

EFFECTS OF INITIAL SPECIES RICHNESS ON
THE SURVIVORSHIP, BIOMASS, AND FINAL
SPECIES RICHNESS OF PLANTS IN
TERRESTRIAL MICROCOSMS

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CHAPTER I

PLANT SURVIVORSHIP AT DIFFERING SPECIES RICHNESSES IN TERRESTRIAL MICROCOSMS.

ABSTRACT

I observed cultivated plants in terrestrial microcosms at four different levels of initial species richness and examined their effects on plant survivorship. I transplanted eight individual plants chosen from *Lycopersicon esculentum*, *Brassica oleracea*, *Ocimum basilicum*, *Lactuca sativa*, *Glycine max*, *Capsicum annuum*, *Tagetes patula*, and *Zinnia violacea* into each of 200 terrestrial microcosms. A power outage caused a "simulated drought" which resulted in high mortality of the transplants. All eight species had significantly different survivorship over the four richness classes. Survivorship of *Brassica oleracea*, *Lactuca sativa*, and *Lycopersicon esculentum* decreased from low species richness to high, while *Zinnia violacea* survivorship decreased as a function of species richness. Survivorship versus richness of *Ocimum basilicum*, *Glycine max*, *Capsicum annuum*, and *Tagetes patula* was nonlinear. These results imply that survivorship does not necessarily increase as a function of diversity.

Key Words: species richness, survivorship, diversity, stability.

INTRODUCTION

Recent studies indicate that the species richness of communities may affect their dynamics, resilience, and ecosystem processes (Pimm 1984, 1991, Tilman and Downing 1994, Naeem et al. 1994). Stability is a measure of both a community's resistance to change and its resilience in recovery following a disturbance. The species richness of plant communities may influence the survivorship of the component species in several ways. If plant survivorship increases with species richness, then "diversity breeds stability;" and species-rich communities are likely to be "resistant" and maintain their initial diversity and species composition. For example, Frank and McNaughton (1991) found that plant community composition was more resistant, or stable, at higher levels of species richness during a drought in Yellowstone National Park. This observation is consistent with the diversity-stability hypothesis, which states that increased biodiversity increases resistance to disturbance (Pimm 1984, Schulze and Mooney 1993, Tilman and Downing 1994).

If, however, plant survivorship decreases as species richness increases, the number of surviving plants would be lower in a species-rich community than in a less species-rich community, and the resulting species richness may be low. In this case, more diverse communities are less likely to maintain their initial diversity and so are less resistant to disturbance. In a simulation study, Pimm

(1984) found that species-rich communities which were more complex were less likely to be resistant. The greater complexity of the community increased its vulnerability by adding more elements which could be disturbed. Diverse communities intrinsically have more rare species, and because these rare species exist in smaller numbers, they may be more vulnerable to extinction (Tilman and El Haddi 1992).

The relationship between plant survivorship and species richness may be more complex, however. Plant survivorship may respond to species richness by peaking and/or decreasing at various intermediate levels in a number of possible patterns. The relationship between plant survivorship and species richness may not be constant (Chapter 2) but rather different for each plant species. Because of these individual plant responses to the initial species richness, overall community structure and stability depend upon each community's component species. This interrelatedness can cause the complexity observed by Pimm (1984) which decreases a community's overall resistance.

The nature of the stresses upon a community may determine which species richness level is most stable (Tilman and El Haddi 1992). Drought is one condition which stresses many plant communities. It can decrease species richness under some conditions (Tilman and Downing 1994) and affect communities of differing species richness in different ways (Tilman and El Haddi 1992).

The purpose of this chapter is to determine how survivorship is related to initial species richness of cultivated plant species in terrestrial microcosms. Previous studies have used diversity gradients and comparisons of plots to assess resilience (Tilman and Downing 1994, Tilman and El Haddi 1992). This study treats the survivorship of plants in terrestrial microcosms as resistance. Unlike Naeem et al. (1994), I relied on the initial species richness of the microcosms instead of attempting to maintain a constant species richness by adding individuals throughout the experiment. By experimentally controlling species richness, I was able to correct for the effects of differing species composition as well.

METHODS AND MATERIALS

I chose basil (*Ocimum basilicum*), cabbage (*Brassica oleracea* cv. capitata), lettuce (*Lactuca sativa*), marigold (*Tagetes patula*), pepper (*Capsicum annuum*), soybean (*Glycine max*), tomato (*Lycopersicon esculentum*) and Zinnia (*Zinnia violacea*) to provide the eight species for this experiment. I conducted a literature search and a pilot study to find species with similarities in environmental requirements, size, growth rate from seedling stage, and lifespan. The eight chosen species germinated and grew reliably under the same standard greenhouse conditions in this pilot study. The pilot study also indicated the appropriate time before the experiment's starting date to sow each of the eight

species' seeds in order to have same-sized seedlings to transplant into the microcosms. I planted basil seeds 3 1/2 weeks before; tomato, cabbage, lettuce, and pepper 3 weeks before; marigold and zinnia 2 1/2 weeks before; and soy 1 1/2 weeks before transplantation. I transplanted the seedlings into trays on July 28-31, 1995.

The original purpose of this study was to assess how species richness of experimental polycultures affects species richness of weeds emerging from the soil seed bank. I therefore constructed an artificial seed bank in the microcosm soil by blending equal volumes (4 l) of soils from six different habitats into 500 liters of standard greenhouse soil mix. For reasons discussed below, I changed the focus of this study and instead monitored the survival of the cultivated plant species.

The microcosms were 26 x 25 x 6 cm plastic trays containing soil with native seed bank mix and eight transplants maintained in standard greenhouse conditions. The microcosms were constructed by filling 200 trays with 2.5 l of the soil mix and transplanting eight same-size cultivated plants according to the treatment plan (Table 1).

I arranged the microcosm trays in grids on three tables with gaps of at least 25cm between adjacent trays. I assigned transplanting order and location for each microcosm randomly. The trays were randomly rotated to new cells every two weeks during the trial to eliminate the effects of

variation in the greenhouse environment. The trial ran seven weeks.

I fertilized the seedlings weekly before transplanting them into the microcosms. All trays were fertilized on the first day of the trial with Peters Professional 15-30-15 mix. No more fertilizer treatments were applied during the trial.

I established four initial, or cultivated, species richness classes consisting of one, two, four, and eight plant species per tray (Table 1). For the two species class, two replicates of each of the 28 possible species combinations were established. Thirty-two microcosms provided two replicates each of 16 different four species combinations of the eight cultivated species. These four-species mixtures were chosen to equally represent all eight species. Eight-species mixes contained one individual each of all eight species; the placement of each species within the trays was random.

A power failure in the greenhouse at the beginning of the third week of the experiment caused high temperatures and dry conditions. This resulted in massive mortality of the transplanted species over the following weeks. I therefore changed the focus of the study to consider the effects of this "simulated drought" on survivorship in the microcosms.

I harvested the microcosms between September 13 and 15, 1995, to determine survivorship of individuals. I also

recorded the number of emerged weeds, and identified them to species where possible.

I discuss the weed communities and their effects on the transplants separately (Chapter 2), but effects of weed biomass, species richness and density were negligible. My analyses revealed no significant effects on cultivated plant survivorship.

I plotted survivorship for each species richness class to reveal trends in plant survivorship. I also plotted each of the eight species' survivorship separately at the four species richness levels. I used contingency table analyses of the eight transplant species' survivorship over the four species richness classes. I also examined the 95% confidence intervals for binary variables (Diem 1962) to determine whether plant survivorship for each species was different from low species richness to high.

RESULTS

Total plant survivorship generally decreased as species richness increased for all microcosms in the study (Fig. 1). However, the eight species behaved differently with respect to survivorship (Fig. 2). Comparison of percent survivorship (Diem 1962) at the four richness levels revealed no differences in survivorship of basil, soybean, pepper, marigold, and zinnia at the $p < .05$ level (Fig. 2: a, b, c, d, and e). Zinnia, however, was significantly different at the $p < .10$ level. The overall survivorship of

cabbage, lettuce, and tomato plants clearly decreased as a function of increasing species richness (Fig. 2: f, g, and h). This means a higher proportion of these species survived in low richness (SR=1) microcosms than in high richness (SR=8) microcosms. Lettuce also showed a difference in survivorship between the species richness levels of two and four and four and eight (Fig. 2g). Contingency table analyses of each species' survivorship showed that the species had different survivorship patterns among the four species richness classes (Table 2).

DISCUSSION

Decreased survivorship with species richness is consistent with the hypothesis "diversity breeds instability." Total plant survivorship was higher in species-poor microcosms and lower in species-rich microcosms. The experimental design allows us to note that species-rich microcosms were less resistant from the point of view of mortality. Because every microcosm started with eight individuals, and each species was equally represented in those microcosms, higher richness microcosms contained fewer representatives of each component species. Species-rich microcosms (SR=8) also lost the most individuals, and because each species was represented by only one individual, each individual lost meant a species lost. Species-poor microcosms and those with intermediate richness (SR= 1,2, or 4) not only lost fewer individuals but also had two, four,

or eight individuals of each species. These microcosms thus better maintained their level of diversity. This study's species-rich microcosms were more fragile by artifact because they were more likely to lose component species when individuals were lost. The results (Fig. 1 and Fig. 2: f, g, and h) show that these species-rich microcosms were also more likely to lose individuals and thus overall are less resistant to the disturbance of drought.

These results are the same as those predicted by Pimm (1984). My microcosms contained eight plants in close proximity, using the same resources. This potential for interspecific competitive interactions could cause a high connectedness and strong competitive interactions. Pimm's hypothesis is that a high degree of connectedness and complexity decreases the stability of a community and the resilience of its component populations. Pimm's (1984) hypotheses also predict that the species-rich communities are more likely to lose even more species after one is lost due to the disturbance caused by the species losses.

These results are contrary to the effect predicted by Frank and McNaughton (1991). Their study of prairie plant communities responding to drought revealed that plant community composition can be more stable at higher species richnesses. From an individual species point of view, none of the communities analyzed in my study seemed to indicate this tendency. A longer term study such as Frank and McNaughton's (1991) contains the potential for richness to

be maintained by immigration. A greater number of species also provides more possible species that are suited to the conditions of drought. Yet another consideration is that Frank and McNaughton's study used larger communities with a greater number of both species and individuals. A larger scale experiment based on my protocol might reveal whether there is an interaction between spatial scale and the resistance of species-rich communities.

Basil, soybean, and pepper (Figure 1: a, f, and e) had complex responses to microcosm richness. These species appear more likely to survive at intermediate levels of species richness. Survivorship was different among the four levels of species richness (Table 2), but there was no clear increase or decrease in survivorship with increased species richness to indicate what type of relationship occurs for these particular species.

Although the survivorship of each individual species in the microcosms decreased (or at least failed to increase) at higher richness, much more research is needed to determine whether per-species extinction rates are influenced by initial species richness. More species survived in these high richness communities; however, it is difficult to determine whether this is merely an artifact of the higher initial diversity or some internal tendency to maintain the species. This is related to the findings of Moffat (1996) and Tilman (1996), who argued that there is a fundamental

difference between population-level stability and higher-level stability.

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Table 1. Replications of cultivated polycultures and monocultures. SR = species richness of the transplants, #/tray = the number of plants of each species represented in the tray, #trays/trt = the number of trays each species appears in for that species richness, and #rep/trial = the number of replicates of that SR used in the experiment.

SR	#/tray	#trays/trt	#rep/trial
1	8	10	80
2	4	14	56
4	2	16	32
8	1	32	32

Table 2. Chi-squared values from 2 x 4 (i.e. alive vs. dead, in four richness classes) contingency tables of survivorship of the eight cultivated species.

Species	chi-squared	p
basil	12.99	<.005
cabbage	33.51	<<.005
lettuce	24.09	<<.005
marigold	18.31	<.005
pepper	22.81	<<.005
soybean	8.93	<.050
tomato	17.54	<.005
zinnia	30.91	<<.005

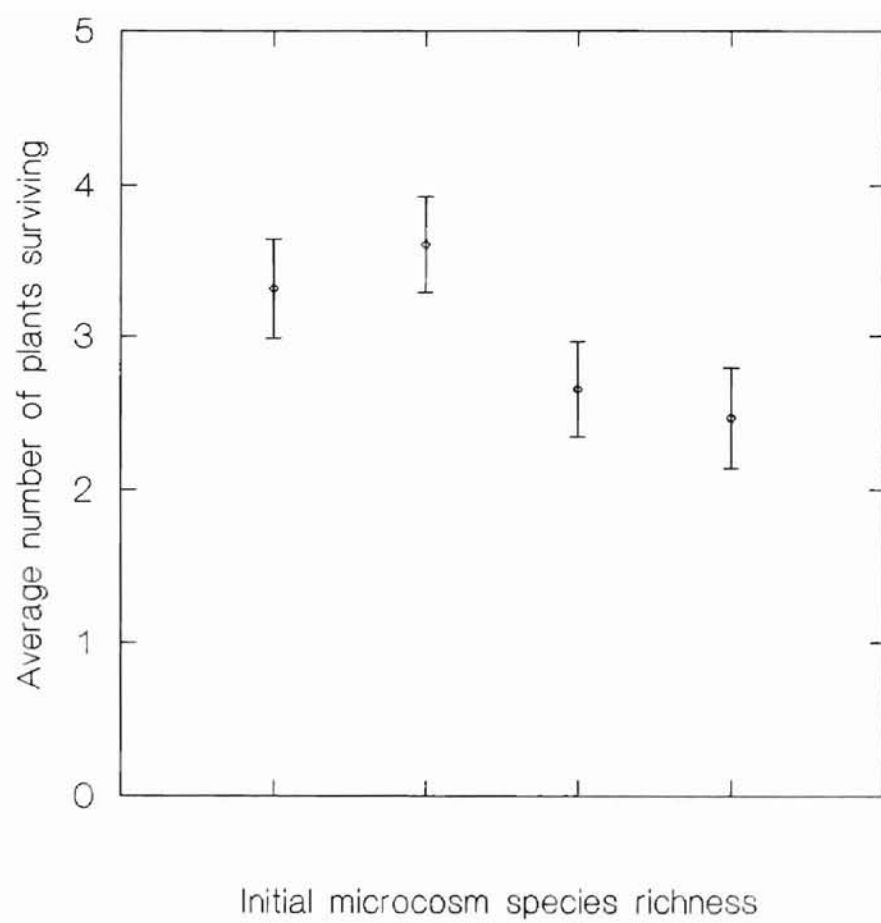


Figure 1. Average total plant survivorship vs. initial microcosm species richness for all 200 microcosms, with 95% confidence intervals.

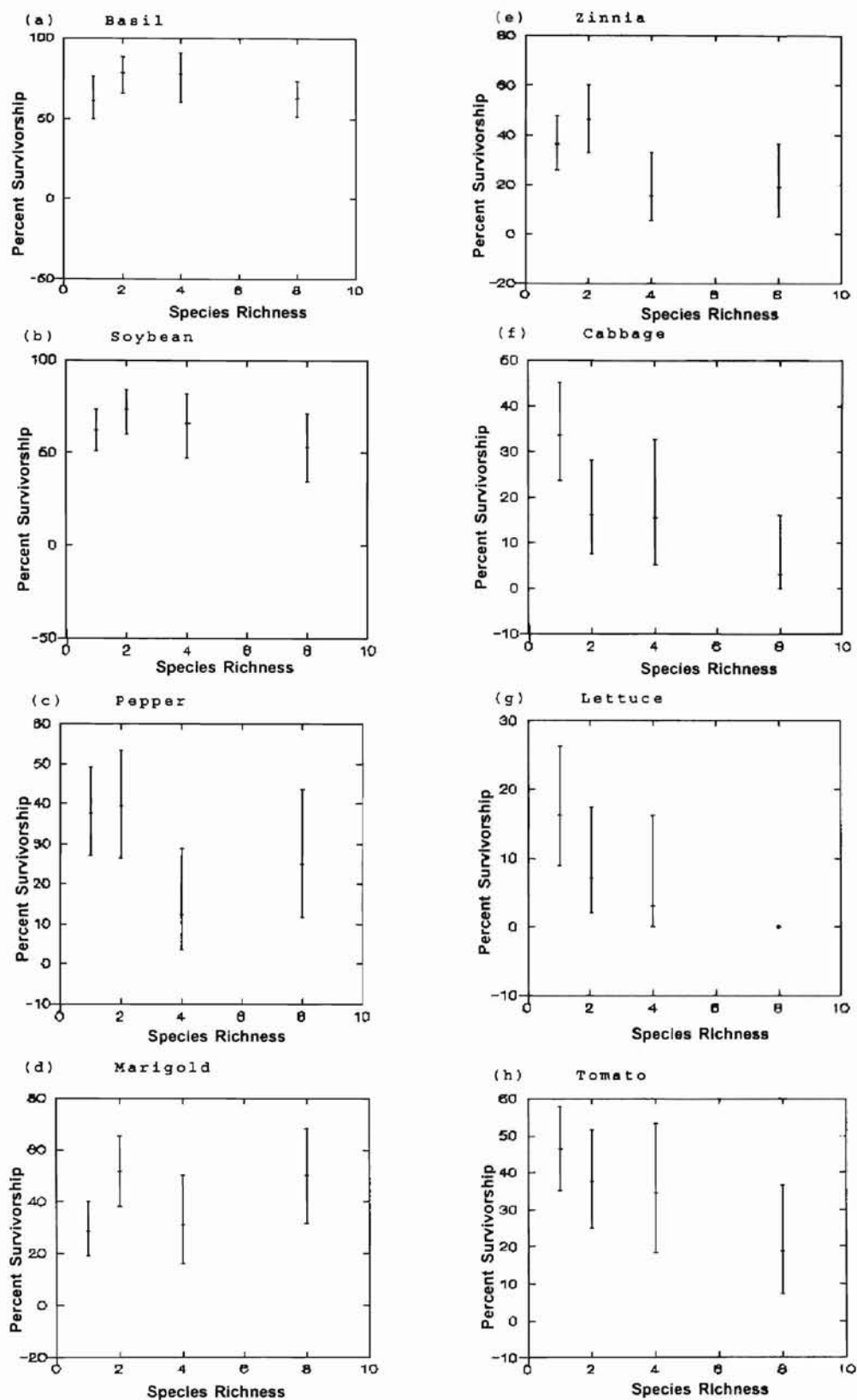


Figure. 2. Survivorship of eight plant species at different species richnesses. Error bars show 95% confidence intervals.

CHAPTER II

RELATIONSHIPS BETWEEN CULTIVATED PLANTS AND EMERGING WEEDS AFTER DROUGHT DISTURBANCE IN TERRESTRIAL PLANT MICROCOSMS.

ABSTRACT

I assessed the relationships between initial and resulting species richness, biomass, and number of surviving individuals of cultivated plants in 200 terrestrial microcosms. To do this, I established four species richness classes, ranging from one to eight, with each species evenly represented in each microcosm. The microcosms contained eight transplant species: *Brassica oleracea*, *Capsicum annuum*, *Glycine max*, *Lactuca sativa*, *Lycopersicon esculentum*, *Ocimum basilicum*, *Tagetes patula*, and *Zinnia violacea* as well as soil containing an artificially constructed seed bank. The microcosms were disturbed by a simulated drought in the greenhouse. I harvested, counted, and weighed all emerged and surviving plants after seven weeks to determine the effects of this drought on the microcosms. Emerged weed species richness, the number of weeds, cultivated plant biomass and cultivated plant survivorship differed significantly among the eight monocultures. There were no significant correlations between the weeds and initial transplant species richness, the number of surviving transplants, or surviving transplant species richness. The weeds emerging into the microcosms did not appear to affect the resulting biomass,

survivorship, or species richness of the transplants. Total biomass of the microcosms was positively correlated with the final species richness of the microcosms, but not with initial species richness. Biomass per individual was negatively related to initial species richness.

Key Words: biomass, diversity, drought, disturbance, resistance, species richness, survivorship, weeds.

INTRODUCTION

Many ecologists have found significant relationships between species richness and the biomass of plant communities (Moore and Keddy 1989, Klinkhamer and de Jong 1985, Hussain 1994, and Naeem et al. 1994). The effect of initial species richness on a plant community's resulting richness and biomass after a disturbance, however, is still unclear. There are many possible relationships among these variables.

Species richness in plant communities may be important in many ways. New species colonize a community by dispersal, or by emergence from a seed bank (Fenner 1985). New colonists may change the species richness and perhaps the overall biomass of the community. Colonization by these species may then influence the stability, or maintenance, of the community's initial species by the growth requirements, biomass, and other characteristics these colonizing taxa possess.

In turn, a community's stability is influenced in many ways by the identity of the species present. Different taxa respond to disturbances differently. The identity and nature of these taxa also may influence the chances of new species to successfully colonize that community. Following a stress or disturbance, the species composition of a community may change as a result of colonizing species' particular abilities to resist that disturbance.

Species richness is a measure which may be taken of any plant community and quantitatively compared to the species richness of other communities. Species richness may also be taken before and after a disturbance such as drought for comparison of community response. Though the species composition may change in a multitude of ways after a disturbance, e.g., the number of species in the community may either decline, increase, or remain constant after the disturbance. The initial and resulting species richness of the community will have a built-in correlation, as the first comprises a large part of the latter; but it is still relevant to examine the change in species richness over the time of the experiment.

Some current literature indicates that species-rich communities are less likely than species-poor communities to lose species after a disturbance. Species-poor communities, by comparison, may contain even fewer species than they began with after a disturbance. The change in species richness may thus be a more important measure than the actual species richness. Though the focus of their study was on biomass, Frank and McNaughton (1991) found that communities with higher species richness were more likely to maintain their species during a drought in Yellowstone National Park. In a comparison of perennial grain polycultures at four species richness levels, Crockett (1995) determined that resulting diversity, evenness, and percent cover of the individual plant families increased as

initial species richness of the polycultures increased. Her findings predict that diversity tends to persist through time. High initial diversity may effect the resistance of species and members of species to disturbances such as drought (Frank and McNaughton 1991, Tilman and El Haddi 1992). I observed (Chapter 1) that resistance, as measured by plant survivorship, was higher at low species richness than at high species richness for several taxa in terrestrial plant microcosms subjected to an artificial drought.

Biomass and productivity are often related to the species richness of a community. Naeem et al. (1994) measured the highest plant productivity in high diversity microcosms in their study of three trophic levels. If productivity is measured simply as biomass as in Naeem et al. (1994), it is important to differentiate between average and overall biomass production. Total community biomass and average biomass per individual may be highest at different richness levels. Naeem et al. (1994) were interested in total biomass while Vermeer and Berendse (1983) were interested in finer distinctions of biomass. Vermeer and Berendse (1983) found a negative correlation between shoot biomass and species number (richness) in their grassland sites but a positive correlation at their fen sites. By examining the biomass (as productivity) of the sites, they concluded that species richness is highest at intermediate levels of biomass (Vermeer and Berendse 1983). Indeed,

Klinkhamer and de Jong's (1985) study of coastal dune areas in The Netherlands also indicated that species richness is highest at intermediate biomass. Another pattern of response may be seen in Tilman's studies of grassland plots in Minnesota (Tilman 1996, Tilman and Downing 1994, and Tilman and El Haddi 1992). They concluded that rich communities had low biomass. If the relationship between biomass and richness in this study is unimodal or otherwise nonlinear, linear regression will not appropriately evaluate the relationship between species richness and biomass. However, the focus of this study is solely on detecting linear relationships.

I measured the responses of experimental communities to disturbance and determined the resulting species richnesses and biomasses. The purpose of this paper was to elucidate the relationships between initial species richness and the resulting biomass, emerged species, and species richness.

METHODS AND MATERIALS

In order to collect the soil containing wild seed banks, I sampled six sites at the James K. McPherson Botanical Preserve in Payne County, Oklahoma on February 17, 1995. The sites were: 1) a dry, rocky roadside, 2) an old field dominated by tallgrass prairie species, 3) a high, well-drained dike area dominated by perennial weeds, 4) an upland hardwood forest, 5) a hardwood floodplain forest, and 6) a mud flat along a pond shoreline. Ten shovel loads of

each soil type were collected at a depth of approximately 3 cm. The soils were spread upon aluminum trays to a depth of less than 2 cm. Large pieces of plant material and stone were removed as the soils were spread. The trays were labeled as to site, covered in brown butcher paper to exclude light, and spread on tabletops to dry. Over a period of three weeks, the soils were frequently stirred, mixed, and minced with a trowel to promote even drying and mixing. On March 21, 1995, after the soils were thoroughly dry, the samples were sifted through 0.5 cm mesh and stored in double-thick brown paper bags. Two informal seed bank emergence tests were performed by placing a sample of each soil in 8 cm x 8 cm pots watered and placed under 1) grow lights and 2) natural sunlight. These tests revealed that all six of the soils contained viable wild plant seeds of multiple species.

The methods for the greenhouse portion of this experiment are described more fully in Chapter 1. The experiment used 200 terrestrial plant microcosms divided into four species richness classes ranging from one to eight (Table 1). Each microcosm was a 26 x 25 x 6 cm plastic tray containing 2.5 l of the experimental soil. The experimental soil contained 4 l from each of the six collected soils blended into 500 l of standard potting soil and therefore contained wild seed banks. Eight same-sized cultivated plants were transplanted into each tray from July 28-31, 1995. Each tray received either one, two, four, or eight

cultivated species. The eight species used in the microcosms were: *Brassica oleracea*, *Capsicum annuum*, *Glycine max*, *Lactuca sativa*, *Lycopersicon esculentum*, *Ocimum basilicum*, *Tagetes patula*, and *Zinnia violacea*.

For simplicity, I called the transplants placed in the microcosms at the start of the experiment "cultivated plants". All plants which emerged from the artificial seed bank were termed "weeds". However, these terms are not meant to imply the agronomic roles for either group of species.

I harvested the plants in the microcosms at ground level September 13-15, 1995, identifying the species, counting the number of emerged weeds and the number of the surviving transplants. I then calculated the species richness of cultivated plants, emerged weed species richness, and the total final microcosm species richness for each tray. The harvested plants were oven-dried, and I determined the dry biomass of the emerged weeds and surviving transplants. The species present were identified using Waterfall (1969).

I used analysis of variance (ANOVA) among the monocultures to examine differences in total weed biomass, number of emerged weeds, and richness of emerged weed species. Microsoft Excel 5.0 and SYSTAT 2.0 were used to perform linear regression in order to determine whether relationships existed between all possible pairs of the following variables: weed biomass, richness of emerged weed

species, number of emerged weeds, surviving transplant biomass, total microcosm biomass, surviving transplant species richness, number of surviving transplants, initial transplant species richness, final total microcosm species richness. These were examined to find meaningful patterns and relationships. However, it must be noted that there may be trivial intrinsic correlations between some variables (e.g. weed species richness and total species richness).

RESULTS

Fourteen taxa of weeds emerged from the artificial seed bank (Table 2) with a total of 193 individuals for all 200 trays in the experiment. Individual microcosms contained from 0 to 16 weeds with a mean of 0.965 weeds/microcosm and a standard deviation of 1.942. The greatest emerged weed species richness for any one microcosm was only three, however. On average, emerged weeds only contributed 0.480 species to a microcosm's overall species richness (standard deviation = 0.770). Compared to the number of cultivated plants present in the microcosms, very few weeds emerged from the artificial seed bank (Table 3), and the weeds may be considered negligible. Analyses of variance revealed that both the number of emerged weeds and weed species richness differed among the eight species monocultures (Table 3), so the identity of the cultivated species in the monocultures is important when considering the responses of the weeds.

Cultivated plant biomass and survivorship also differed in the monocultures (Table 3). Some of the variation found in the cultivated plants' survivorship and final biomass lies in the inherent differences among species. Cultivated plant biomass at the end of the experiment ranged from 0 (complete mortality) to 9.30 grams/individual (mean =2.254, s.d.=2.269) while the number of individuals surviving through the experiment ranged from 0 to all 8 (mean =3.155, s.d.=2.486). Contingency table analysis (Chapter 1) also supports this conclusion. ANOVA of the eight species' monocultures (Table 3) indicates that cultivated plant biomass is significantly different among the species. ANOVA did not indicate a difference in total microcosm species richness and weed biomass among the eight species (Table 4).

The survivorship of the cultivated plants depended upon the initial species richness of the microcosms (Figure 1; note that this is another way of plotting the same information in Figure 1 of Chapter 1; see also Table 5). As the microcosms' species richness increased, the chance for individuals within those communities to survive slightly decreased. No correlation emerged between initial species richness and the biomass of the surviving cultivated plants or the total biomass of the microcosms (Figure 2). Initial species richness was not significantly related to the weed biomass, resulting weed species richness, or the number of weeds emerging (Table 5). A clearer pattern emerged when I calculated the average biomass per individual plant (weed

and cultivated) in each microcosm (Figure 3). Initial microcosm species richness was strongly related to biomass per individual in the microcosm. Though an individual's chance of survivorship decreased as the initial species richness increased, those individuals which did survive in higher richness microcosms were larger.

The resulting species richness of the microcosms was related to biomass (Table 5). The resulting species richness of the emerged weeds increased as weed biomass increased. The biomass and richness of the weeds were both dependent upon the presence of weeds, however, so the relationship is skewed and perhaps trivial. Very few weeds emerged in the experiment (mean= 0.965 weeds/microcosm with a range of 0 to 3 weeds), but the relationship seems to indicate that emerged weeds increased the microcosm species richness as well as its biomass. Cultivated plant biomass per microcosm and the resulting species richness were also positively correlated in a stronger relationship (Table 5). The total biomass of the microcosms (weed biomass plus cultivated plant biomass) was, logically, also correlated with the resulting species richness (Figure 4). Weed biomass and cultivated plant biomass showed no correlation (Figure 5). The resulting species richness of the microcosms was positively correlated with both the number and richness of the weeds emerging in the microcosms (Table 5), but these were not truly independent variables. Over

all four initial richness classes, cultivated plant biomass did increase as more of those species survived (Figure 6).

DISCUSSION

Few weeds emerged from the artificial seed bank. As mortality was high among the cultivated transplants during the drought, it is possible that the drought was also responsible for the paucity of weeds. I observed a number of dead weed seedlings during and after the drought. The paucity of weeds was not caused by too few seeds in the seed bank, however: a pilot study revealed very high seed densities within the seed bank. It is also possible that the weed seeds did not break dormancy because the parameters of the experiment did not provide the necessary conditions for germination. Unfavorable or dry conditions often cause continued dormancy in seeds (Fenner 1985). The hot, dry conditions in the greenhouse during the simulated drought may have affected the seeds in the artificial bank, causing many to get a late start or to fail to break dormancy. It is also possible that many of the seeds were too far beneath the surface to germinate (Fenner 1995).

ANOVA revealed that the identity of the eight cultivated species in the monocultures affected the species richness and number but not the biomass of the weeds. Because the polycultures were constructed from these same eight species, the differing influences of the individual species were most likely a factor in the resulting effects

of the weeds in those polycultures. Some species might simply have exerted stronger influences on their communities despite the fact that each species present in a microcosm had an equal number of individuals at the start of the experiment.

The microcosms with high species richness seemed in some respects more resistant, and in other respects less resistant to drought disturbance. Species-rich microcosms had higher overall biomass and higher biomass per individual. The plants which died before the end of the experiment were usually small. On the other hand, resistance when viewed as cultivated plant survivorship was lowest in microcosms with high initial species richness. The resulting biomass and species richness were also highest in these initially species-rich microcosms (though the trend in species richness is most likely a methodological artifact). The weeds emerging from the microcosm seed banks did not appear to play a significant role in the cultivated plants' response to the drought.

The findings of this experiment are consistent with the hypotheses that resulting species richness increases as initial species richness increases and agree with other studies of the relationship between initial and resulting species richness (Crockett 1995, Frank and McNaughton 1991, and Tilman and Downing 1994). The observed positive correlation between biomass and final total species richness is consistent with the observations of Naeem et al (1994)

and Crockett (1995). The biomass of the microcosms did increase as the species richness of those microcosms increased. While some of this relationship is no doubt due to the fact that microcosms with fewer species had fewer plants to provide biomass, the fact remains that the microcosms with higher species richness were those with greater relative biomass and biomass per individual. The overall biomasses of the microcosms in this study were quite low, and so agree with the findings of Vermeer and Berendse (1983). At higher overall productivity levels, another pattern may prevail. In that case, species richness might be highest in communities with intermediate or lower biomass.

Despite its limited scope, this study provides insight into the relationships between the initial species richness and the resulting species richness and biomass in communities disturbed by drought.

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Table 1. Replications of cultivated polycultures and monocultures. SR = species richness, #/tray = the number of plants of each species represented per tray, #trays/trt = the number of trays in which each species is present for that treatment and #rep/trial = the number of replicates of that SR used in the experiment.

SR	#/tray	#trays/trt	#rep/trial
1	8	10	80
2	4	14	56
4	2	16	32
8	1	32	32

Table 2. Weed species emerging from the artificial seed bank. (Nomenclature follows Kartesz (1994))

<u>Scientific name</u>	<u>Common name</u>
<i>Amaranthus spinosus</i> L.	spiny amaranth
Unidentified forb	--
<i>Cynodon dactylon</i> (L.) Pers.	bermuda grass
<i>Cyperus rotundus</i> L.	flatsedge
<i>Cyperus polystachyos</i> Rottb.	
var <i>texensis</i> (Torr.) Fern.	flatsedge
<i>Digitaria ischaemum</i> (Schreb.) Muhl.	crabgrass
<i>Echinochloa crus-galli</i> (L.) Beauv.	barnyard grass
<i>Euphorbia nutans</i> Lag.	eyebane
Grass A	--
Grass B	--
<i>Eclipta alba</i> (L.) Hassk.	yerba de tago
<i>Polygonum pennsylvatica</i> (L.) Small.	smartweed
<i>Scutellaria parvula</i> Michx.	small skullcap
<i>Trifolium repens</i> L.	white clover

Table 3. Number of weeds, weed richness, cultivated plant biomass, and number of survivors. Numbers are means, with standard deviations in parentheses. The *F* and *p*- values from ANOVA are given beneath.

Species	# weeds	species richness	biomass	#survivors
<i>Brassica oleracea</i>	0.5 (0.707)	0.500 (0.707)	1.784 (2.752)	2.8 (2.974)
<i>Capsicum annuum</i>	4.0 (4.830)	1.600 (1.075)	0.403 (0.417)	3.0 (2.625)
<i>Glycine max</i>	0.7 (1.252)	0.400 (0.516)	4.159 (1.859)	5.6 (2.271)
<i>Lactuca sativa</i>	0.7 (1.160)	0.600 (0.966)	0.307 (0.614)	1.3 (2.263)
<i>Lycopersicon esculentum</i>	0.8 (1.687)	0.200 (0.422)	2.507 (2.611)	3.7 (2.946)
<i>Ocimum basilicum</i>	1.1 (1.853)	0.400 (0.516)	4.759 (3.266)	4.9 (2.885)
<i>Tagetes patula</i>	1.6 (2.503)	0.800 (1.135)	1.211 (1.359)	2.3 (3.093)
<i>Zinnia violacea</i>	1.0 (2.108)	0.500 (1.080)	2.158 (1.949)	2.9 (2.767)
<i>F</i>	2.383	2.571	6.070	2.563
<i>p</i>	0.030	0.020	<0.001	0.020

Table 4. Microcosm species richness and weed biomass; numbers are means with standard deviations in parentheses The *F* (from ANOVA) and *p*-values are given beneath.

Species	Species richness	Weed biomass
<i>Brassica oleracea</i>	1.2 (1.135)	1.162 (3.164)
<i>Capsicum annum</i>	2.4 (1.265)	0.668 (0.730)
<i>Glycine max</i>	1.4 (0.516)	0.094 (0.182)
<i>Lactuca sativa</i>	1.0 (1.414)	0.117 (0.228)
<i>Lycopersicon esculentum</i>	1.0 (0.667)	0.063 (0.162)
<i>Ocimum basilicum</i>	1.3 (0.675)	0.064 (0.137)
<i>Tagetes patula</i>	1.3 (1.059)	0.217 (0.377)
<i>Zinnia violacea</i>	1.1 (0.876)	0.185 (0.547)
<i>F</i>	2.012	1.113
<i>P</i>	0.065	0.364

Table 5. Summary results of linear correlations. Abbreviations are as follows: SR= species richness, # = number of, cult= cultivated, surv.= surviving, and ini.= initial.

X	Y	r
emerged weed SR	weed biomass	0.368**
# weeds emerged	weed biomass	0.326***
# weeds emerged	emerged weed SR	0.757***
cult biomass	weed biomass	-0.112
cult biomass	emerged weed SR	-0.054
cult biomass	# weeds emerged	-0.012
surv.cult SR	weed biomass	0.041
surv.cult SR	emerged weed SR	0.036
surv.cult SR	# weeds emerged	0.066
surv.cult SR	crop biomass	0.467***
# cult surviving	weed biomass	-0.053
# cult surviving	emerged weed SR	0.079
# cult surviving	# weeds emerged	0.063
# cult surviving	crop biomass	0.712***
# cult surviving	surv. cult SR	0.480***
ini.cult SR	weed biomass	0.016
ini.cult SR	emerged weed SR	-0.054
ini.cult SR	# weeds emerged	-0.061
ini.cult SR	cult biomass	0.027
ini.cult SR	surv.cult SR	0.519***
ini.cult SR	# cult surviving	-0.145*
ini.cult SR	ave.biomass/ind	0.209**
resulting SR	weed biomass	0.196**
resulting SR	emerged weed SR	0.570***
resulting SR	# weeds emerged	0.469***
resulting SR	cult biomass	0.352***
resulting SR	surv. cult SR	0.837***
resulting SR	# cult surviving	0.435***
resulting SR	ini.cult SR	0.400***
resulting biomass	ini.cult SR	0.032
resulting biomass	final total SR	0.413***
resulting biomass	# cult surviving	0.674***
resulting biomass	surv. cult SR	0.469***
resulting biomass	# weeds emerged	0.106
resulting biomass	emerged weed SR	0.080
resulting biomass	weed biomass	0.252***

*p<.05

**p<.01

***p<.001

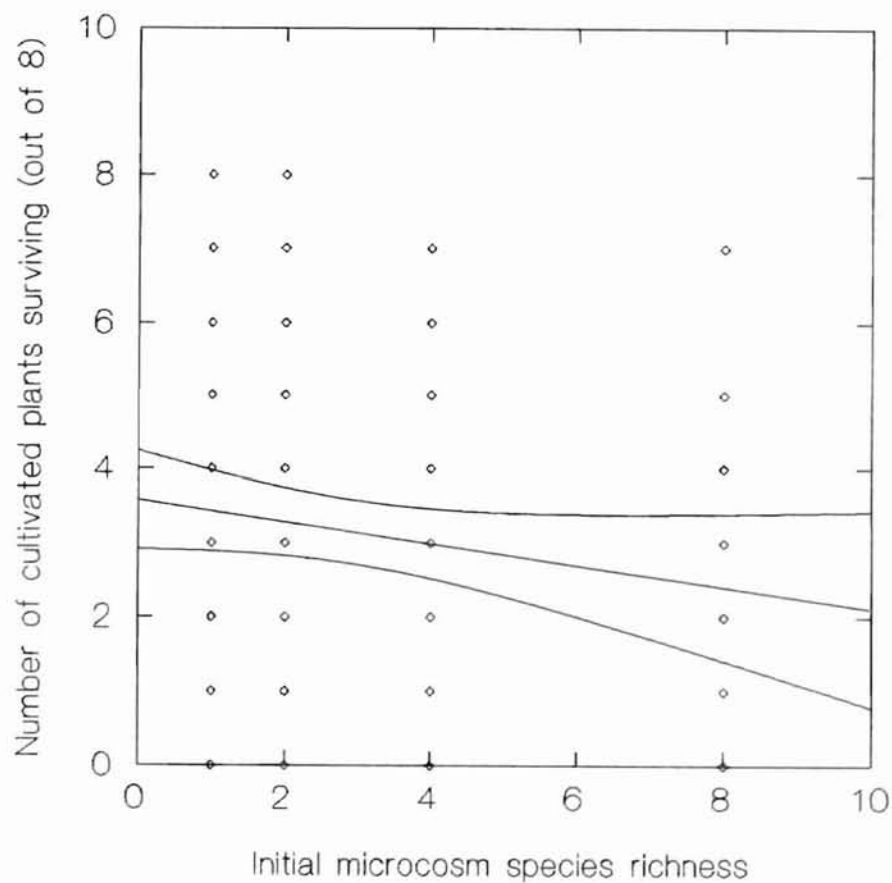


Figure 1. Number of cultivated plants surviving as a function of initial microcosm species richness, along with regression function and 95% confidence bands.

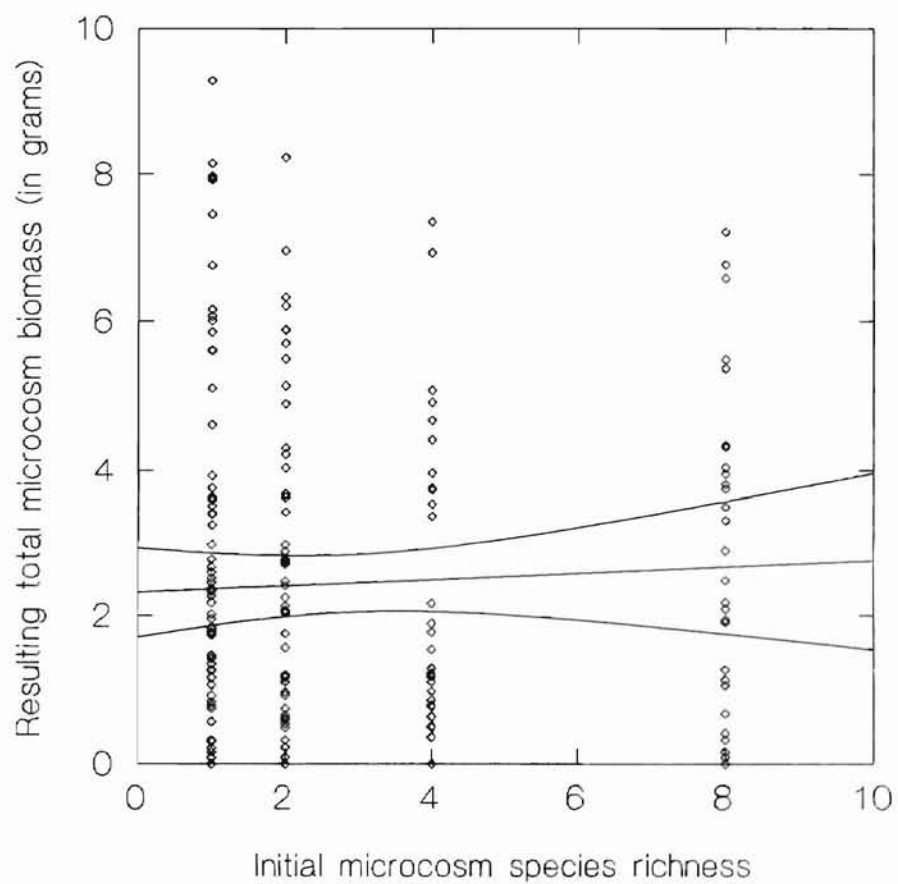


Figure 2. Total microcosm biomass (in grams) as a function of initial species richness, along with regression function and 95% confidence bands.

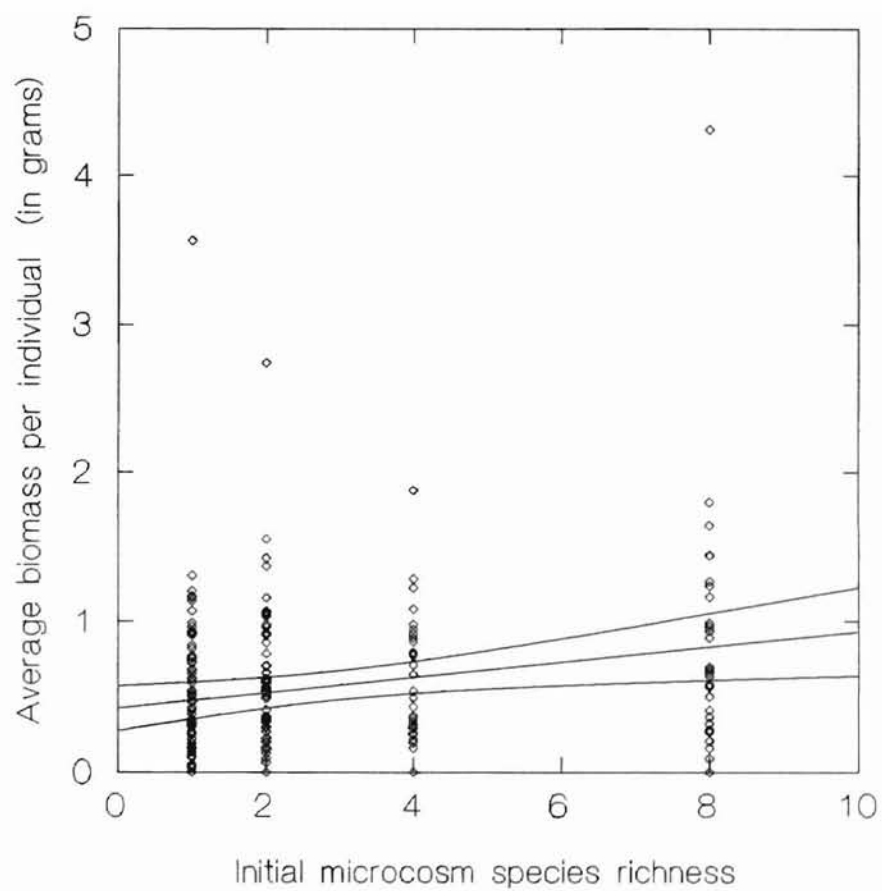


Figure 3. Average biomass per individual as a function of initial microcosm species richness, along with regression function and 95% confidence bands.

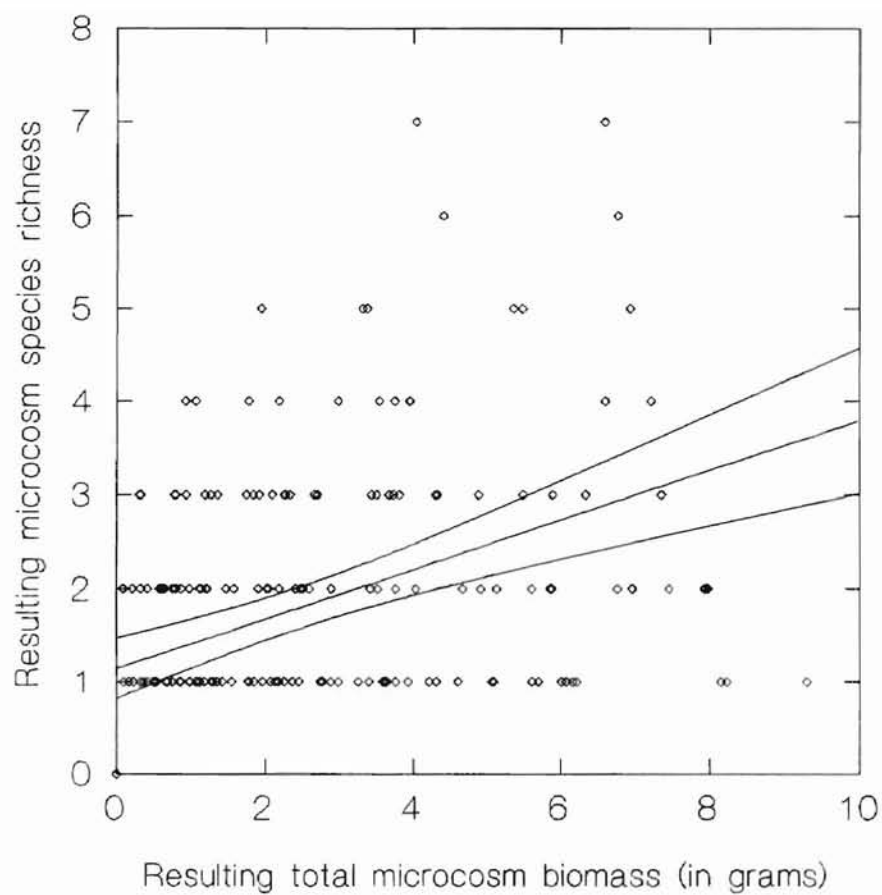


Figure 4. Resulting microcosm species richness as a function of total microcosm biomass, along with regression function and 95% confidence bands.

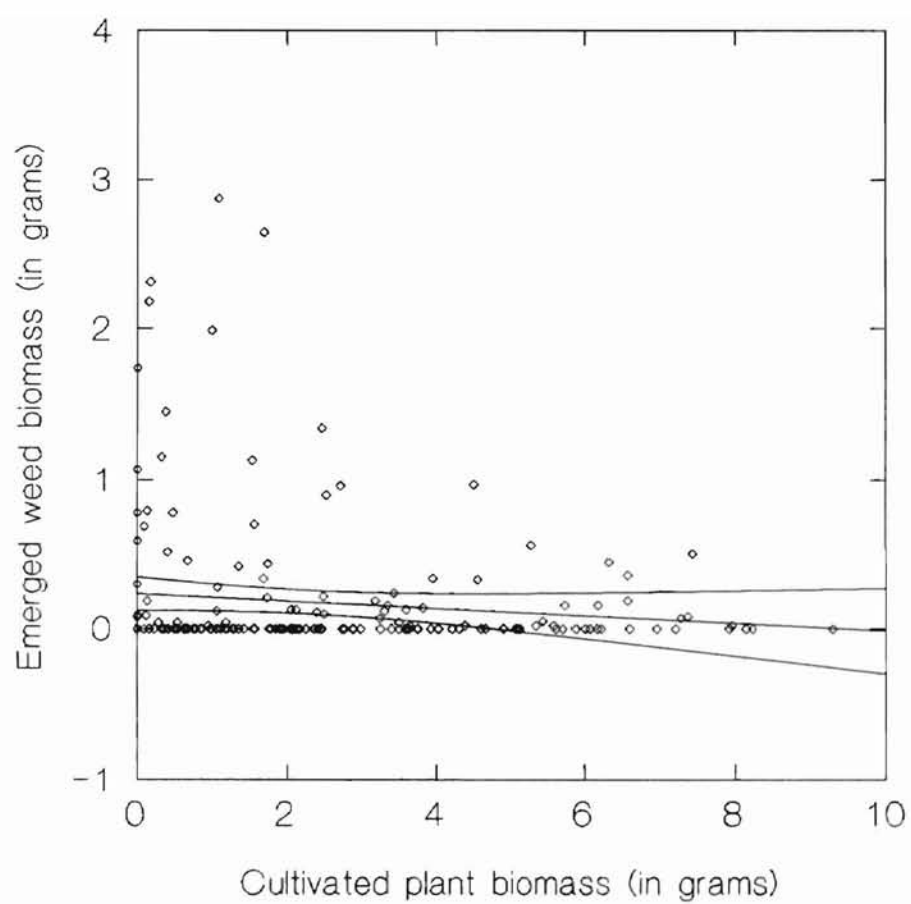


Figure 5. Weed biomass as a function of surviving cultivated plant biomass, along with regression function and 95% confidence bands.

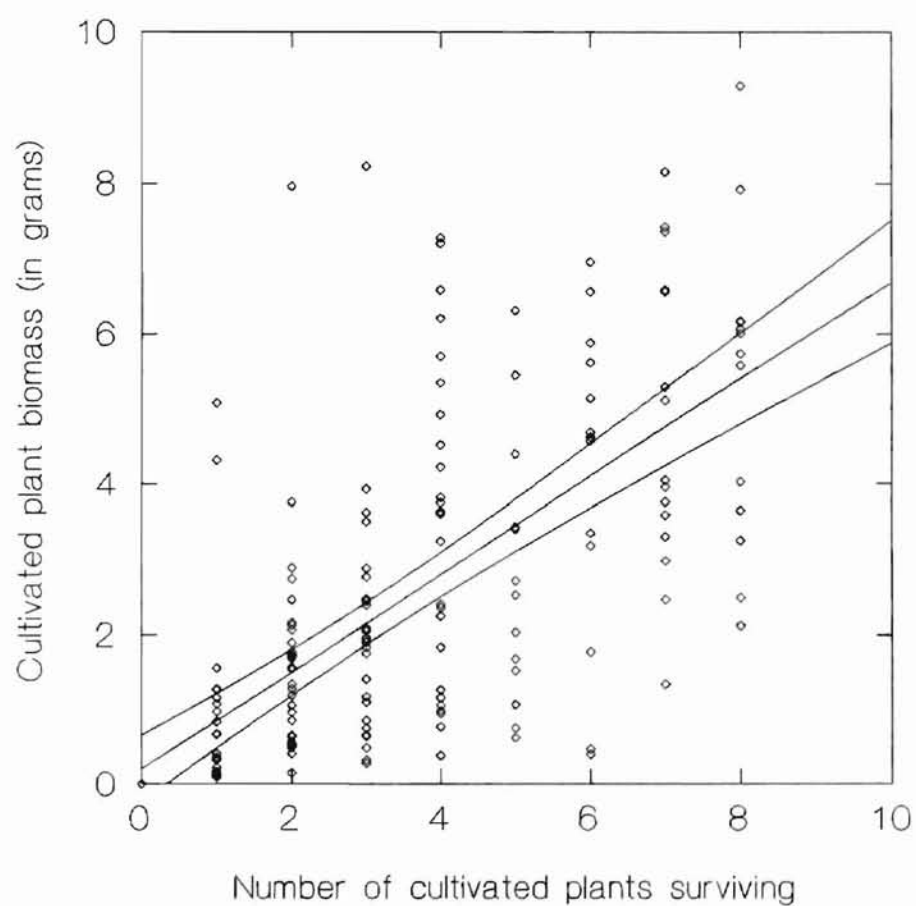


Figure 6. Cultivated plant biomass as a function of the number of cultivated plants surviving, along with regression function and 95% confidence bands.

CHAPTER III.

THE EFFECTS OF INITIAL SPECIES RICHNESS IN ARTIFICIAL SEED BANK-CONTAINING TERRESTRIAL PLANT MICROCOSMS.

ABSTRACT

This study assesses the effects of initial species richness on the cultivated plants and emerging weeds in terrestrial plant microcosms. Eight cultivated, or crop, plants were placed in each of 200 microcosms with an artificial seed bank. After a 13 week period, I measured the resulting species richness and biomass of the crops and the weeds in the microcosms. Four species richness classes, ranging from one to eight species, represented each species evenly in each microcosm and the overall experiment. I constructed the microcosms using transplants from eight commonly cultivated species: *Lycopersicon esculentum*, *Brassica oleracea*, *Ocimum basilicum*, *Lactuca sativa*, *Glycine max*, *Boragio officinale*, *Tagetes patula*, and *Zinnia violacea*. The soil contained an artificially constructed seed bank consisting of 37 "weed" species. All emerged and surviving plants were harvested, dried, and weighed after 13 weeks. Survivorship was significantly different among the four species richness classes for the eight cultivated plant species. Cultivated plant survivorship was also significantly different among *B. officinale*, *B. oleracea*, *T. patula*, and *G. max* monocultures. Resulting biomasses were different among all eight species in the monocultures.

The emerging weeds were not correlated with the cultivated plant biomass, species richness, or number of surviving individuals. Initial species richness was not correlated with cultivated plant survivorship or the number of weed species emerging. Cultivated plant survivorship and biomass were not correlated with the total microcosm biomasses. Initial microcosm species richness was positively correlated with resulting species richness but negatively correlated to the overall change in richness.

Key Words: biomass, diversity, productivity, species richness, survivorship.

INTRODUCTION

The species richness of a community affects that community's overall resilience, nutrient cycling (Naeem et al. 1994) and productivity (Moore and Keddy 1989, Klinkhamer and de Jong 1985, Hussain 1994, Naeem et al. 1994, Grime 1973). Because plants form the community's lowest trophic level, studies of how species richness affects plant communities are relevant to studies of the biodiversity at all trophic levels.

The relationships between species richness and the biomass of plant communities have been explored by many ecologists (Moore and Keddy 1989, Klinkhamer and de Jong 1985, Hussain 1994 and Naeem et al. 1994). The effect of initial species richness on plant communities' resulting species richness and biomass, however, is still unclear.

High initial species richness in plant communities may be important in many ways. "Initial" is used here as an expression of the species richness of the community at a point in time before recruitment or mortality has had a chance to change the community. The initial point in this study, for example, is an experimental starting point with known community members. Over time, a community may acquire additional species (members) from a seed bank or dispersing seeds (Fenner 1985). In the process, these recruits change the species richness and perhaps the biomass of the community. Recruitment of these species may influence the stability, or maintenance, of the community's initial

species. Conversely, the initial plants present may influence community stability in a number of ways.

Plant community species richness may be affected by the biomass of the community as well. Recent literature supports three theories on the relationship of biomass and species richness. The highest richness may result at higher levels of overall community productivity. Naeem et al. (1994) measured the highest plant productivity in high diversity microcosms in their three trophic level study. Recent studies also predict other patterns of response which may be more complex. Vermeer and Berendse (1983) found a positive correlation between species number (richness) and shoot biomass at their fen sites. By contrast, they found a negative correlation between the two at their more productive grassland sites. As a result, they were able to conclude that species richness is highest at high overall biomasses when the community's productivity levels are relatively low. When productivity levels are high, however, species richness decreases as biomass increases (Vermeer and Berendse 1983). Tilman's studies of Minnesota grassland plots (Tilman 1996, Tilman and Downing 1994, and Tilman and El Haddi 1992) found that species richness was greatest at low overall biomass. Species richness, then, may be highest at either low or high community biomass, depending on the specific community being studied. Klinkhamer and de Jong (1985) found that richness was highest at intermediate

levels of community biomass in coastal dunes in the Netherlands.

This study considers two main questions about species richness and biomass. First, how does the initial species richness of a plant community affect the resulting species of that community? Secondly, how is biomass affected by the surviving and emerging species and species richness? The purpose of this study is to demonstrate how initial species richness in terrestrial plant microcosms affects plant survivorship, biomass, and resulting species richness.

METHODS AND MATERIALS

I chose the following species for this study: *Boragio officinale* (borage), *Brassica oleracea* (cabbage), *Glycine max* (soybean), *Lactuca sativa* (lettuce), *Lycopersicon esculentum* (tomato), *Ocimum basilicum* (basil), *Tagetes patula* (marigold), and *Zinnia violacea* (zinnia). A pilot study as well as a previous trial (Chapters 1 and 2) indicated the appropriate time before the experiment's start date to sow seeds in order to have same-sized seedlings. I planted *O. basilicum* seeds 3 weeks before; *L. esculentum*, *L. sativa*, *B. officinale*, and *B. oleracea* 2 1/2 weeks before; *T. patula* and *Z. violacea* 2 weeks before; and *G. max* seeds just 1 1/2 weeks before the experiment began. The experiment began when my helpers and I transplanted the cultivated plant seedlings into the terrestrial microcosms October 9-12, 1995.

The microcosms were 26x25x6 cm plastic trays containing standard greenhouse potting soil, an artificially constructed seed bank, and 8 cultivated plant transplants. The seed bank contained 37 "weed" species obtained from wildflower seed mixes and agricultural supply (Table 1). We determined the approximate number of seeds per volume for each of the species obtained from the Agricultural Supply by counting the number of seeds per cm³ (ml). The wildflower seed canisters listed the estimated number of total seeds enclosed as well as the percentage supplied by each species. I calculated the average number of seeds provided by each of the wildflower mix species. In an attempt to use approximately the same amount of seeds from each species, we added this average amount by volume of the seven species from the Agricultural Supply. My helpers and I blended this artificial seed bank into the potting soil and filled each tray with 4 l of soil. Each tray received eight same-sized transplants according to the treatment plan (Table 2) for a total of 200 microcosms with four initial species richness classes of 1, 2, 4, and 8. I arranged the microcosm trays in grids so that they were spaced with at least a one tray width gap on all sides, then rotated the trays into randomly assigned spaces every two weeks during the experiment to eliminate potential bias due to their position in the greenhouse.

After 13 weeks in standard greenhouse conditions, we harvested the plants in the microcosms at ground level on

January 9-12, 1996. The plants were frozen, oven-dried, identified using Steyermark (1963) and Waterfall (1969), seedling descriptions and photos from Wildseed Farms, and comparison with herbarium specimens in the O.S.U. Teaching Herbarium. I recorded the number and biomass per species of the cultivated plants harvested from the microcosms. Emerged weed plants were identified, sorted and weighed by species.

I used contingency table analyses to test for independence in survivorship for the eight cultivated species at the four initial species richness levels. I then used analysis of variance (ANOVA) among the eighty monocultures to discover differences among monocultures in the following variables: cultivated plant survivorship, cultivated plant biomass, emerged weed biomass, emerged weed species richness, resulting overall species richness, and resulting total biomass. Microsoft Excel (5.0) and SYSTAT (5.0) were used to organize the raw data, calculate ANOVA, and perform linear regression. The regressions were used to reveal relationships between the following variables: initial species richness, resulting species richness, weed biomass, emerged weed species richness, surviving cultivated plant biomass, surviving transplant species richness, and number of surviving transplants.

RESULTS

Table 1 shows the identity of the 18 weed species that emerged from the 37 species of seeds in the microcosm seed bank. The emerged weeds provided over half the species in the trays and approximately seven times more of the biomass than the cultivated plants. On average, 6.4 weed species emerged into the microcosms from the artificial seed bank (s.d.=5.0, range 4 - 12). The average weed biomass per tray was 8.2 grams (s.d.=5.0, range 0.8 - 27.6) while cultivated plants provided an average biomass of only 1.2 grams (s.d.=0.9, range 0.0 - 6.6).

Survivorship was significantly different among species richness classes in *B. officinale*, *B. oleracea*, *T. patula*, and *G. max* (Table 3). *B. oleracea*, *Z. violacea*, *T. patula*, and *G. max* had the highest survivorship over the 13 week period of the experiment. By contrast, *L. sativa* and *L. esculentum* had the lowest survivorship (Table 3). ANOVA of the number of surviving cultivated plants among the monocultures indicated that survivorship was different among the eight cultivated plant species (Table 4). ANOVA revealed that cultivated plant biomasses differed among the eight species' monocultures (Table 4). ANOVAs also indicated that emerged plant biomasses and total plant biomasses per microcosm were different among all eight species in monocultures (Table 5). The emerged weed species richness and the resulting total species richness were not

significantly different among the monocultures, however (Table 5).

Linear regressions (Table 6) revealed several positive correlations when all pairs of variables were compared, but relationships between many are expected because they are not truly independent. Initial species richness was not significantly correlated with either the biomass or the species richness of the emerged weeds. The initial species richness of the microcosms did affect the biomass of the cultivated plants and perhaps the total resulting biomass of the microcosms (Table 6). Figure 1 indicates that there may be a slight positive correlation between initial species richness and the resulting biomass in the microcosms at lower significances. Resulting species richness and biomass were positively correlated (Figure 2). The number of cultivated plants surviving, however, was not correlated with initial species richness when analyzed with linear regression. Resulting species richness of the microcosms did increase as initial species richness increased (Figure 3), but the change in species richness over the time period of the experiment was negatively correlated with initial species richness (Figure 4).

DISCUSSION

The ANOVAs revealed that the identity of the species in the monocultures affected the species richness, number, and biomass of the weeds in some cases. When considering the

effect on emerged plants in communities, then, it is important to take into account the identity of the established plants in that community. Because the polycultures in this study were constructed from eight different species, their differing influences could factor into the resulting effects on the weeds in those polycultures. Despite the fact that each species was evenly represented in the experiment and in each polycultures it was a part of, there is the possibility that the effects of each species was not even within the experiment. Some species might simply have exerted stronger influences on their communities, and therefore there may have been interaction effects.

The findings of this experiment are consistent with the hypotheses that resulting species richness increases as initial species richness increases. These findings are also consistent with the findings of other recent studies considering the relationship between initial and resulting species richness (Crockett 1995, Frank and McNaughton 1991, Tilman and Downing 1994, and Tilman and El Haddi 1992). Of course, this relationship is in part trivial, since the initial species richness makes up a part of the resulting species richness of the microcosm.

The observed positive correlation between biomass and resulting species richness is consistent with the observations of Naeem et al. (1994) and Crockett (1995). Overall productivity levels in the microcosms were lower

than those studied by Naeem et al. (1994) and Crockett (1995), but the biomass of the microcosms increased slightly as species richness increased. This is in accordance with the findings of Vermeer and Berendse (1983) as well.

This study reveals some of the relationships between initial species richness and the emergence of species from a seed bank. Further studies will be needed to clarify how the initial species richness and the identity of the cultivated plant species relate to the resulting species richness, composition, and biomass of plant communities at small spatial scales.

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species richness in grasslands and wetland communities.
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edition. Published by the author, Stillwater,
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Table 1. Species present in and emerged from the artificial seed bank. 18 species emerged during the experiment. Seven species were obtained from the Stillwater Agricultural Supply while the rest were obtained from two canisters of Sam's Choice Wildflower Farms Cutting Garden mixes. Nomenclature follows Kartesz (1994).

<u>Species</u>	<u>Family</u>	<u>Est.# seeds/ tray</u>	<u>emerged</u>	<u>source</u>
<i>Achillea millefolium</i> L.	Asteraceae	62	no	mix
<i>Adonis vernalis</i> L.	Ranunculaceae	38	no	mix
<i>Amaranthus caudatus</i> L.	Amaranthaceae	57	no	mix
<i>Aquilegia vulgaris</i> L.	Ranunculaceae	38	no	mix
<i>Briza maxima</i> L.	Poaceae	48	yes	mix
<i>Centaurea cyanus</i> L.	Asteraceae	48	no	mix
<i>Cirsium vulgare</i> (Savi) Ten.	Asteraceae	70	yes	Ag. Supply
<i>Clarkia unguiculata</i> Lindl.	Onagraceae	57	no	mix
<i>Coreopsis tinctoria</i> Nutt.	Asteraceae	76	yes	mix
<i>Cynodon dactylon</i> (L.) Pers.	Poaceae	70	yes	Ag. Supply
<i>Delphinium ajacis</i> (L.) Schur	Ranunculaceae	57	no	mix
<i>Erysimum asperum</i> (Nutt.) DC.	Brassicaceae	48	no	mix
<i>Eschscholzia californica</i> Cham.	Papaveraceae	71	no	mix
<i>Festuca rubra</i> L.	Poaceae	70	yes	Ag. Supply
<i>Gaillardia pulchella</i> Foug.	Asteraceae	67	no	mix
<i>Gypsophila paniculata</i> L.	Caryophyllaceae	67	yes	mix
<i>Helichrysum bracteatum</i> (Vent.) Andr.	Asteraceae	57	no	mix
<i>Hesperis matronalis</i> L.	Brassicaceae	48	no	mix
<i>Kummerowia stipulacea</i> (Maxim.) Makino	Fabaceae	70	yes	Ag. Supply
<i>Limonium</i> sp.	Plumbaginaceae	62	no	mix
<i>Linum lewisii</i> Pursh.	Linaceae	62	yes	mix
<i>Linum</i> sp.	Linaceae	62	no	mix
<i>Lolium temulentum</i> L.	Poaceae	70	yes	Ag. Supply
<i>Lupinus perennis</i> L.	Fabaceae	62	yes	mix
<i>Lupinus texensis</i> Hook.	Fabaceae	67	no	mix
<i>Moringa oleifera</i> Lam.	Moringaceae	38	no	mix
<i>Nigella damascena</i> L.	Ranunculaceae	38	no	mix
<i>Oenothera biennis</i> L.	Onagraceae	67	no	mix
<i>Oxalis stricta</i> L.	Fabaceae	62	no	mix
<i>Panicum virgatum</i> L.	Poaceae	48	no	mix
<i>Papaver rhoeas</i> L.	Papaveraceae	62	yes	mix
<i>Phacelia</i> sp.	Hydrophyllaceae	48	yes	mix
<i>Rudbeckia hirta</i> L.	Asteraceae	62	yes	mix
<i>Silene laciniata</i> Cav.	Caryophyllaceae	57	no	mix
<i>Trifolium campestre</i> Schreb.	Fabaceae	70	yes	Ag. Supply
<i>Vicia sativa</i> L.	Fabaceae	70	yes	Ag. Supply
Mystery forb B	--	-	yes	--
Mystery forb C	--	-	yes	--

Table 2. Replications of cultivated polycultures and monocultures. SR = species richness, #/tray = the number of plants of each species represented per tray, #trays/trt = the number of trays in which each species is present for that treatment and #rep/trial = the number of replicates of that SR used in the experiment.

SR	#/tray	#trays/trt	#rep/trial
1	8	10	80
2	4	14	56
4	2	16	32
8	1	32	32

Table 3. Results of contingency table analyses of % cultivated plants surviving for the eight cultivated species in microcosms with initial species richnesses of 1, 2, 4, and 8.

Species	chi-squared	% surviving/SR class				p-value
		1	2	4	8	
<i>Boragio officinale</i>	27.5312	43.75	50.00	75.00	68.75	<0.001
<i>Brassica oleracea</i>	24.2399	100.00	94.64	96.88	84.38	<0.001
<i>Glycine max</i>	17.7347	76.25	82.14	81.25	96.88	<0.001
<i>Lactuca sativa</i>	2.3662	46.25	46.43	40.63	37.50	<0.500
<i>Lycopersicon esculentum</i>	3.1502	47.50	44.64	35.50	43.75	<0.500
<i>Ocimum basilicum</i>	0.9786	67.50	66.07	68.75	62.50	<0.900
<i>Tagetes patula</i>	24.8023	91.25	89.29	96.88	75.00	<0.001
<i>Zinnia violacea</i>	4.8717	77.50	71.43	78.13	84.38	<0.250

Table 4. The number of surviving cultivated plants and cultivated plant biomass in monocultures, along with the results of ANOVA. Numbers are means with standard deviations in parentheses.

<u>Species</u>	<u>Number of survivors</u>	<u>mean biomass</u>
<i>Borago officinale</i>	3.5 (3.064)	0.584 (0.594)
<i>Brassica oleracea</i>	8.0 (0.000)	2.515 (2.096)
<i>Glycine max</i>	6.1 (1.595)	1.415 (0.896)
<i>Lactuca sativa</i>	3.7 (2.214)	0.275 (0.184)
<i>Lycopersicon esculentum</i>	3.8 (2.616)	0.351 (0.269)
<i>Ocimum basilicum</i>	5.4 (1.776)	0.621 (0.229)
<i>Tagetes patula</i>	7.3 (0.823)	1.093 (0.424)
<i>Zinnia violacea</i>	6.8 (1.135)	0.978 (0.527)
F	7.881	6.965
p	<0.001	<0.001

Table 5. The biomass of the emerged weeds (grams), resulting total microcosm biomass (grams), emerged weed species richness, and total microcosm species richness, along with results of ANOVA. Numbers are means with standard deviations given in parentheses.

<u>Species</u>	<u>weed biomass</u>	<u>total biomass</u>	<u>weed richness</u>	<u>total richness</u>
<i>Borago officinale</i>	9.641(3.858)	10.225(4.107)	5.70(0.675)	6.40(0.699)
<i>Brassica oleracea</i>	9.275(2.947)	11.790(3.587)	6.25(1.488)	7.25(1.488)
<i>Glycine max</i>	7.843(4.834)	9.258(4.234)	6.70(1.252)	7.70(1.252)
<i>Lactuca sativa</i>	9.654(5.479)	9.929(5.449)	6.40(0.516)	7.20(0.789)
<i>Lycopersicon esculentum</i>	6.521(1.897)	6.872(1.973)	6.90(1.595)	7.70(1.767)
<i>Ocimum basilicum</i>	5.475(4.429)	6.096(4.438)	6.80(1.398)	7.80(1.398)
<i>Tagetes patula</i>	10.345(5.458)	11.438(5.526)	6.30(0.823)	7.30(0.823)
<i>Zinnia violacea</i>	11.088(6.338)	12.066(6.503)	6.70(0.675)	7.70(0.675)
F	1.741	2.185	1.227	1.567
p	0.114	0.046	0.300	0.160

Table 6. Summary of linear correlations. Abbreviations are as follows: SR= species richness, surv.= surviving, # = number of, cult.= cultivated, andn ini.= initial.

X	Y	r
emerged weed SR	weed biomass	0.087
cultivated biomass	weed biomass	0.126
cultivated biomass	emerged weed SR	0.054
surv.cultivated SR	weed biomass	0.086
surv.cultivated SR	emerged weed SR	0.076
surv.cultivated SR	cultivated biomass	0.358***
# cult.surviving	weed biomass	0.131
# cult.surviving	emerged weed SR	0.081
# cult.surviving	cultivated biomass	0.523***
# cult.surviving	surv. Cultivated SR	0.225***
ini.cultivated SR	weed biomass	0.069
ini.cultivated SR	emerged weed SR	0.086
ini.cultivated SR	cultivated biomass	0.279***
ini.cultivated SR	surv.cultivated SR	0.917***
ini.cultivated SR	# cult.surviving	0.006
ini.cultivated SR	change in SR	-0.480***
resulting SR	weed biomass	0.120
resulting SR	cultivated biomass	0.353***
resulting SR	surv. Cultivated SR	0.831***
resulting SR	# cult. surviving	0.227***
resulting SR	ini.cultivated SR	0.771***
resulting biomass	ini.cultivated SR	0.120
resulting biomass	resulting SR	0.184**
resulting biomass	# cult. surviving	0.226***
resulting biomass	surv. Cultivated SR	0.152*
resulting biomass	emerged weed SR	0.109
resulting biomass	weed biomass	0.982***

*p <.05

**p <.01

***p <.001

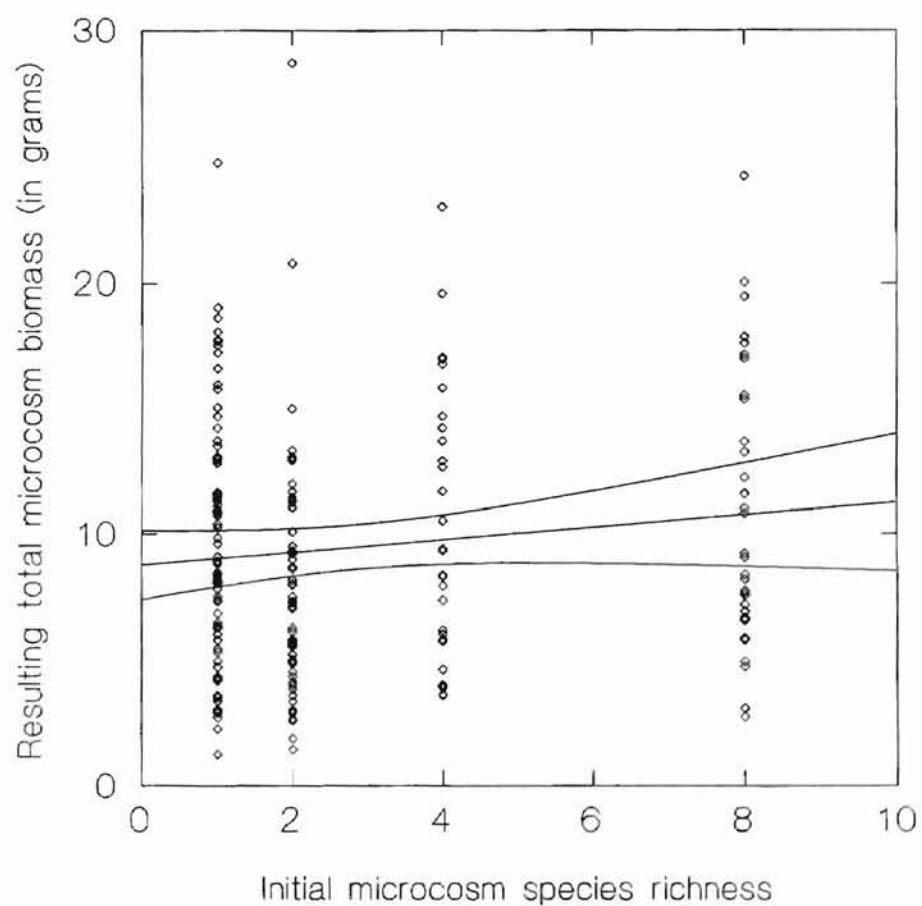


Figure 1. Resulting total microcosm biomass (in grams) as a function of initial microcosm species richness ($r=.120$, $t=1.692$, $p=.092$).

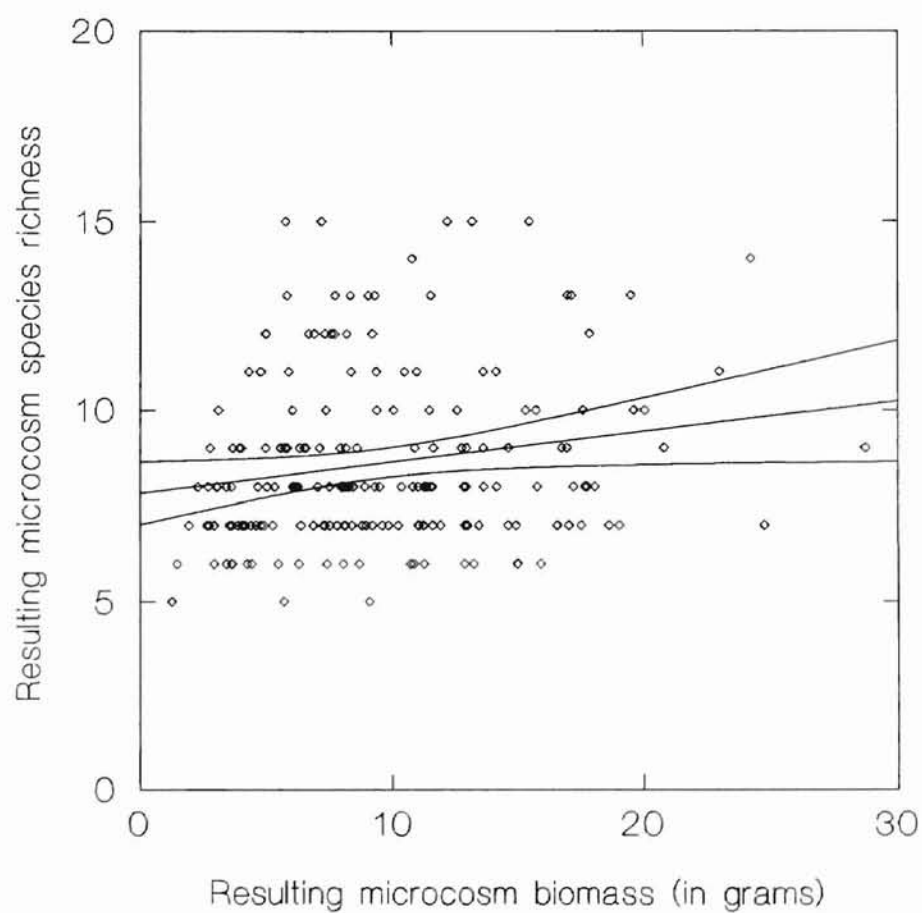


Figure 2. Resulting total microcosm biomass (in grams) as a function of the final, or resulting, microcosm species richness ($r=.184$, $t=2.619$, $p=.010$).

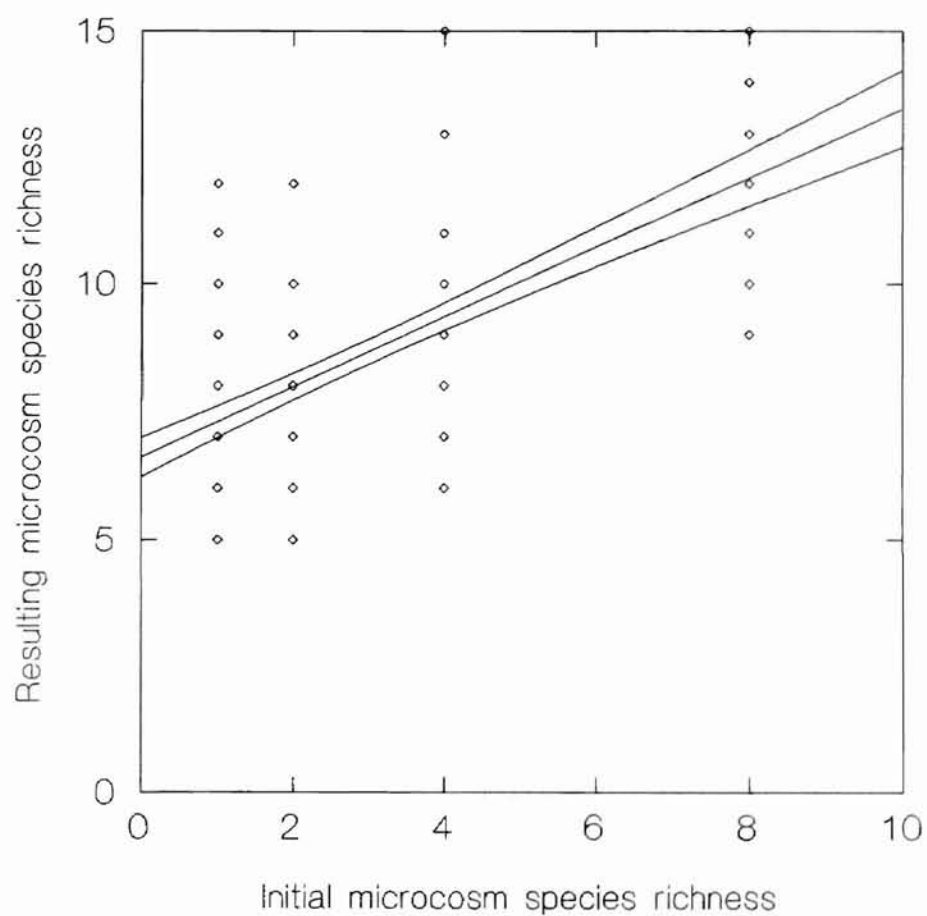


Figure 3. Resulting total microcosm species richness as a function of initial microcosm species richness ($r=.771$, $t=16.947$, $p<.0001$).

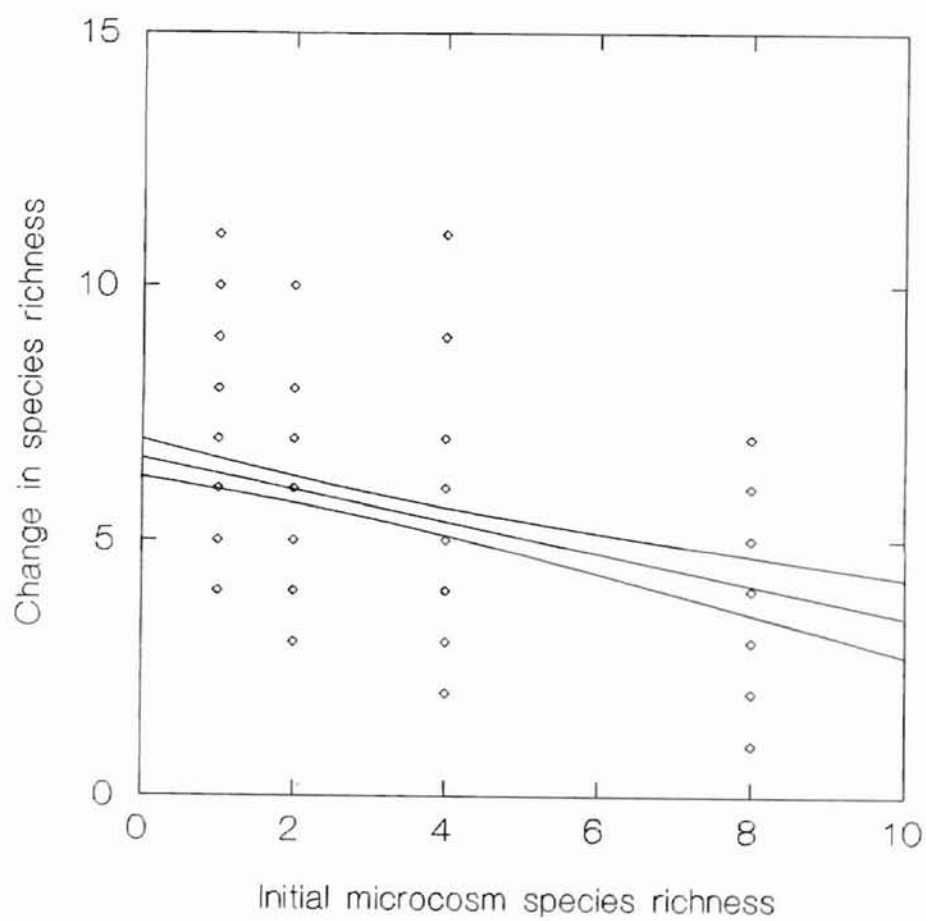


Figure 4. Overall change in microcosm species richness as a function of initial species richness ($r=.480$, $t=7.664$, $p<.0001$).

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VITA

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Candidate for the Degree of

Master of Science

Thesis: EFFECTS OF INITIAL SPECIES RICHNESS ON THE
SURVIVORSHIP, BIOMASS AND FINAL SPECIES RICHNESS OF
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