yield of any associate species. However, increases in the yield of Agropyron did significantly decrease the growth of Plantago, Trifolium, and Chenopodium. This also is in agreement with the hierarchy of competitive ability previously discussed.

The growth of Plantago responded only to changes in the yield of Agropyron. As discussed above, Ambrosia appears to have a large effect on the growth of Plantago, but the magnitude of this effect does not change significantly over the range of yields of Ambrosia used in this

Figure 4.2. The interspecific effects of the yield (dry weight biomass/m^2) of various associate species on the growth of individuals of five focal species in Year 2. Each associate species was grown in two-species mixtures with the focal species and the data organized on a single axis. Each letter indicates the yield of a specific associate species: A= *Ambrosia*, G=*Agropyron*, P=*Plantago*, T=*Trifolium*, C=*Chenopodium*.

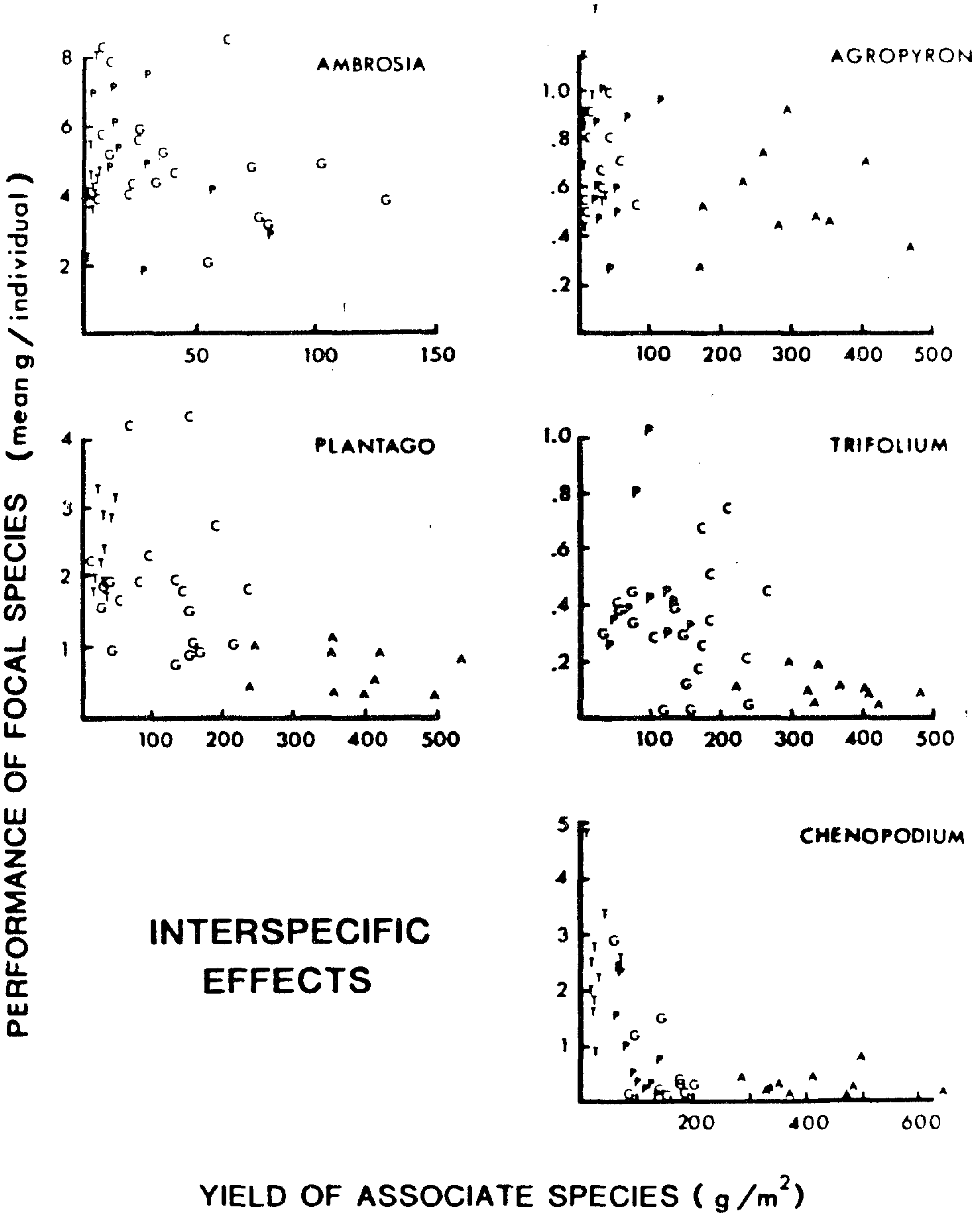

PERFORMANCE OF FOCAL SPECIES (mean g/individual)
AMBROSIA
8
6
4
2
50
100
150
AGROPYRON
1.0
.8
.6
.4
.2
100
200
300
400
500
PLANTAGO
4
3
2
1
100
200
300
400
500
TRIFOLIUM
1.0
.8
.6
.4
.2
100
200
300
400
500
CHENOPODIUM
5
4
3
2
1
200
400
600
INTERSPECIFIC EFFECTS
YIELD OF ASSOCIATE SPECIES (g /m²)

Figure 4.2

Table 4.2. Linear correlations between mean weight of focal species and the yield of different associate species in two-species mixtures. N=10 for all species pairs. (* - Significant, P<.05; ** - Significant, P<.01; a dash indicates that the correlation was not determined for that situation).

Focal Species	Associate Species Ambrosia	Agropyron	Plantago	Trifolium	Chenopodium
Ambrosia	-	-.35	-.57	.04	.32
Agropyron	.02	-	.40	-.03	.06
Plantago	-.15	-.65*	-	.49	.06
Trifolium	-.43	-.65*	.00	-	.01
Chenopodium	.22	-.60*	-.77**	-.14	-

study. Increasing yields of Plantago did significantly reduce the growth of Chenopodium, but had no effect on the other three species. This is not in complete agreement with the hierarchy of competitive ability. In the previous experiments, the presence of Plantago also significantly affected the growth of Trifolium, yet no evidence of that effect was demonstrated here.

Both Trifolium and Chenopodium had no significant effect on the growth of any focal species, at least at the yields obtained for these two species as associates. The general competitive ability determined for these two species is precisely that found previously: both species have little effect on any focal species and are often strongly suppressed by the presence of associates.

The results presented in Table 4.2 and Figure 4.2 document three very interesting patterns in the data. First, species which appeared to have a low competitive effect did so because they have an extreme response to competition. That is, Trifolium and Chenopodium were highly suppressed when grown with any of the other species and this poor growth seems to be why these two species had very little competitive effect on any of the other species. On the other hand, Agropyron grew relatively unimpeded by the presence of other species and this may be the reason why Agropyron had a large competitive effect on many of the other species. However, there is a some circularity to this argument that demonstrates the interdependence of interactions in this community. Does the competitive response of a species determine its competitive effect (as argued above), or does effect determine response? In fact, both portions of competitive ability in part determine one another and so cannot be completely separated.

Second, there seems to be a general per-amount equivalence of competitive effects among the five species. The important factor in determining the competitive effect of a species appears to be the yield (dry weight biomass/m^2) of that species rather than its identity. In fact, there is no evidence that the per-amount competitive effects of the species are different at any particular yield. A test of this hypothesis would be to compare the competitive effect of two associate species on the same focal species over the same range of associate yield. Unfortunately, the yield of associate species generally did not overlap to a sufficient degree to allow a statistical analysis of the competitive abilities of the species. Thus, for example, I cannot statistically compare the effect of Chenopodium and Ambrosia on Plantago because these two associate species did not occur at the same yield. However, two lines of evidence do support the hypothesis of equivalence of competitive effects. First, the relationship of associate yield, regardless of identity, and focal species growth is significant for Agropyron, Plantago, Trifolium, and Chenopodium. Second, in the one instance where a significant overlap in the yield of two associate species was found, no significant difference in per-amount competitive effects could be found (analysis of covariance of Agropyron and Plantago yield on Chenopodium growth; F=1.2668, P>.28). Table 4.3 gives the amount of variance in growth of individuals of focal species explained solely by the total yield of all associates. This suggests that yield is a factor in determining competitive effect, though it does not provide conclusive evidence for per-amount equivalence of species.

The third pattern exhibited by the data is the shape of the response curve of the growth of focal individuals as a function of the

Table 4.3. The variance explained (R^2) by three different equations describing the mean growth of individuals of focal species at a single density as a function of associate species yield. The linear equation describes the mean weight of the focal species as a linear function of the associate species yield; the reciprocal yield equation describes the reciprocal of the mean weight of the focal species as a linear function of the associate species yield; the log-log equation described the logarithm of the mean weight of the focal species as a linear function of the logarithm of the associate species yield. N=40 in each case. (* - Significant, P<.05; ** - Significant, P<.01)

Species	Linear	Reciprocal Yield	log-log
Ambrosia	.06	.06	.02
Agropyron	.10	.08	.08
Plantago	$.29^{**}$	$.50^{**}$	$.40^{**}$
Trifolium	$.23^{**}$	$.11^{*}$	$.26^{**}$
Chenopodium	$.34^{**}$	$.18^{**}$	$.55^{**}$

yield of the associate species. Ambrosia and Agropyron as focal species are not strongly affected by changes in the yield of associates. This is similar to the patterns observed between growth and density in monocultures. The relationship of associate yield, regardless of identity, and focal species growth for the species having a lower competitive ability (Plantago, Trifolium, and Chenopodium) strongly resembled a negative hyperbolic function, demonstrating an asymptotic effect of associate yield on focal species growth.

3. Total Competitive Effect

It is evident that several different types of interactions may occur in two species mixtures. The monoculture experiments indicate that there is at least the potential for all five species to limit their own growth (intraspecific effects). The analysis of two-species mixtures both in the above section and in Chapter 3 demonstrates that there are significant interspecific effects limiting some of the species. If both of these types of interactions simultaneously limit a focal species in a two-species mixture, then it is also possible that complex intraspecific effects are occurring, with the simple interspecific effect changing the magnitude of the intraspecific effect. This section is an attempt to understand the relative importance of simple intraspecific, simple interspecific, and complex intraspecific effects in each of the two-species mixtures.

The difficulty in understanding even simple two-species systems is in interpreting the net results of the several simultaneous cause-effect pathways which limit the growth of individuals. The approach I have taken here is to determine the mean success of individuals of the focal species at various combinations of abundance of both the focal and associate species. These results will then be applied to several simple a priori models of species interactions. If a model provides an adequate description of the data, it will be assumed that the model in some way reflects the functional nature of the species interactions. This same approach has been used in several studies using laboratory populations of Drosophila (e.g. Ayala 1971, Ayala et al. 1973).

Four different models were used, either because they have been previously used in plant studies, or because they were an extension of a another model. An infinite number of other models could have been used; I have restricted the analysis to only these four in an attempt to make as few assumptions as possible about the form of any interaction. Most of the terms have reasonable biological interpretations, although they do not describe details of any particular mechanism of interaction.

The first model is the simplest possible two-species model, which describes the growth of individuals of a focal species as a linear function of the density of both the focal and associate species:

$$wt_1 = A + B_1N_1 + B_2N_2 \tag{1}$$

where A represents the growth of an isolated individual of species 1 and B_1 and B_2 represent the constant per-amount effects of individuals of species 1 and 2, respectively.

The second model is the two-species reciprocal yield model proposed by Watkinson (1981) and Spitters (1983a). This model is very similar to model 1 and describes the reciprocal of the mean growth of individuals as a linear function of the density of both the focal and associate species:

$$1/wt_1 = A + B_1N_1 + B_2N_2 \tag{2}$$

This model has been successfully used to describe interactions between corn and peanuts (Spitters 1983a, 1983b). The model does incorporate an implicit complex effect (intraspecific higher-order or indirect effect) in that the per-amount effect of species 2 on wt_1 cannot be determined without knowledge of N_1. However, this complex term was not noted or discussed by any of the previous studies.

The third model uses yield (dry weight biomass/m^2) of the associate species as the independent variable rather than density. The single species reciprocal law states that the growth of a focal species is a linear function of the yield of the species. This yield model could be extended to a two-species equation which would predict wt_1 as a linear function of the yields of species 1 (B_1Y_1) and species 2 (B_2Y_2). However, this would be mathematically intractable as the yield of species 1, Y_1, is a function of its mean growth, wt_1. Instead, I have constructed an equation that combines models 1 and 2:

$$wt_1 = A + B_1N_1 + B_2Y_2 \tag{3}$$

This model does not include a term describing any complex intraspecific interaction.

The fourth model is identical to model 3 with the addition of an explicit cross-product term which describes a complex intraspecific effect of the yield of the second species (Y_2) on the performance of the focal species (wt_1):

$$wt_1 = A + B_1N_1 + B_2Y_2 + C_3N_1Y_2 \qquad (4)$$

where C_3 represents a constant complex effect. Neither model 3 or 4 have previously been used.

The data used above to evaluate interspecific effects were also used in this section to evaluate each of the models of total effects. Mean biomass of individuals and the densities and total yields of each species were determined in each of the fifteen plots that contained a unique combination of two species. Models 1, 3, and 4 were analyzed using multiple linear regression analysis, while model 2 was analyzed using non-linear regression (BMDP Biomedical Computer Program - PAR). Partial regression coefficients were determined for model 2 by transforming the equation into a linear model in the form:

$$wt_1 = 1/A - (B_1/A)Y_1 + (B_2/A)N_2wt_1$$

The amount of variance explained by the four models for each possible species pair is given in Table 4.4. R^2 values close to unity suggest that the model provides a very good description of the species dynamics. At least one of the models significantly described the interaction in eleven of the twenty possible cases. In general, if any one of the models provided a significant fit to the data, all of the models were significant.

The relative importance of each individual term in the equations (intraspecific/interspecific/complex intraspecific) can be determined

Table 4.4. Coefficients of determination (variance explained) for four different models of two-species mixtures. (* - Significant, P<.05; ** - P<.01; *** - P<.001).

		Model			
Focal sp.	Associate sp.	1	2	3	4
Ambrosia	Agropyron	$.58^{**}$	$.58^{**}$	$.46^{*}$	$.51^{*}$
Ambrosia	Plantago	$.59^{**}$	$.72^{***}$	$.58^{**}$	$.64^{**}$
Ambrosia	Trifolium	$.68^{***}$	87^{***}	$.57^{***}$	$.58^{*}$
Ambrosia	Chenopodium	$.58^{**}$	$.62^{**}$	$.57^{**}$	$.61^{*}$
Agropyron	Ambrosia	.05	.05	.02	.03
Agropyron	Plantago	.02	.00	.01	.09
Agropyron	Trifolium	.09	.16	.11	.18
Agropyron	Chenopodium	.28	.30	.08	.10
Plantago	Ambrosia	.25	.15	.08	.14
Plantago	Agropyron	$.59^{**}$	$.69^{***}$	$.52^{**}$	$.58^{**}$
Plantago	Trifolium	$.38^{*}$	.36	.28	.28
Plantago	Chenopodium	.24	.07	$.42^{*}$	.42
Trifolium	Ambrosia	$.39^{*}$	.23	.03	.07
Trifolium	Agropyron	$.65^{**}$	$.42^{**}$	$.58^{**}$	$.63^{**}$
Trifolium	Plantago	$.38^{*}$	$.75^{***}$	.25	.30
Trifolium	Chenopodium	.01	.04	.11	.11
Chenopodium	Ambrosia	.34	.39	.23	.23
Chenopodium	Agropyron	.29	.21	.32	.32
Chenopodium	Plantago	$.63^{**}$	$.61^{***}$	$.68^{***}$	$.77^{***}$
Chenopodium	Trifolium	.27	.17	.23	.36

using partial correlation coefficients (Table 4.5). Coefficients near zero suggest that a term contributes little to the overall success of the model, while values near 1 or -1 suggest that, because a large portion of the total variance is explained, this term has some biological significance.

None of the models appears to be generally better than any other (Table 4.4). In particular, models 2 and 4, which include complex intraspecific effects, do not appear to be generally better than 1 and 3, which only include simple interactions. However, different models appear to apply somewhat better for specific species pairs. For example, only model 2 accounted for a high amount of the variance in the effects of Plantago and Trifolium on Trifolium.

All of the equations were significant that described the growth of Ambrosia as a function of its own abundance and the abundance of a competitor. The partial correlation coefficients (Table 4.5) indicate that the primary reason for this result is that Ambrosia generally had a strong intraspecific effect on its own performance. Only Agropyron and Plantago also affected the performance of Ambrosia. On the other hand, variation in the abundance of Ambrosia as an associate had very little effect on the growth of any of the other species. This is suprising as the previous experiments had demonstrated that Ambrosia significantly suppressed the growth of other species. However, as discussed above, this may be due to the fact that most species have a non-linear response to the presence of Ambrosia and at the high range of densities of Ambrosia used, very little response would be expected.

On the other hand, Agropyron was not affected by the abundance of any of the species, including itself. There was no indication from

Table 4.5. Partial correlation coefficients from multiple regression analysis of two-species mixtures. The values give the partial coefficient associated with different effects: intraspecific /interspecific/higher-order (only model 4). For models 1, 2, and 3, coefficients greater than .62 are significant (P<.05). For model 4, values greater than .67 are significant (P<.05). The .m. indicates independent variables which could not be entered into multiple regression equations because of high correlations with the variable first entered into the model.

		Model			
focal sp.	associate sp.	1	2	3	4
Ambrosia	Agropyron	-.64/-.54	.65/.52	-.65/-.32	-.04/.18/-.29
Ambrosia	Plantago	-.63/-.54	.76/.62	-.73/-.53	-.69/-.52/.37
Ambrosia	Trifolium	-.81/-.51	.93/.18	-.76/.m.	-.40/.08/-.09
Ambrosia	Chenopodium	-.75/.33	.79/-.04	-.71/.29	-.37/.39/-.33
Agropyron	Ambrosia	-.10/-.17	.14/.15	-.11/.05	.08/-.04/-.10
Agropyron	Plantago	-.12/.04	.04/-.05	-.12/.m.	-.28/-.23/.28
Agropyron	Trifolium	-.14/-.30	-.16/.29	-.22/-.32	-.30/-.42/.28
Agropyron	Chenopodium	-.17/.47	.23/-.47	-.26/-.06	-.29/-.16/.14
Plantago	Ambrosia	-.03/-.48	-.06/.39	-.26/-.24	-.32/-.34/.26
Plantago	Agropyron	-.58/-.66	.57/.78	-.56/-.59	-.56/-.56/.37
Plantago	Trifolium	-.58/-.39	.60/.23	-.34/.21	-.25/.04/.09
Plantago	Chenopodium	-.35/.22	.26/.11	-.64/-.52	-.63/-.40/.02
Trifolium	Ambrosia	-.39/-.57	-.08/.48	.09/-.13	.20/.13/-.19
Trifolium	Agropyron	.60/-.60	.10/.62	.12/-.57	.36/.07/-.36
Trifolium	Plantago	-.50/-.51	.83/.75	-.50/-.21	-.40/-.31/.26
Trifolium	Chenopodium	-.12/-.03	-.19/-.14	-.28/-.31	-.20/-.23/.06
Chenopodium	Ambrosia	.52/-.40	-.58/.40	.45/.13	.13/.05/.01
Chenopodium	Agropyron	-.08/-.53	-.15/.39	.04/-.56	-.02/-.23/.05
Chenopodium	Plantago	-.54/-.80	-.03/.74	-.48/-.83	-.61/-.77/.50
Chenopodium	Trifolium	-.47/-.46	.38/.35	-.43/-.39	-.50/-.49/.43

either the R^2 values or the partial correlation coefficients that the growth of *Agropyron* was affected by variation in the abundance of any species. However, the abundance of *Agropyron* did significantly affect the performance of *Ambrosia*, *Plantago*, and *Trifolium*. This also is in general agreement with the interspecific studies discussed above in section 2.

The growth of *Plantago* was strongly limited by the abundance of *Agropyrón*. *Plantago* also demonstrated a significant intraspecific effect when grown with the competitive subordinates *Trifolium* and *Chenopodium*. Variation in the abundance of *Ambrosia*, the competitive dominant from the previous studies, had no effect on the growth of *Plantago*. *Plantago* did demonstrate significant competitive effects on all species but *Agropyron*, with model 2 describing a particularly strong effect of the abundance of *Plantago* on *Trifolium* and *Chenopodium*.

The growth of individuals of *Trifolium* and *Chenopodium* was strongly suppressed by variation in the abundance of *Agropyron* and *Plantago*. Neither *Trifolium* or *Chenopodium* appeared to ever limit their own abundance. The abundances of *Trifolium* and *Chenopodium* did appear to have some effect on the growth of *Plantago*; however, in each case, this effect was only apparent in one of the four possible models. These results are also in agreement with my previous experiments which had suggested that *Chenopodium* and *Trifolium* were competitive subordinates (Chapter 3).

The term for complex intraspecific effects in model 4 never exhibited a significant partial correlation coefficient. This can be interpreted two very different ways. It is possible that complex effects are simply not important in these two species mixtures.

However, the models only reflect the dynamics that change within the range of abundances of the two species used in the experiments. It is also possible that complex effects are important in these mixtures but are not changing in intensity over the ranges of abundance used. It is not possible to separate these two alternatives using the ranges of abundance obtained in this study.

This general approach of comparing the results to several a priori models is susceptible to several types of errors. First, the curve-fitting approach is only correlational. The equations may provide a mathematical description of the interrelationships among the variables, but they provide only circumstantial evidence for any particular biological mechanism. That is, the models may demonstrate that two variables arranged in a particular mathematical form are highly correlated, but they do not claim that a change in the value of one variable actually causes a change in another in the manner described by the model.

Second, the models can only be used to understand dynamics that both occur and change over the range of abundances investigated. This is particularly important when exploring non-linear systems. Both this study and many others (e.g. the reciprocal yield law) suggest that plants exhibit a negative hyperbolic response to an increasing abundance of competitors. This suggests that at very high yields, there will be very little change in the effect of the competitor on the focal species, even though the overall magnitude of the effect may be very large. This phenomena appears to be occurring, for example, when Ambrosia was grown with Chenopodium (Figure 4.2). Models based on multiple regression are dependent upon the range of the parameter values: variation in the yield

Ambrosia demonstrates no significant effect upon the growth Chenopodium because a high range of yields was used, not because Ambrosia does not suppress Chenopodium.

CONCLUSIONS

The species interactions in a multispecies mixture can be viewed as a web of reciprocal cause-effect pathways. The abundance of an associate species affects the growth of a target, which then changes the yield of the target species, which changes the effect of the target species on itself and its reciprocal effect upon the original associate species, etc. I have measured the mean response of individuals of each species to varying the abundance of competitors. This has been done in increasingly complex communities, varying the abundance of intraspecific competitors alone, interspecific competitors alone, and both intra- and interspecific competitors simultaneously.

The experiments suggest that individuals of most species in this community exhibit a highly non-linear response to competition. The response curve demonstrated by Plantago, Trifolium, and Chenopodium resembles a negative hyperbolic response, with increases in the yield of an associate species reducing the success of focal individuals more at lower total yields. This type of pattern has been previously noted in many studies, both in agricultural monocultures (as expressed by the reciprocal yield equation) and in natural communities (e.g. Weiner 1982).

This non-linear response may, in part, explain the hierarchy of competitive effect demonstrate both in Chapter 3 and here. The yield of Ambrosia in this community is always quite high, as the growth of individuals of Ambrosia is not affected by the presence of other species. The result is that the yield of Ambrosia as an associate is generally past the point of inflection of the non-linear response curve for most focal species: the presence of Ambrosia strongly suppresses the growth of other species. This in turn may explain why other species have no competitive effect on Ambrosia; they exhibit a large competitive response to Ambrosia and so never achieve a large biomass which might affect the growth of Ambrosia. In contrast, the yield of Chenopodium is very low in almost all situations, as individuals of this species are strongly suppressed by the presence of most other species. Thus, the presence of Chenopodium has very little effect on the growth of other species, which in turn allows these other species to achieve a size which influences the growth of Chenopodium. So, it appears that competitive effect and response are inversely correlated, but it is not clear how much each actually determines the other. These processes cannot be easily disentangled.

I can find no evidence that the competitive effects of species are in any way independent of their yield. The five species examined appear to have a general equivalence of competitive effect. The appropriate test of this hypothesis is to examine the competitive effect of two different associates at the same yield on a single focal species. Unfortunately, it is very difficult to reduce the yield of Ambrosia because of the large size achieved by individuals and it is very difficult to increase the yield of Chenopodium and Trifolium because individuals never achieve a large size when in the presence of a competitor. It may be impossible to achieve equal yield of these species because cause and effect cannot be separated

Finally, no strong evidence was found for the importance of complex intraspecific interactions in two-species mixtures. The results were generally explained sufficiently by the simple intraspecific and interspecific effects.

Chapter 5

ANALYSIS OF MULTISPECIES INTERACTIONS

The major challenge for community ecology is to understand how all the intraspecific and interspecific interactions mesh together in a multispecies system. In multispecies systems, each species potentially can be limited by not only simple intraspecific and interspecific effects, but also by a host of different complex effects derived from interactions between simple effects. The purpose of this chapter is to determine what types of species interactions are important in this plant community and how the interactions combine to generate the full community structure. Specifically, the questions to be addressed are 1) what are the strengths of the various types of biotic interactions (simple intra- and interspecific and complex intra- and interspecific) for each of the species when in the full community and 2) how do the different interaction effects of several associate species "sum-up" to a net effect on a focal species?

The fact that ecologists have a very poor understanding of the importance of the different types of interactions in multispecies systems is due in part to two problems. The first problem is a methodological problem inherent in complex systems, termed the "multi-body problem". Simply put, it is very difficult and sometimes impossible to find general analytic solutions to problems which have many interacting variables. Examples include attempts to understand how planetary motion is affected by the gravitational influences of other bodies and in understanding the motion of charged atomic particles in relation to one another (Pines 1961). In community ecology, the interacting variables are the abundances of the various species and the analytic solution we are attempting to determine would include terms for each of the different types of species interactions.

The second problem is that complex interspecific effects do not exist as separate, distinct interactions; complex effects are the result of combinations of two or more direct effects (simple intra- or interspecific effects). The complex effects occur when one or more of the direct effects changes the magnitude of another direct effect on a focal species. This can occur in at least three distinctly different ways. 1) Indirect Effect - A second associate species has a direct effect on the abundance of a first associate species (Figure 1.1d). This in turn changes the effect of the first associate species on the focal species. 2) Higher-order Effect - A second associate species has a direct effect on the mechanism of interaction between the first associate species and a focal species without affecting the abundance of the first associate species (Figure 1.1f). This also changes the direct effect of the first associate species on the focal species. 3) There is a distinct type of higher-order interaction that I will discuss separately in this chapter. Compound Effects do not involve a loop of direct effects, but involve two or more direct effects both operating on the same focal species. A second associate species has a direct effect on the focal species that changes the ability of the focal species to respond to the presence of the first associate species. Once again, the presence of the first associate species changes the effect of the second associate species on the focal species. Compound effects have not previously been noted, but might be quite important in species which experience highly plastic growth such as found in most plants.

All three types of complex interspecific interactions can be quantified by determining how much the direct interactions between two species is changed by the presence of a third species. In each case, the mathematical representation of the complex effect on the focal species is a term that included both the abundance of the first and the second associate species (e.g. N_1N_2 or $1/(N_1+N_2)$). Finally, to make things a bit more complex, it is quite conceivable that two or more different complex interactions might be occurring simultaneously.

In this chapter, I present the results of species growth in the four- and five-species experiments. These experiments provide a measure of the total effects between all possible pairs of species. I then propose a model of plant interference that describes the success of individuals as a function of the abundance of their competitors. This model is discussed and supported using data from all of the experimental plots. The model is used to estimate the relative importance of simple and complex interspecific effects in the full five-species community.

Summary of Methods

All experiments were performed in Bailey Field during 1982 (Year 1) and 1983 (Year 2). The general methods will be summarized here; a detailed description of the methods can be found in Chapter 2.

Most of the analysis in this chapter uses the results of species growth in four- and five-species mixtures. Both years of the study used the species *Ambrosia*, *Agropyron*, *Plantago*, and *Chenopodium*, with the fifth species being *Lepidium* in Year 1 and *Trifolium* in Year 2. All other species were removed from the plots. Six different treatments were used, consisting of all the possible one-species removals (resulting in four-species mixtures) and the five-species "full" community. Three (Year 1) or five (Year 2) replicates of each treatment were maintained in plots arranged in a random block design. The species removals were initiated by hand weeding in early May and then maintained throughout the summer through weeding or the use of a contact herbicide. At the end of September in both years, all plants within the center section of the plots were harvested for above-ground biomass, oven dried, and weighed. The data from Year 1 were analyzed using a nested analysis of variance, with individual plant weights nested within plot. The greater replication used in Year 2 allowed the use of the Welsh Step-up test (Sokal and Rohlf, 1981) to determine pairwise differences in treatment effects.

Analysis of the Field Data

Species can respond in several different ways to the presence of an associate species. I have measured two different types of response in this study: survival and growth. *Trifolium* is the only species that demonstrated a significant survivorship response to competitive effects from different species (Table 5.1), although *Chenopodium* demonstrated a similar but non-significant pattern. The survival probability of *Trifolium* is extremely low in the full community (26% survival) and with only *Chenopodium* or *Plantago* removed (2% and 27% respectively). However, removal of either of the dominant species, *Ambrosia* or *Agropyron*, increased the survival of *Trifolium* to over 60%. Neither *Ambrosia* or *Plantago* had any mortality in any of the treatments. It was impossible to quantify the survivorship of *Agropyron* genets due to its

Table 5.1 Percent survival of focal individuals following the removal of different associate species in Year 2. Values in the same row with different letters are significantly different ($p<.05$, Welsch Step-up Test). A dash indicates that the mortality could not be observed for that situation.

Focal	Associate Species Removed					full
Species	Ambr.	Agro.	Plan.	Trif.	Chen.	community
Ambrosia	–	1.00a	1.00a	1.00a	1.00a	1.00a
Agropyron	–	–	–	–	–	–
Plantago	1.00a	1.00a	–	1.00a	1.00a	1.00a
Trifolium	.67a	.61a	.27ab	–	.02ab	.26b
Chenopodium	.88a	1.00a	.92a	1.00a	–	.78a

rhizomatous growth, but no death of shoots or culms was noted in any of the treatments.

These experiments demonstrate the response in the growth of a focal species to the removal of different associates and, looked at a different way, the effect of a single associate on the growth of different focal species. Data on the mean individual growth for each species in the five-species and all of the possible four-species combinations are shown in Figure 5.1. The most obvious pattern is the large effect the removal of Ambrosia has on the growth of Plantago, Lepidium, Trifolium and Chenopodium (Figure 5.1). In the most extreme case, the removal of Ambrosia increased the growth of Chenopodium in Year 2 by almost 900% (from .054 to .479 g/individual). Ambrosia did not have a significant effect on the yield of Agropyron in either year of the study. The removal of no other species had as great an effect on the growth of a focal species. In fact, only the removal of Agropyron, and in one instance, Plantago (with Lepidium), had any effect at all on the growth of any focal species. This is in general agreement with the two-species experiments which found a hierarchy of competitive effect with Ambrosia > Agropyron > Plantago > Lepidium = Trifolium = Chenopodium. However, in the two-species studies, Agropyron generally had a large competitive effect and Plantago had a smaller, but significant, competitive effect on species lower in the hierarchy. In the removal studies, both of these species only have either very small competitive effects, or they have no effect at all.

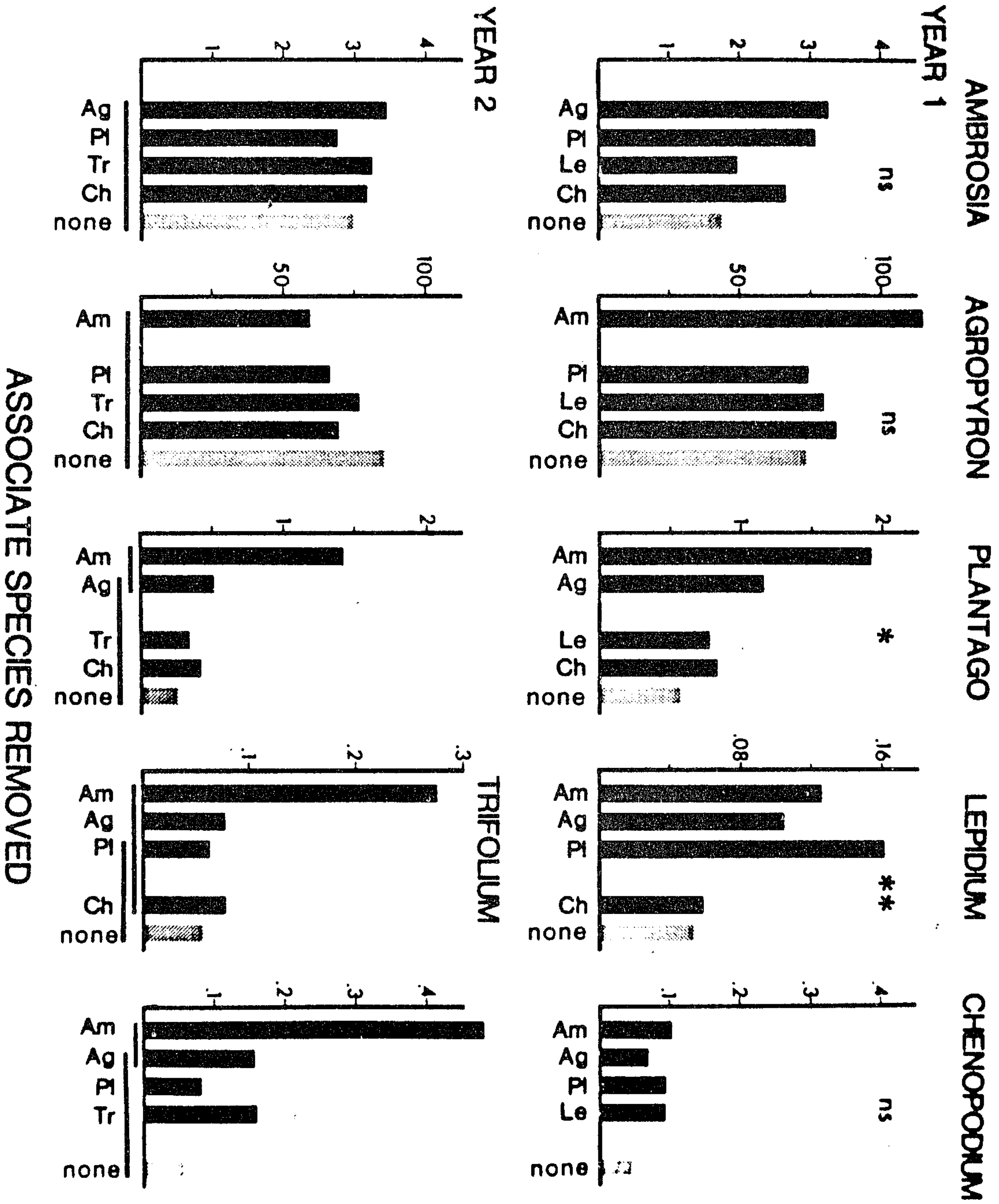
The hierarchy of competitive response is also similar to that found in the two-species experiments. Ambrosia and Agropyron demonstrated almost no response to the removal of any other species, while

Figure 5.1. The mean growth of individuals of each species in the full community and in all possible single species removals (four-species treatments) in Year 1 (top) and Year 2 (bottom). Below the bars in each figure are the results of all-pairs analysis for the effect of removing different associate species on growth of the focal species. Species mixtures underlined by the same line do not differ significantly ($p<.05$, Welsh step-up test).

Figure 5.1

PERFORMANCE OF FOCAL SPECIES

mean g/individual (g/m for Agropyron)



Chenopodium, Lepidium, and Trifolium all demonstrated a strong response to the removal of Ambrosia. Again, the hierarchy is not as clear-cut as it is in the two-species experiments. In general, the focal species in the full community do not respond as dramatically to the removal of an associate as they did in the one- and two-species experiments.

There were some differences in the growth of the species between the two years of the study. Individuals of Ambrosia in the five-species community were smaller in Year 1 than in Year 2 (1.72 g and 2.98 g, respectively). Plantago showed the opposite response, obtaining a larger individual size in Year 1 than in Year 2 (.57 g and .26 g, respectively). The other two species demonstrated very similar performance in the two years. This is in general agreement with the between-year patterns exhibited by the monoculture plots (see Chapter 3).

A Model of Plant Interference

The response of a focal species to the removal of a single associate species provides a measure of the total effect of this associate in suppressing the focal species in the full community ('press' experiments, Bender et al. 1984). Because direct (simple) and complex interspecific effects are simultaneously relieved following the removal of an associate, neither can be directly and independently measured. The total effect is the only interaction that we can experimentally measure.

To estimate the interspecific direct (simple), indirect, and higher-order components of the total effect, I have constructed a general model of plant interference that describes the mean performance of each species as a function of the abundance of the other species in the community. The model provides estimates of the simple and complex effects between species, allowing an understanding of the relative importance of the different types of interactions occurring in a multispecies community. The model is supported using data from plots containing one, two, four, and five species in various combinations.

The structure of the model is based on the response demonstrated by each focal species to the increasing abundances of different associate species. In a n-species system, the response would be represented in (n+1)-dimensional space, each independent axis representing the effect of a different associate species. The difficulty expressed by the multi-body problem is that the predicted response in (n+1)-dimensional space is usually extremely difficult to determine.

The results of the two-species experiments provide a method to overcome this dilemma. The two-species experiments suggest that there may be a general per-amount equivalence of effects (see Goldberg and Werner 1983). That is, any single focal species seems to respond to the same degree to the presence of a set amount of any associate species, no matter the identity of the associate species. The biomass of the neighboring individual is the most important factor determining its competitive effect upon a focal individual. It should be noted that different focal species do respond in different ways, i.e. it is an equivalence of competitive effect, not response. If we can assume that there is an equivalence of effect, then the axes in the n-dimensional space that give the abundance of each associate species can be collapsed into a single axis. Figure 5.2 demonstrates the general model in which the total combined yield (dry weight biomass/m^2) of the associates

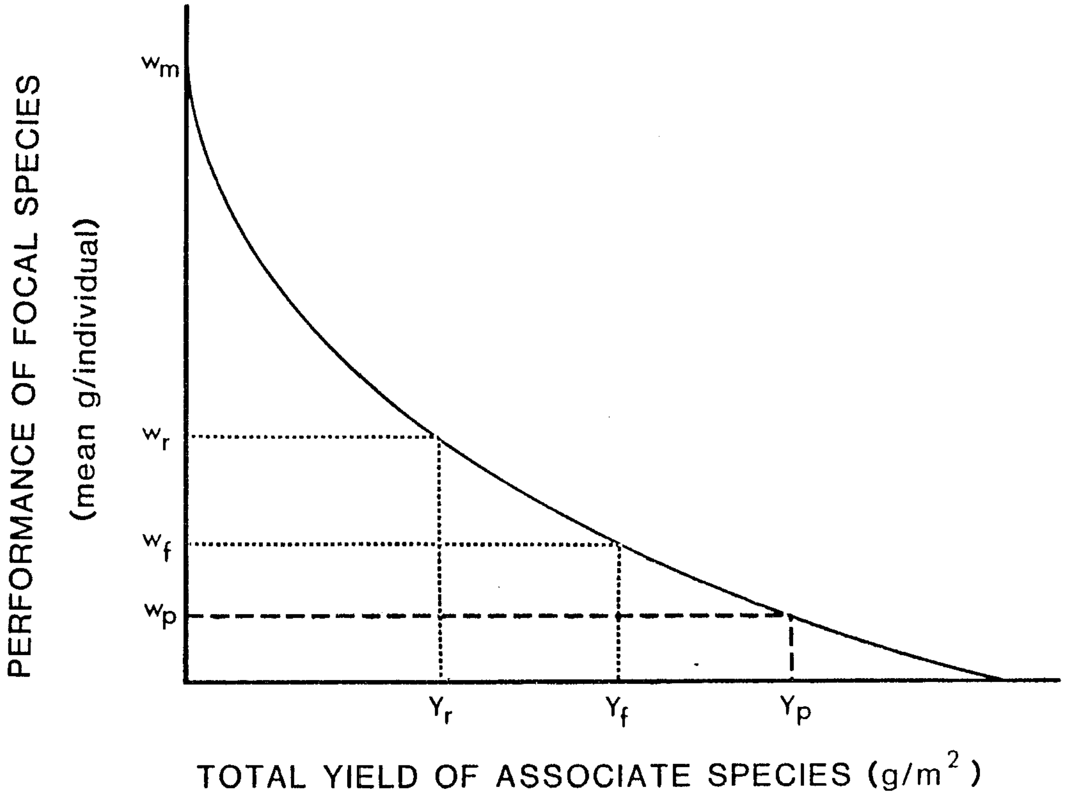


Figure 5.2. The hypothetical relationship between the mean growth of individuals of the focal species and the total yield of the associate species (biomass/m^2). Y_f is the total yield of associate species in the full community, Y_r is the total yield of associate species when a selected associate species has been removed from the community, and Y_p represents the predicted total yield of associate species if the selected associate species has no indirect effects on the focal species. w_m is the expected mean growth of individuals of the focal species when no competitors are present, while w_f, w_r, and w_p represent the expected mean growth of individuals of the focal species at Y_f, Y_r, and Y_p, respectively.

determines the mean biomass of individuals of the focal species. The total combined yield of the associate species in the full community (Y_f) describes the mean success of individuals of the focal species in the full community (w_f). The value w_m represents the expected success of the focal species when no associates are present (without competitors; see Table 5.2).

Note that in this model, the total yield (dry weight biomass/m^2) of associates does not include the yield of the focal species. This is a methodological problem. I could only directly control species density, which can have an intraspecific effect on both mean performance and yield. So, I was not able to manipulate the yield of a focal species independent of mean performance. By not including the effect of the yield of the focal species on itself, the model is restricted to analyzing species which are not affected by strong intraspecific effects. However, if a response curve such as that in Figure 5.2 can be established for a focal species, it would suggest that the abundance of this species does not affect its own success (no intraspecific effects). This might occur if either the density of the focal species was low and/or the sizes of individuals were small, so that the plants effectively had no interactions with conspecific individuals.

This model allows a straightforward quantification of the total, direct (simple interspecific) and indirect interspecific competitive effects of an associate species on a target species. Given equivalence, the effect of a particular group of associate species on a focal species is a function of the sum of the yield of these associates. This net effect of all associates can be quantified as the percent reduction of the focal species:

Table 5.2 Definitions of terms for a model of multispecies interactions.

Y_n = yield (biomass/m^2) of the associate species of interest when grown in the full (five-species) community.

Y_f = total yield of all associate species when grown in the full community.

Y_r = total yield of all associate species when grown in community with the associate species of interest removed.

Y_p = predicted total yield of all associate species when grown in the full community if no indirect effects occur.

w_m = mean weight of individuals of the focal species when no individuals of the associate species are present.

w_f = mean weight of individuals of the focal species when grown in the full community and associate yield = Y_f.

w_p = predicted weight of individuals of the focal species in the full community if no indirect effects occur and associate yield = Y_p.

$$\text{effect of total associate yield on the focal species} = \frac{(w_m - w_f)}{w_m} \qquad (1)$$

where w_m and w_f are the mean weight of individuals of the focal species in monocultures and the full community, respectively (see Table 5.2). The contribution of each associate to this net competitive effect is directly proportional to its contribution to the total yield of associates. So, the total effect of a particular associate species on the focal species can be quantified as the percent reduction of the focal species caused by the yield of a specific associate species:

$$\text{total effect of species } n = \left(\frac{Y_n}{Y_f}\right)\left(\frac{w_m - w_f}{w_m}\right) \qquad (2)$$

where Y_n is the yield of the specific associate species in the full community. The value of the total effect of species n will range from negative infinity to 1, with values less that 0 indicating a facilitative effect and values greater than 0 indicating an antagonistic (competitive) effect.

Because the model allows us to predict the growth of the focal species based only on the total yield of associate species, the direct and indirect effects can be understood as the effect of adding a selected associate species on the total yield of associates previously found when this selected associate species was not present. The addition of a selected associate species affects the total yield in two distinctly different ways. First, the yield of the selected associate (Y_n) directly increases the total yield of associates (Y_r). This is quantified by the model as how much the mean growth of individuals of the focal species is affected by this change in the total yield of the associate species. Secondly, the presence of the selected associate species can change the yields of the other associates (and so change Y_r). This is quantified as the indirect effect of the selected associate on the focal species.

The data to estimate the direct and indirect effects is thus obtained from the four- and five-species mixtures. The direct effect is quantified from the direct increase in yield expected from the addition of the selected associate species. The expected total yield of associates in the five-species mixture is then:

$$Y_p = Y_r + Y_n \tag{3}$$

Using this total yield of associates as an estimate of the direct effects of the whole associate species group, an estimate of the direct effect of the single selected associate species on the focal species can be obtained:

$$\text{direct effect} = \left(\frac{Y_n}{Y_f}\right)\left(\frac{w_m - w_p}{w_m}\right) \tag{4}$$

where w_p is the predicted success of the focal species at Y_p (see Table 5.2). The estimated indirect effect can be found simply by difference:

$$\text{indirect effect} = \text{total effect} - \text{direct effect} = \left(\frac{Y_n}{Y_f}\right)\left(\frac{w_p - w_f}{w_m}\right) \tag{5}$$

Both the direct and indirect effect represent a percent reduction in the maximum potential growth of individuals of a focal species. Note that when there are no indirect effects, $Y_p = Y_f$ and $w_p = w_f$ and equations 2 and 4 are equivalent.

Evaluation of the Model

The critical requirement of this model is that the success of the focal species is a function of the total yield of the associate species. To test this assumption and to allow an estimation of the direct and indirect effects, response curves were evaluated for all species in both Year 1 and Year 2 using all experimental plots which included each focal species with any associate species or combinations of associate species. The mean performance of individuals of the focal species was measured as a function of the total combined yield of all of the other species in the plot for Year 1 (Figure 5.3) and Year 2 (Figure 5.4).

The data were analyzed using regression analysis. The choice of the relationship used to describe each curve was somewhat subjective. I wished to determine equations which would demonstrate the shape of the whole response curve and at the same time minimize the variance over the portion of the curve used to estimate direct and indirect effects. The portion of curve used for predictions is the right-hand side: where necessary, transformations were used to weight the residuals over the whole length of the response curve (generally log-log transformation). The equations for each curve are presented in Figures 5.3 and 5.4. The value of w_m, the success of the focal species in the absence of associates, was determined from monocultures of each species maintained at the natural density (see Chapter 3).

The response curves support use of the model for species which are lower in the competitive hierarchy. The responses of Plantago, Lepidium, Trifolium, and Chenopodium in both years are clearly a function of the total yield of associates (Figures 5.3 and 5.4). And in

Figure 5.3. The effects of the total yield of associate species on the growth of individuals of the five focal species in Year 1. The points indicate the mean wt/individual of the focal species across all treatment plots (grown with either one, three, or all four of the associate species). The value w_m is the yield of a species when found in monoculture (no competitors present). The equations and r^2 values describe the line indicated on each figure.

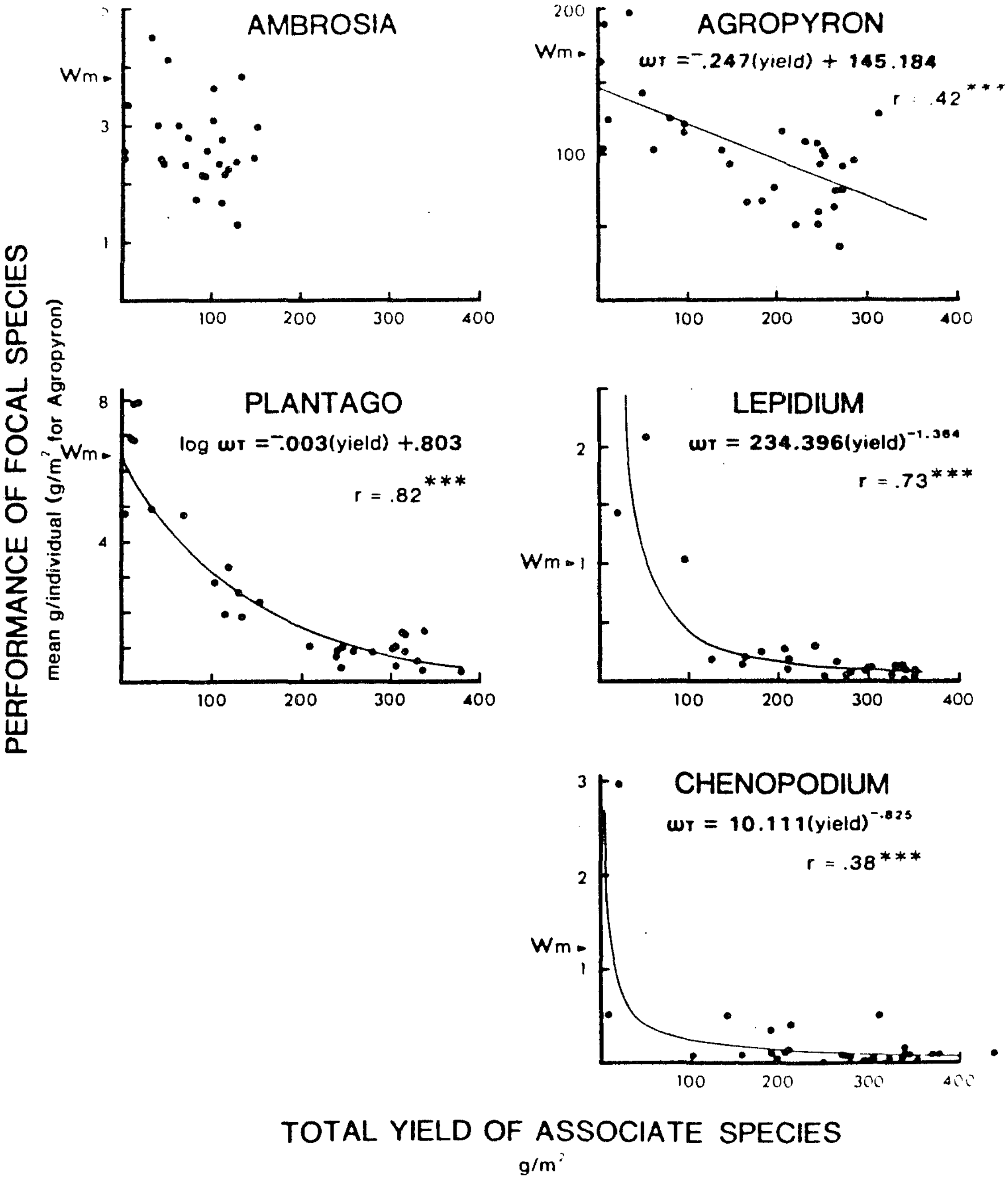

PERFORMANCE OF FOCAL SPECIES
mean g/individual (g/m² for Agropyron)
TOTAL YIELD OF ASSOCIATE SPECIES
g/m²
AMBROSIA
Wm
3
1
100
200
300
400
AGROPYRON
200
100
Wm
ωT = ⁻.247(yield) + 145.184
r = .42***
100
200
300
400
PLANTAGO
8
4
Wm
log ωT = ⁻.003(yield) +.803
r = .82***
100
200
300
400
LEPIDIUM
2
Wm 1
ωT = 234.396(yield)^-1.364
r = .73***
100
200
300
400
CHENOPODIUM
3
2
Wm
1
ωT = 10.111(yield)^-.825
r = .38***
100
200
300
400

Figure 5.3

Figure 5.4. The effects of the total yield of associate species on the growth of individuals of the five focal species in Year 2. The points indicate the mean wt/individual of the focal species across all treatments plots (grown with either one, three, or all four of the associate species). The value w_m is the yield of a species when found in monoculture (no competitors present). The equations and r^2 values describe the line indicated on each figure.

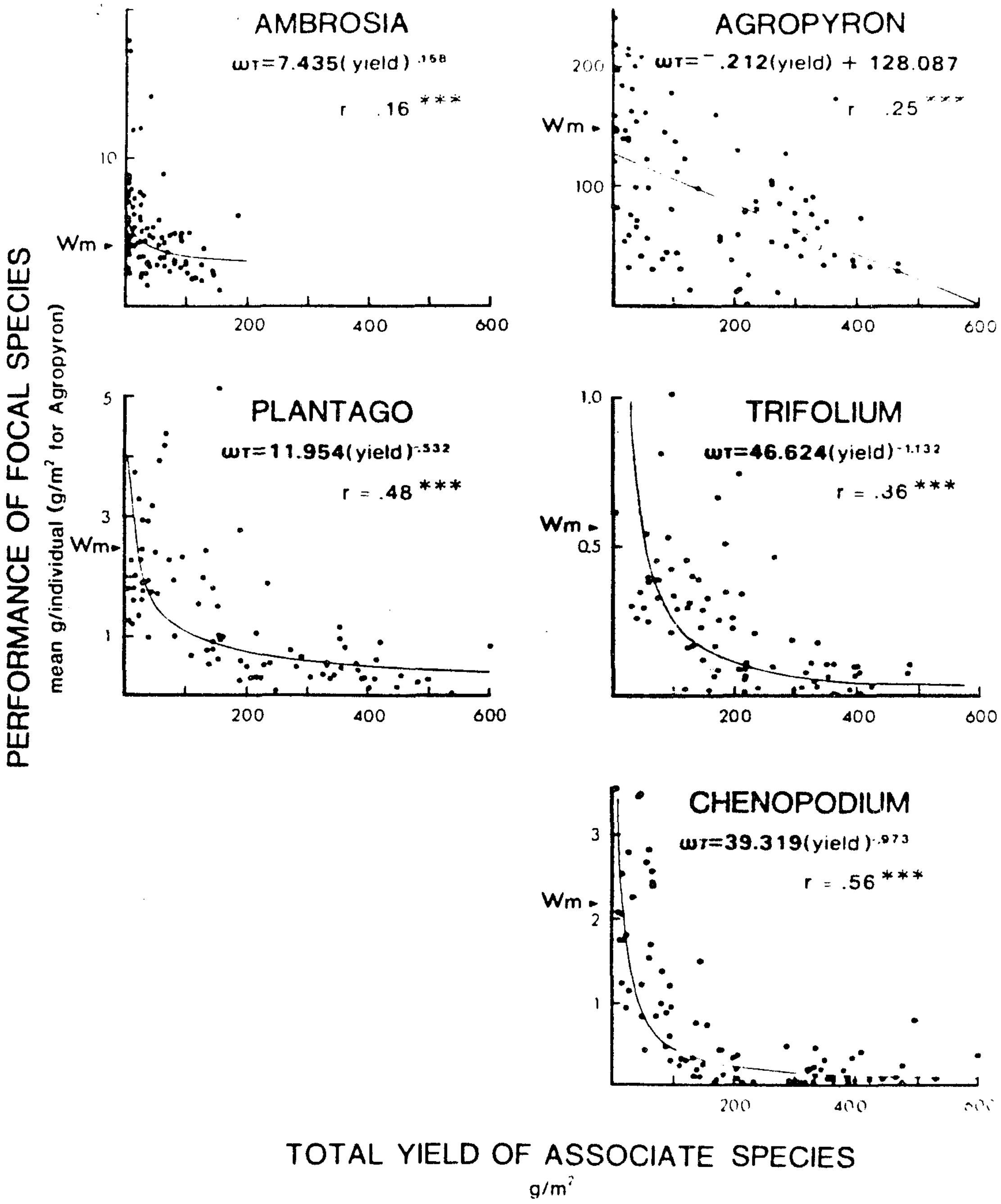

AMBROSIA
ωT=7.435(yield)-.158
r .16 ***
10
Wm
200
400
600
AGROPYRON
ωT= -.212(yield) + 128.087
r .25 ***
200
Wm
100
200
400
600
PLANTAGO
ωT=11.954(yield)-.532
r = .48 ***
5
3
Wm
1
200
400
600
TRIFOLIUM
ωT=46.624(yield)-1.132
r = .36 ***
1.0
Wm
0.5
200
400
600
CHENOPODIUM
ωT=39.319(yield)-.973
r = .56 ***
3
Wm
2
1
200
400
600
PERFORMANCE OF FOCAL SPECIES
mean g/individual (g/m² for Agropyron)
TOTAL YIELD OF ASSOCIATE SPECIES
g/m²

Figure 5.4

each case, the response curve appears to be highly non-linear. The data were generally described best using a log-log transformation of the data, which also provided a homogeneous variance (r^2 values are given in Figures 5.3 and 5.4). The yield of Agropyron was a linear function of the total yield of associates in both years of the study. For Ambrosia, there was no significant effect of total yield of associates on mean growth in Year 1 and there was only a very weak relationship in Year 2 (R^2=.16). This may, in part, be caused by the small range in the yield of associate species found with Ambrosia.

The Y_r and Y_n for each associate-focal species pair were determined from the results of the four- and five-species experiments and used to predict the total yield in the absence of an indirect effect, Y_p. The equations describing the relationship between focal species success and total yield (Figure 5.3 and 5.4) were then used to determine w_p, the predicted success of the focal species in the absence of indirect effects. Since no strong effect of yield on growth was found for Ambrosia in either year of the study, it was impossible to estimate the direct and indirect effects of other associate species on Ambrosia. The direct, indirect, and total effects for the remaining associate-focal species pairs were determined using equations 2, 4, and 5.

The results are presented for both Year 1 and 2 in Table 5.3. Each value represents the direct or indirect effect of the associate species in changing the maximum growth of the focal species (w_m). Positive values indicate an antagonistic competitive effect while negative values indicate a facilitative effect.

Note that all of the direct effects are positive in value (or zero), indicating a competitive effect of the associate species on the

Table 5.3 The estimated direct (D) and indirect (I) effects between species in Year 1 and 2. Values represent the percent reduction in maximum potential growth of individuals of the focal species. Positive values indicate a competitive effect; negative values indicate a facilitation effect.

YEAR 1.

	Associate Species									
	Ambrosia		Agropyron		Plantago		Lepidium		Chenopodium	
Focal species	D	I	D	I	D	I	D	I	D	I
Agropyron	.428	-.063	-	-	.062	-.011	.001	.000	.006	-.001
Plantago	.598	-.038	.276	-.030	-	-	.001	.000	.008	-.001
Lepidium	.580	-.024	.257	-.012	.079	-.003	-	-	.007	.000
Chenopodium	.591	-.011	.260	-.006	.081	-.001	.001	.000	-	-

YEAR 2.

	Associate Species									
	Ambrosia		Agropyron		Plantago		Trifolium		Chenopodium	
Focal species	D	I	D	I	D	I	D	I	D	I
Agropyron	.560	-.097	-	-	.066	-.010	.000	.000	.007	-.001
Plantago	.563	-.008	.218	-.006	-	-	.000	.000	.007	.000
Trifolium	.596	-.012	.228	-.005	.072	-.001	-	-	.008	.000
Chenopodium	.627	-.003	.240	-.002	.076	-.001	.000	.000	-	-

focal species, while the indirect effects were negative (or zero), indicating a facilitative effect. Some of the direct effects were quite large; for example, the presence of Ambrosia in the five-species community in Year 2 reduced the growth of Chenopodium by 63 percent. In many cases the effects were quite small; Lepidium, Trifolium, and Chenopodium had virtually no effect on the other species.

The main factor determining the magnitude of the direct effect was the identity of the associate species, with the Ambrosia reducing the growth of other species by from 43 to 63 percent, Agropyron by 22 to 28 percent, Plantago by 6 to 8 percent, and Trifolium, Lepidium, and Chenopodium never reducing the growth by more than 1 percent. This is a remarkably consistent competitive effect of each associate. The identity of the focal species also affects the value of the direct effect, with Agropyron being the least affected by any associate species and Chenopodium generally being the most affected. Once again, the hierarchy of competitive effect and response was apparent.

Of particular interest is that the indirect effects are both negative (or zero) and very small, contributing very little to the total effect. The relationship between the direct and the total effects was examined using the reduced major axis method to determine an independent regression line between the pairs of total and the direct effects (Kermack and Haldane 1950). If there were no significant indirect effects, the relationship between the total and direct effects would be described by a line of 45 degrees passing through the origin. In both years, the relationship was defined by lines with slopes slightly less than one (Year 1 - .95, Year 2 - .96), yet still passing through or very near the origin (Figure 5.5). So, the data indicate not only that the

Figure 5.5. The relationship between the direct and total effects of associate species on focal species for each associate-focal species pair in Year 1 (top) and Year 2 (bottom). The line in each figure represents where total effect = direct effect and the indirect effect = 0. The indirect effect is the deviation between the line and each point along the abscissa.

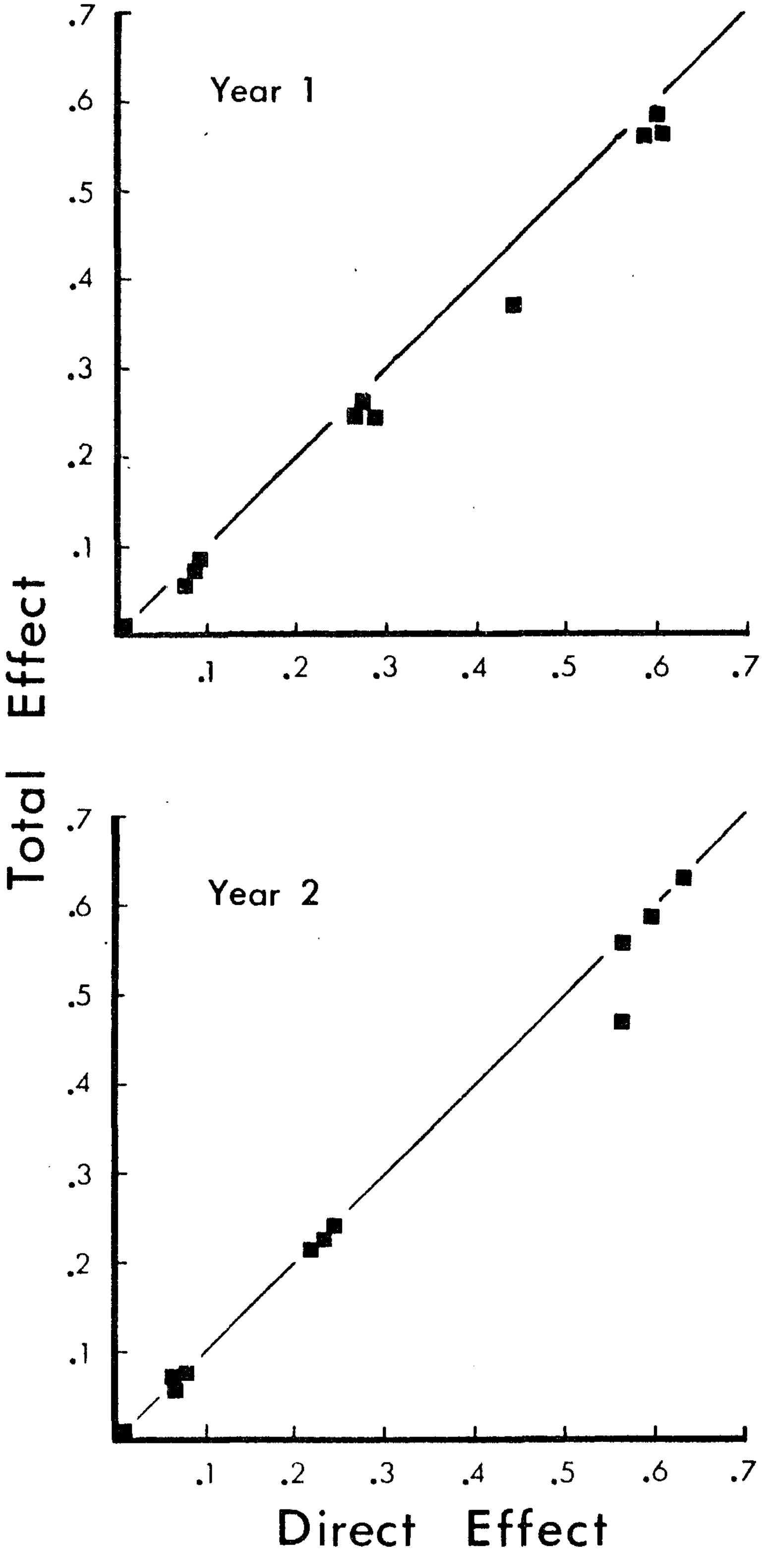


Figure 5.5

indirect effects in this community were small relative to the direct effects, but also that they generally increased as the direct effect increased (Table 5.3). The fact that the indirect effects were always negative or zero indicates that, in this community, the addition of an associate always decreased or had no effect on the abundance of other associates.

The measure of indirect effects (equation 5) only includes effects in which an associate species changes the abundance of a second associate and thus changes the effect of the second associate on the focal species. If there were significant higher-order effects, in which the mechanism of interaction is affected without affecting the abundance of the associate, then the response curves could not have been generated. That is, the fact that the total yield of associates predicts the success of the focal species suggests that higher-order effects are not important in this weedy plant community.

DISCUSSION

The use of the model to quantify the direct and indirect effects indicates that most of the total effect between species is caused by the direct interactions, and not by indirect pathways of interaction (Table 5.3). The indirect effects were also all facilitative; they acted in the opposite direction as the direct competitive effects. This would be expected as the presence of a dominant associate species in the community reduces the yield and potential competitive effect of each of the other associate species.

It was somewhat unexpected that the indirect effects would be very small. For example, it was known from the two-species studies that

Agropyron has a strong competitive effect on Chenopodium and that Ambrosia had a strong competitive effect on Agropyron. My expectation was that Ambrosia would have a strong facilitative indirect effect on Chenopodium because of its effect in reducing the abundance of Agropyron. However, because the yield of Ambrosia in the full community is large, the direct effect of Ambrosia is to reduce the size of Chenopodium to a very small size. As the size of Chenopodium is reduced, its response to the changes in total yield decrease. The response curve for Chenopodium in Figures 5.2 and 5.3 demonstrates that the curve appears to asymptotically approach zero success for the focal species as the total yield increases. At this point any affect that Ambrosia has in reducing the abundance of Agropyron simply has little net effect on Chenopodium.

Two factors seem to be important in restricting the importance of indirect effects: the shape of the response curve and the amount of the direct effect. Because of the hierarchy of competitive effect found in this community, any large direct effect 'pushes' the response curve into the asymptotic region where neither direct or indirect effects have large effects on the focal species. Species having small direct effects on the focal species generally have small direct effects on the other associates as well, and again the potential for indirect effects is quite small.

It appears that the assumption of equivalence of competitive effects can be relaxed somewhat without changing the general conclusions about the importance of indirect effects. For example, if one gram of Ambrosia had the same competitive effect as three grams of Chenopodium, the conclusions of the model would still hold. In fact, the simple model presented here could be used by converting grams of *Chenopodium* into an amount of *Ambrosia* "units" having the same competitive effect. The assumption of equivalence is only important in allowing the construction of a simple model of competitive effects.

The third type of complex interspecific effect, compound effects, do appear to be very important in this community; however they are difficult to quantify. A measure of the importance of compound effects is given by the shape of the response curve. The response curve demonstrates the ability of the focal species to respond to the presence of a competitor. If the response curve is linear, then the per-amount response of the focal species to competitors is constant and there are no compound effects. If the response is curvilinear, then the ability of the focal species to respond to competitors changes with the total yield of the community and the per-amount effect of any associate species on the focal species would be dependent upon the total yield of the rest of the associates. The data indicate that the response curve for *Agropyron* is fairly linear, indicating only that the magnitude of the compound effects, if present, is not changing over the range of associate yield investigated. However, *Plantago*, *Lepidium*, *Trifolium*, and *Chenopodium* all exhibit highly nonlinear response curves, indicating that compound effects are operating, particularly at higher yields.

The model requires making two critical assumptions. First, it assumes that there is a general equivalence of competitive effects by different associates. That is, the effect of a unit of associate species on the focal species is constant, no matter what the identity of the associate. Secondly, the model assumes that the intraspecific effects on the focal species are minimal.

The assumption of equivalence is critical because it allows the determination of a simple relationship between focal species success and the abundance of competitors. This assumption is not unreasonable for this community (see Chapter 4). Non-equivalence would lead to a very poor relationship between focal species success and total associate yield. In fact, the relationship is actually quite good, except when *Ambrosia* is the focal species. It is not clear whether a poor relationship between *Ambrosia* success and total associate yield is due to non-equivalence, high intraspecific effects, or to the very small range of associate species yields that were produced when grown with *Ambrosia*.

A similar general equivalence of competitive effects was found by Peart (1982) in grassland plant communities and Goldberg (in review) in a mid-successional old-field community. Goldberg and Werner (1983) argue that equivalence should be expected among plant species of similar growth form. They suggest that a homogeneity of resource requirements, diffuse competition, and strong size asymmetries between competing individuals will lead to a general equivalence of competitive effect. The weedy community in Bailey Field generally meets these requirements: though all individuals begin as similar-sized seedlings, a strong size asymmetry develops with 4-6 weeks.

The assumption of low intraspecific effects on the focal species also appears to be valid for most of the species. When grown in the full community, the individual plants of *Plantago*, *Lepidium*, *Trifolium*, and *Chenopodium* are so small that it is rare for individuals of the same species to be in contact with one another. However, intraspecific effects do appear to restrict the growth of *Ambrosia* and, to a more limited extent, Agropyron. If the intraspecific effect is strong, it can seriously bias the response curve. As pointed out earlier, it was for this reason and because of the possible non-equivalence, that the model was not used to investigate the growth of Ambrosia in the full community.

Several other studies have proposed measures of total, direct, and indirect competitive interactions. In fact, three studies proposed measures requiring data from single-species removal studies similar to the experiments used here (Lawlor 1977, Silander and Antonovics 1982, Bender et al. 1984). However, the mathematics used to determine Lawlor's gamma value and Bender et al.'s a_{ij} require that the community return to equilibrium following the removal of species. This would be impossible in this study and, in fact, neither Lawlor or Bender et al. provide evidence from studies in any natural system. Silander and Antonovics applied their measure of "removal response" (total effect) to a set of coastal plant communities. While their measure provides an estimate of relative total effects, it cannot be separated in direct and indirect components. But all of the proposed measures, including that proposed in this study, are very similar. All of the studies quantify an interaction effect as a function of the amount of response of the focal species and the amount of associate species present.

One of the questions originally set out in the beginning of this chapter was to understanding the relative importance of the different types of interactions that can potentially affect each species in the full community. The species in this community are restricted by different types of interactions. Ambrosia is the competitive dominant, strongly suppressing most of the other species. No evidence was found that the presence of any other species affects the growth of *Ambrosia*. It is likely that *Ambrosia* has a strong competitive effect on itself. The four- and five-species experiments do not allow a quantification of the intraspecific effect. However, the monoculture and two-species experiments suggest that increasing *Ambrosia* density does lead to reduced growth. So, it is probable that the growth of *Ambrosia* in the full community is strongly affected by intraspecific effects, but not by any other type of interaction.

At the other end of the hierarchy, *Plantago*, *Lepidium*, *Trifolium* and *Chenopodium* are all strongly suppressed in the full community. These species are strongly restricted by direct effects from both *Ambrosia* and *Agropyron* (Table 5.3). The growth of *Plantago*, *Lepidium*, *Trifolium*, and *Chenopodium* in the full community are also strongly affected by compound effects, as indicated by the highly non-linear response curves. It is likely that the growth of these species is not affected by intraspecific effects, on the basis of the response curves and the fact that these species have very little effect on other species. Individuals are very small and, because they are small, only rarely can be found in contact with one another. This suggests that the intraspecific simple and complex effects are not important in regulating the growth of these species. Indirect effects affecting the growth of these species are quite minor. The general pattern is that all of these species are highly suppressed in the full community and that individuals of these species persist in the first-year field only because they become less responsive to increases in competition as they are increasingly suppressed by direct competitive effects.

Agropyron, the species in the middle of the hierarchy, may be the only species that is limited by both strong intraspecific and interspecific effects. The response curves for *Agropyron* (Figures 5.3 and 5.4) do not explain a high amount of the variance in the success of *Agropyron* in different plots. This may be due to the experimental difficulty in controlling the initial density of tillers, but it may also be that the response curve does not include a significant intraspecific effect. Only *Ambrosia* exhibits a strong direct competitive effect on *Agropyron*. The strongest indirect effect found (-.097) is also an effect of *Ambrosia* on *Agropyron*. It is unknown if there is a strong intraspecific higher-order effect of *Ambrosia* on *Agropyron*.

In summary, this plant community seems to be structured by hierarchical, asymmetric direct competitive effects with strong intraspecific effects on the dominant species, *Ambrosia* and *Agropyron*. Indirect effects do not appear to be generally important for two reasons: dominant species are not strongly affected by direct effects of other species and so cannot be affected by indirect effects, while subordinate species are suppressed by direct effects to a size at which they show very little further response to direct or indirect competition.

General Implications

What do the results of this study suggest about complex interactions and the structure of communities? The major factors contributing to the importance of different types of complex interactions in this community are 1) the non-linear response curve exhibited by most species as foci and 2) the hierarchy of species competitive ability. The non-linear curve seems to be a general phenomenon in herbaceous plant species (e.g. reciprocal yield law), and may also occur in other species which exhibit very plastic growth. Unfortunately, very few studies have attempted to determine the form of the response curve of different species to increasing competition (see Schoener 1983).

The hierarchy of species competitive abilities is equally important in determining the importance of complex effects in this community. While few studies have looked at rankings of relative competitive abilities, hierarchies or transitive competitive relationships have been found in other herbaceous plant communities (Pemadasa and Lovell 1974, Pemadasa 1976, Handel 1978, Fowler 1982) and in several other types of sessile communities (e.g. intertidal organisms - Connell 1961, corals - Lang 1973, macroalgae epiphytes - Stebbing 1973). It is interesting to note that all of these other types of communities are space limited systems. As with the plant community in this study, the species in these systems all appear to be limited by and possibly competing for a single resource. It may be this characteristic that leads to competitive hierarchies (however, see Buss and Jackson 1979).

Then most herbaceous plant communities also have non-linear competitive response curves and hierarchies of competitive ability. This suggests that interspecific compound effects may be important in these communities, while interspecific indirect effects will not be important. It is also interesting to consider where these predictions would not hold. First, a linear response curve for any focal species will both eliminate any compound effects and increase the potential magnitude of the indirect effects. This situation was found for

Agropyron in this study, which was affected by the strongest indirect effects of all the species. Second, any disruption of the hierarchy may also produce strong indirect effects in the community, though it may or may not influence the magnitude of the compound effects. For example, species-specific allelopathy by a subordinate species on a competitive dominant might produce strong indirect effects of this subordinant species on other species in the community.

What other types of communities might exhibit non-linear response curves and competitive hierarchies? Possibly sessile marine communities such as barnacles, corals, or algae may exhibit such patterns, but since response curves and patterns of competitive interactions have been very rarely determined for communities, I am not able to answer this question. It appears from this study that the potential for different types of complex interactions to be important exists in many communities. However, it is also clear that we have very seldom sufficiently explored the dynamics of communities to even predict the importance of these interspecific forces.

Chapter 6

GENERAL CONCLUSIONS AND SUMMARY

The results presented in this dissertation on the types and importance of species interactions in a five-species plant community yielded several conclusions:

1. The five species investigated in each year exhibited a consistent hierarchy of competitive ability. *Ambrosia* had the greatest competitive effect on other species and demonstrated the least competitive response to the presence of other species. *Ambrosia* was followed in the hierarchy by *Agropyron* and *Plantago*, while *Lepidium*, *Trifolium*, and *Chenopodium* all had almost no competitive effect on and were highly suppressed by other species. This hierarchy was established by midsummer and was consistent in both years of the study.

2. The data from one-, two-, four-, and five-species mixtures suggest that most species exhibit a non-linear response to an increasing abundance of competitors. Increasing the yield (dry weight biomass/m^2) of competitors had a negative effect on the success of *Plantago*, *Trifolium*, *Lepidium*, and *Chenopodium* with the slope of this relationship asymptotically approaching zero.

3. There appeared to be a general per-amount equivalence of competitive effects among the species. The important factor determining the competitive effect of a species was the yield of that

species, rather than its identity. No differences could be found in the competitive effects of different associate species on a single focal species when the associate species were at the same yield.

4. Single-species removals were performed in the full five-species community to measure the response of focal species to the removal of single associate species. These removal experiments provided a measure of the total effect (direct + indirect interspecific effects) of each species as an associate on each species as a focus. The results show that the hierarchy of competitive ability observed in the two-species experiments persisted in the full community. However, the competitive effects of two species with intermediate competitive ability, Agropyron and Plantago, were less in the full community than in two-species mixtures.

5. The relationship between focal species growth and the total yield of associate species, regardless of identity of the associate or associates, was highly significant for the focal species Agropyron, Plantago, Lepidium, Trifolium, and Chenopodium. This relationship was used to separate the total competitive effect of an associate species on a focal species into a direct effect of the associate species acting to increase the summed yield of associate species and an indirect effect of the associate species in decreasing the yield of other potential competitors and thus decreasing the sum yield of associate species. The results suggest that a) the direct effects between species were always competitive (antagonistic) and often quite large and b) the indirect effects were always very small or zero, and facilitative, acting to

increase the growth of the focal species.

6. There was no evidence that interspecific indirect effects were important in structuring this community; however, compound effects were important for some species. Compound effects are a type of higher-order effect and occur when the direct effect of one associate species on a focal species changes the ability of the focal species to respond to another associate species. The highly non-linear curves demonstrated by the growth response of individuals of *Plantago*, *Lepidium*, *Trifolium*, and *Chenopodium* to increasing yields of competitors suggest that compound effects must be considered to predict the success of these species in the full community.

7. The plant community studied was structured by hierarchical, asymmetric competitive effects. Growth of the competitively dominant species, *Ambrosia*, was restricted by strong intraspecific effects. The species of intermediate competitive ability, *Agropyron*, was restricted by both intra- and interspecific effects. The competitively subordinate species, *Plantago*, *Lepidium*, *Trifolium*, and *Chenopodium*, were restricted by interspecific and compound effects.

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