THE STRUCTURE OF PLANT MICRO-COMMUNITIES EMERGING FROM SOIL SEED BANKS

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Chapter 1

ROLE OF DISTURBANCES, FERTILIZATION, AND SOIL SEED BANKS IN STRUCTURING PLANT COMMUNITIES

Before human alterations, natural plant communities occupied vast areas of the Earth's land surface and were maintained by natural disturbances (Bormann & Likens 1979; Burton at al. 1988). With the introduction of anthropogenic disturbance, intensive deforestation to open new land for agriculture (Boza 1993) and extensive exploitation of grasslands for cattle raising (Peet et al. 1983) in different parts of the world has markedly reduced the size of natural plant communities. The remaining natural plant communities are also losing their species richness at an alarming rate as a result of clearcutting (Johnson et al. 1993), introduction of exotic plant species (Berger 1993) and deteriorating environmental conditions such as the greenhouse effect (Root & Schneider 1993; Grabherr, et al. 1994). These circumstances have lead ecologists to seek suitable strategies for the conservation of the remaining plant communities, especially those that are endangered.

Research endeavors in the last few decades have revealed that some prescribed disturbances (burning, grazing, and mowing), and use of soil seed banks can contribute tremendously towards conservation of plant communities (Bakker 1987; Young et al. 1987; Collins & Glenn 1988; Schiffman & Johnson 1992). I present a review of the relevant literature addressing the role of disturbances, fertilization, and soil seed banks in maintaining the structure of natural plant communities.

Disturbances

Grime (1979) defined "disturbances" as "mechanisms that limit the plant biomass by causing its partial or total destruction." Disturbances, either natural (lightning, drought, soil erosion and floods) or anthropogenic (burning, grazing, and mowing) have a decisive influence on plant community structure, especially in grasslands. The most important effect of disturbances in grasslands is to remove the heavy litter accumulations (Adams et al. 1982; Dudley and Lajtha 1993). If not disturbed, the thick litter layer blocks light penetration (Silvertown 1980) and releases some allelopathic chemicals (Abdul-Wahab & Rice 1967; Muller et al. 1968; Bokhari 1978; del Moral & Muller 1970) which negatively influence the germination and establishment of many species. Willems (1983) found that in a chalk grassland in the Netherlands, the withdrawl of herbivores and other management practices resulted in heavy litter accumulations and dominance of only a few species . He attributed the reduction in species richness to poor seedling emergence and survival rates because of low light intensity and red : far-red ratio caused by the above ground biomass. Similarly, Facelli (1988) reported a sharp decrease in species richness as a result of dense litter accumulations. In a related study, Bobbink and Willems (1993) observed that the removal of thick litter layers by cutting improved the germination of short-lived forbs that markedly increased the species richness of a chalk grassland in the Netherlands.

Another important effect of disturbance is to check the encroachment of trees and shrubs in herbaceous plant communities (Peet et al. 1983). Without disturbance, trees and shrubs rapidly invade grasslands and change them into closed woodlands or shrublands (Adams et al. 1982; Bobbink & Willems 1993). Like the litter layer, the canopy cover of trees has a negative influence on the understory vegetation (Specht et al. 1990). The competitive exclusion of shade intolerant species, deprived of suitable light, space, and moisture conditions by canopy species, results in low species richness (Collins & Glenn

1988). Gehring and Bragg (1992) found that the rapid invasion of eastern red cedar (*Juniperus virginiana*) significantly influenced the species composition in an eastern Nebraska bluestem prairie. Fowler (1990) observed similar significant effects of the canopy cover of *Juniperus ashei* on the growth of *Bouteloua rigidiseta* and seedset of *Aristida longiseta.*

The monopoly of even a single species on resources without disturbance can adversely influence the species richness of plant communities (Collins 1990; Bobbink & Willems 1993). In riverine marsh vegetation, Day et al. (1988) found that the dominance of *Typha latifolia* considerably reduced species richness. In contrast, Glenn & Collins (1993) observed an increase in the species richness following the removal of *Schizachyrium scoparium* in tallgrass prairie communities in Oklahoma and Kansas. Experiments designed to study the interspecific competitive effects have confirmed the existence of competitive hierarchies among species (Keddy & Shipley 1989) and their possible influence on their coexistence (Fowler 1990). Some recent studies (Miller 1994; Tilman 1994) also indicate that direct and indirect interspecific competitive interactions profoundly influence the species richness of plant communities.

By reducing the vigor of fast growing dominant species and counteracting the competitive exclusion process , disturbances promote the existence of competitively inferior species (Collins 1990; Fowler 1990; Pacala & Crawley 1992). Following disturbance, the improved red : far-red light ratio, temperature, and moisture conditions at soil surface stimulate seed germination. Consequently, the successful establishment of subordinate species yields high species richness (Peet et al. 1983; Rabinowitz & Rapp 1985; Platt & Weis 1985; Belsky 1986; Collins 1987; Young et al. 1987; Goldberg & Gross 1988; Fowler 1990; McGinley & Tilman 1993). Armesto & Pickett (1985) found that the disruption of canopy cover in an old-field community dominated by *Solidago canadensis* improved the germination and growth of suppressed species and resulted in high species richness. Ellison & Farnsworth (1993) also recorded similar seedling survivorship and growth responses following canopy removal by tidal disturbance in a Belizean mangal.

The intensity and frequency of disturbance are also of specific importance in regulating the species richness of plant communities (Bakker 1987). Armesto and Pickett (1985) imposed three intensities of disturbance (low, intermediate, and high), to remove biomass accumulations and disrupt the canopy cover. Following disturbance, they found a positive relationship between species richness and the intensity of disturbance, which caused maximum species richness in the highly disturbed plots. Collins (1987) also noted rapid increase in the species richness of a tallgrass prairie in response to increasing intensity of disturbance.

Normally infrequent and low disturbance levels prove ineffective in removing the thick litter layers and in reducing the vigor of dominant species to provide suitable environmental conditions for the germination and establishment of fugitive species (Connell 1978). After very intense and frequent disturbances as well, some species lose their regenerative capability. Therefore, both very high and very low disturbance levels result in low species richness. However, intermediate disturbance regimes disrupt the canopy cover and thick litter layers to appropriate levels, which facilitate the establishment of new recruits and yield high species richness (Zeevalking & Fresco 1977; Collins & Glenn 1988).

Grime (1973, 1979) after surveying several vegetation types proposed his well-known curvilinear model for the relationship between species richness and biomass (Fig. 1). He attributed the low species richness at the upper extreme to competitive exclusion caused by fast growing species, and at the lower extreme to the stress caused by disturbances or poor resource levels. The maximum species richness in his model was related to intermediate biomass levels. Al-Mufti et al. (1977) further refined the model and related high species richness to a specific biomass range (350-750 g m^{-2}) for herbaceous plant communities. This model has been tested and found valid for a large

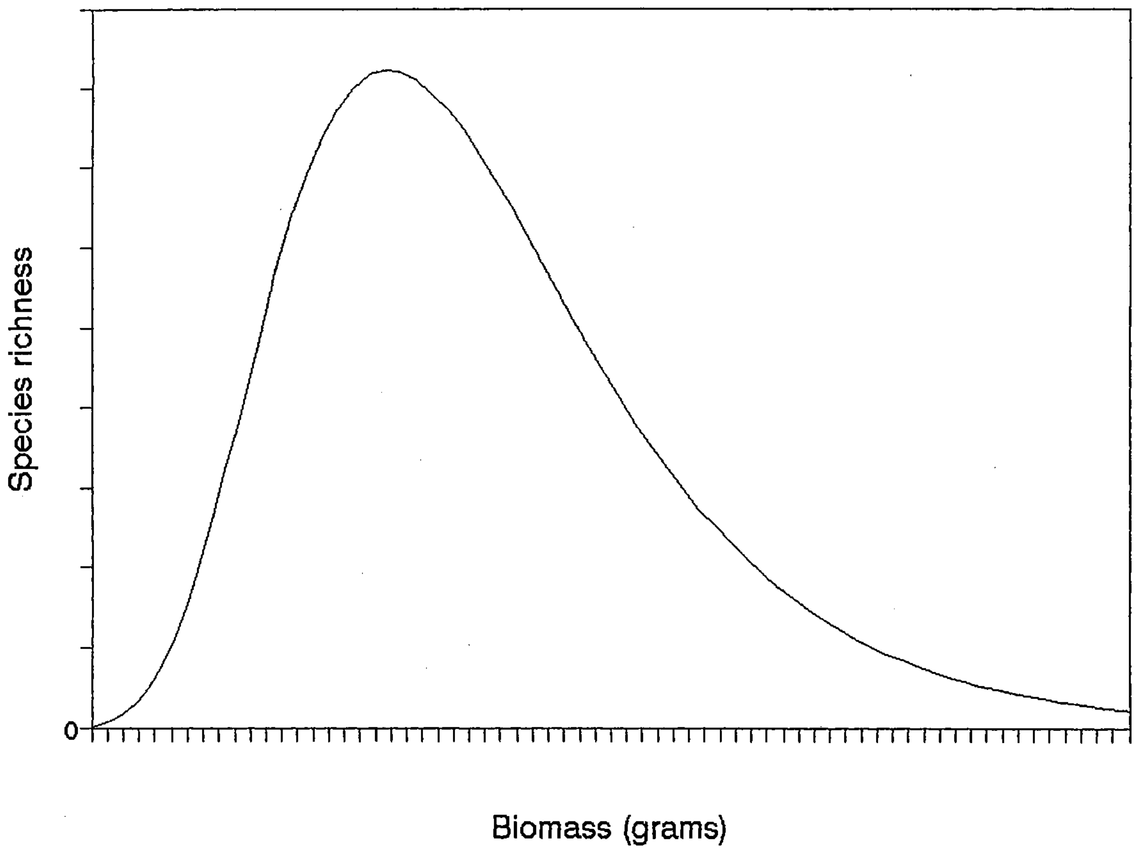

Fig. 1. The relationship between species richness and biomass according to Grime's model, modified from Grime (1973, 1979).

variety of plant communities (Klinkhamer & De Jong 1985; Kutiel & Danin 1987; Belcher et al. 1992).

The timing of disturbance of plant communities also has a profound importance (Goldberg & Gross 1988; Dudley & Lajtha 1993). As noted above, the effectiveness of a disturbance depends on how efficiently it removes plant litter. Perhaps because of biomass dryness and therefore high flammability, summer burning has proved more effective than dormant season disturbances for achieving high species richness (Wheeler & Giller 1982). Armesto and Pickett (1985) also reached the same conclusion. In an old-field community, they observed that mid-summer and late-summer disturbances proved more effective than early-summer disturbance in enhancing species richness. In contrast, in an Oklahoma grassland, Adams et al., (1982) observed that dormant season (winter) burning reduced the richness of woody species more effectively than the summer season burning.

Different types of disturbances affect grassland vegetation differently (Willems 1983; Collins & Glenn 1988). In some grasslands grazing has proved more effective than burning and mowing in promoting species richness (Willems 1983; Belsky 1992; Montalvo et al. 1993), but in other instances, monophagous behaviors of herbivores (Vinton et al. 1993) promoted the dominance of only a few palatable species such as *Leontodon autumnalis* and *Ambrosia trifida* (Ter Heerdt et al. 1991). A long time period is needed to remove heavy biomass accumulations by grazing (Bakker 1987). Extensive defoliation and uprooting by mammals also sometimes reduces survival and fecundity (Collins & Glenn 1988; Pacala & Crawley 1992). Bock and Bock (1993) observed that livestock grazing caused partial destruction of the native flora in a grama grassland in southeastern Arizona. A review by Van Wieren (1991) indicates that heavy grazing by domestic livestock in Scandinavia caused the elimination of several palatable species. Nutrient recycling via defecation by herbivores, causes further enrichment of already fertile soils, and undermines the importance of grazing in grasslands. Frequent and intense burning can also cause the elimination of some species (Collins & Glenn 1988).

Studies by Olff & Bakker (1991) and Bobbink & Willems (1993) indicate that mowing proves very effective in rapid, safe, and uniform removal of thick litter accumulations. Additionally, mowing withdraws nutrients from the system at faster rates than grazing to create nutrient impoverished conditions (Bakker 1987) that facilitate the coexistence of several species. Oomes (1992) observed that cutting twice a year for ten years substantially decreased the dry matter production and N-, P-, and K-, content in the soil, and simultaneously enhanced the species richness.

The differential response of plant species to disturbances (Belsky 1992; Ikeda & Okutomi 1992; Vinton & Hartnett 1992) is also worth mentioning. Some grasses and forbs are well adapted to recurrent fires. Such species can resist burning through "the hide-below-ground" strategy (Collins & Glenn 1988), while species lacking adaptations for such a strategy are adversely affected. The premature death of such species and low contribution to the soil seed banks increases their extinction chances in the long term. Wilson & Keddy (1988) evaluated the survivorship of twelve species along a lakeshore gradient exposed to wave action. They observed that different species responded differently to disturbances and showed huge variability in their survivorship. This differential response of coexisting species sometimes influences the interspecific competitive interactions that ultimately alter the entire community organization (Ikeda & Okutomi 1992).

Soil fertility

Soil fertility has a profound effect on the species richness of plant communities. Carson & Barrett (1988) investigated the effects of nutrient enrichment on succession in two old-field plant communities. Species richness in the fertilized plots was significantly higher than in the control plots in the first year, but thereafter gradually declined. Some grassland and wetland studies (Vermeer & Berendse 1983; Klinkhamer & De Jong 1985) also indicate a positive correlation between soil fertility and species richness.

The Park Grass Experiment at Rothmond England, initiated in 1856, is a classic example of experimental fertilization of grasslands (Silvertown 1980) where following fertilization rapid increase in above-ground biomass levels caused a simultaneous decline in species richness. Similarly in the North American prairies (Reed 1977; Tilman & Olff 1991; Wilson & Shay 1991; Tilman 1993) and in some chalk grasslands in the Netherlands (Bobbink 1991; Willems et al. 1993), fertilization significantly decreased species richness. Ecological surveys of riverine marsh (Day et al. 1988), fen (Wheeler 1988), and grassland (Olff & Bakker 1991), communities have also revealed that sites with enriched soils had lower species richness than the sites with impoverished soils. Peet et al. (1983) attributed this apparent paradox of enrichment leading to low species richness to the competitive exclusion process caused by the rapidly growing dominant species. The use of a growth retardant leading to low biomass levels but high species richness confirms this view (Yemm & Willis 1962).

Nutrient-poor sites are generally invaded by several early successional, short-lived, and short-statured species and show high species richness (Olff & Bakker 1991). In contrast, at sites with fertile soils the invasion and rapid growth of long-living perennial species with high nutritional demand during late successional stages results in low species richness (Tilman 1987; Nilsson & Wilson 1991). Peet & Christensen (1988) examined changes in species diversity during secondary forest succession in the North Carolina Piedmont. They found that at infertile sites, species richness steadily increased in the earlier stages of succession, but in the later stages, it started declining with the increase in fertility. Similarly, Milchunas et al. (1990) observed considerable increase in species richness following nitrogen enrichment in a short grass steppe in Colorado.

Interaction between disturbance and fertilization

The complex interactive effects between disturbance and fertilization have made it difficult to examine their roles separately in plant communities (Wilson & Tilman 1991), but it is known that these interactive effects greatly influence the relationship between species richness and biomass of plant communities. Models proposed by Grime (1973, 1979) and Al-Mufti et al. (1977), predict that the maximum species in a plant community relates to intermediate biomass levels. An increasing number of studies (Klinkhamer & De Jong 1985; Kutiel & Danin 1987; Moore & Keddy 1989; Belcher et al. 1992) has revealed similar unimodal curves for the relationship between species richness and biomass for a great variety of vegetation types. In all these reports, the low species richness beyond intermediate biomass level has been attributed to competitive exclusion, and below this limit, to the higher degree of environmental stress caused by disturbances or poor resource levels.

Tilman's (1982) resource model predicts high species richness at intermediate resource levels, but in Connell's (1978) model, high species richness is related to intermediate disturbance. A collective understanding of both models provides an insight in inferring the similar role of disturbance and soil fertility on the species richness. At fertile sites when fast growing species tend to competitively exclude the subordinate species (Wheeler 1988; Wilson & Shay 1990), moderate disturbances yield high species richness by counteracting competitive exclusion. In addition to decreasing the vigor of dominant species, they establish nutrient poor conditions. Disturbance-mediated decrease in soil fertility leading to high species richness has been experimentally observed in some grasslands in the Netherlands (Olff & Bakker 1991; Bobbink & Willems 1993).

Soil seed banks

Soil seed banks are an integral part of plant communities. They have the potential to contribute to secondary succession (Hill & Stevens 1981; Young et al. 1987; Brown 1991). Whenever the aboveground vegetation is severely damaged by natural or anthropogenic disturbance and has lost the regenerative capability, soil seed banks prove very effective in recolonization (Bobbink & Willems 1993; del Moral & Wood 1993). Newman (1963) examined the germination behavior of winter annuals. He found that seeds stored for some time germinated at higher rates than fresh seeds. In a lowland forest in Malaysia, Putz & Appanah (1987) found that the seedlings emerging from soil seed banks were several times more abundant than those from recently dispersed seeds. Following deforestation in Costa Rica, Young et al. (1987) also observed an overwhelming number of seedlings emerging from the soil seed banks as compared to those from the fresh seed rain.

The similarity between the species composition of seed banks and the associated above-ground vegetation still remains a controversial topic. Resemblance between the soil seed banks and the associated vegetation usually covary with the intensity and frequency of disturbance (Beatty 1991). Seed banks of grasslands (Major & Pyott 1966; Thompson 1987; Bigwood & Inouye 1988) and woodlands (Pratt et al. 1984) experiencing only low disturbance levels show little resemblance to their associated above-ground vegetation. Ingersoll & Wilson (1992) after assessing the buried propagule bank of a high subalpine site and comparing it with aboveground vegetation reported that the seeds that are abundant in the soil have extremely low colonization. Thompson & Grime (1979) after evaluating the seasonal variation in the seed banks of herbaceous species in ten contrasting habitats also reported a lack of correspondence between the species composition of the seed flora and the vegetation. In contrast, the correlation between the species composition of seed banks and the associated plant communities has been found very high in frequently disturbed habitats such as arable fields (Wilson et al. 1985; Levassor et al. 1990). During a comparatively recent study, Unger & Woodall (1993) determined the relationship between the seed bank and species composition of plant communities in two British salt marshes. They found significant positive correlation between vegetation and seed banks in annual dominated zones, in contrast, perennial dominated zones showed low correlation.

Disturbances prove very effective in burying seeds in the deep soil layers thus providing protection from predation and preventing untimely sprouting. Deeply buried, small-sized seed from frequently disturbed grasslands have been reported to live longer than the seeds of forest species buried near the soil surface (Rampton & Ching 1970; Kellman 1970; Hill & Stevens 1981; Schiffman & Johnson 1992), because seed banks in the upper soil profiles are more susceptable to disturbances such as fire, predation, and fungal attack (Warr et al. 1993).

Soil type also influences the longevity of seed banks. Fertile soils with high mineral content have a higher number of viable seeds than infertile such as peat and acidic soils (Hill & Stevens 1981). Anaerobic conditions in wet soils improve seed longevity in comparison to well aerated soils which promote seed germination (Schafer & Chilcote 1970). Depending upon the soil type, seed banks may exhibit a tremendous amount of spatial heterogeneity (Dessaint et al. 1991; Warr et al 1993). Schneider & Sharitz (1986) assessed the seed bank dynamics of two woody and herbaceous plant communities in South Carolina. They found that woody seed banks had more dissimilarity in their species composition than did the herbaceous seed banks. Schiffman & Johnson (1992) observed large variation among sites in the species composition of buried seed banks in a Southern Appalachian oak forest.

As is apparent from the above discussion, the coexistence of species does not depend on disturbance or soil fertility alone. Ecologists are beginning to study the interactive effects of disturbance and fertility on species richness of plant communities.

At present, there is considerable testing of different models dealing with species richness in natural plant communities, where the influence of a specific environmental factor can not be completely evaluated. Plant communities emerging from soil seed banks may prove very helpful in testing the role of different factors. The controversies in different models dealing with the relationship between species richness and biomass may also be resolved by experimentally manipulating plant communities in different ways. Therefore, the objective of my study is to determine experimentally:

1. the relationship between species richness and biomass in plant micro-communities emerging from soil seed banks.

2. the differences between plant micro-communities emerging from different soil seed banks.

3. the influence of disturbances and fertilization on the structure of plant micro-communities emerging from soil seed banks.

4. the interactive effects of disturbance and fertilization on the structure of plant micro-communities emerging from soil seed banks.

References

Abdul-Wahab, A. S. & Rice, E. L. 1967. Plant inhibition by Johnson grass and its possible significance in old-field succession. *Bull. Torrey Bot. Club*. 94: 486-497.

Adams, D. E.; Anderson, R. C. & Collins, S. C. 1982. Differential response of woody and herbaceous species to summer and winter burning in an Oklahoma grassland. *Southwest. Nat.* 27: 55-61.

Al-Mufti, M. M.; Syeds, C. L., Furness, C. L., Grime, J. P., & Band, S. R. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *J. Ecol.* 65: 759-791.

Armesto, J. J. & Pickett, S. T. A. 1985. Experimental disturbance in old-field plant communities: impact on species richness and abundance. *Ecology* 66: 230-240.

Bakker, J. P. 1987. Grazing as a management tool in the restoration of species rich grasslands. *Proceedings of the Koniklijke van Watenschappen Series* C., 90: 404-429.

Beatty, S. W. 1991. Colonization dynamics in a mosaic landscape: the buried seed pool. *J. Biogeog.* 18: 553-563.

Belcher, J. W., & Keddy, P. A. 1992. Protecting alvar vegetation : will the sum of the parts equal the whole? Pages 327-321 in. Wilson, J. H. M., Bondrup-Nielsen, S., Drysdale, C., Herman, T. B., Munro, N. W. P. & Pollock, T. L. 1992. eds. *Science and the management of protected areas.* Elsevier, Amsterdam.

Belcher, J. W. Keddy, P. A. & Catling , P. M. 1992. Alvar vegetation in Canada: a multivariate description of two scales. *Can. J. Bot.* 70: 1279-1291.

Belsky, J. 1986. Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania. I. Colonization of grazed and ungrazed plots. *J. Ecol.* 74: 419-438.

Belsky, J. 1992. Effects of grazing ,competition, disturbance and fire on species composition and diversity in grassland communities. *J. Veg. Sci.* 3: 187-200.

Berger, J. J. 1993. Restoration and non indigenous plant species: A review. *Rest. Ecol.* 74-82.

Bigwood, D. W. & Inouye, D. W. 1988. Spatial pattern analysis of seed banks: An improved method and optimized sampling. *Ecology* 69: 487-507.

Bobbink, R. 1991. Effects of nutrient enrichment in Dutch grasslands. *J. Appl. Ecol.* 28: 28-41.

Bobbink, R. & Willems, J. H. 1993. Restoration management of abandoned chalk grasslands in the Netherlands. *Biodiv. & Conserv.* 2: 616-626.

Bock, C. E. & Bock, J. H. 1993. Cover of perennial grasses in southeastern Arizona in relation to livestock grazing. *Conserv. Biol.* 7: 371-377.

Bokhari, V. G. 1978. Allelopathy among prairie plants and its possible ecological significance. *Ann. Bot.* 42:142-136.

Bormann, F. H. & Likens, G. E. Catastrophic disturbance and the steady state in northern hardwood forests. *Am. Sci.* 67: 660-669.

Boza, M. A. 1993. Conservation in action: past present, and future of the National Park system in Costa Rica. *Conserv. Biol.* 7: 239-247.

Brown, D. 1991. Estimating the composition of a forest seed bank: a comparison of the seed extraction and seedling emergence methods. *Can. J. Bot.* 70: 1603-1612.

Burton, P. J.; Robertson, L. R.; Iverson, L. R. & Risser, P. J. 1988. Use of resource partitioning and disturbance regimes in the design of restored prairies. In: Allen, E. B. (ed.), *The restoration of disturbed arid lands.* AAAS selected symposium, 109. Western Press, Boulder, Co. 46-48.

Carson, W. P. & Barrett, G. W. 1988. Succession in old-field communities: Effects of contrasting types of nutrient enrichment. *Ecology* 69: 984-994.

Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. *Ecology* 68: 1243-1250.

Collins, S. L. 1990. Patterns of community structure during succession in tallgrass prairie. *Bull. Torrey. Bot. Club* 117: 397-408.

Collins, S. L. & Glenn, S. M. 1988. Disturbance and community structure in North American prairies, pp. 131-143. In: During H. J.; Werger, M. J. A. & Willems J. H. (eds.). *Diversity and pattern in plant communities.* SPB Academic Publishers, The Hague, The Netherlands.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.

Day, R. T., Keddy, P. A.; Mc Neil, J. & Carleton, T. 1988. Fertility and disturbance gradients: a summary model for riverine marsh vegetation. *Ecology* 69: 1044-1054.

del Moral, R. & Muller, C. H. 1970. The allelopathic effects of *Eucalyptus camaldulensis. Am. Midl. Nat.* 83: 254-282.

del Moral, R. & Wood, D. M. 1993. Early primary succession on a barren volcanic plain at Mount St. Helens, Washington. *Am. J. Bot.* 80: 981-991.

Dessaint, F., Chadoeuf, R. & Barralis, G. 1991. Spatial pattern analysis of weed seeds in the cultivated soil seed bank. *J. Appl. Ecol.* 28: 721-730.

Dudley, L. J. and Lajtha, K. 1993. The effects of prescribed burning on nutrient availability and primary production in Sandplain grasslands. *Am. Midl. Nat.* 130: 286-298.

Ellison, A. M. & Farnsworth, E. J. 1993. Seedling survivorship growth, and response to disturbance in Belizean mangal. *Am. J. Bot.* 80: 1137-1145.

Facelli, J. M. 1988. Response to grazing after nine years of cattle exclusion in a flooding pampa grassland, Argentina. *Vegetatio* 78: 21-25.

Fowler, N. L. 1990. The effects of competition and environmental heterogeneity on three coexisting grasses. *J. Ecol.* 78: 389-402.

Gehring, J. L. & Bragg, T. B. 1992. Changes in prairie vegetation under Eastern Red Cedar (*Juniperus virginiana* L.) in an eastern Nebraska Bluestem prairie. *Am. Midl. Nat.* 128: 209-217.

Glenn, S. M. & Collins, S. L. 1993. Experimental analysis of patch dynamics in tallgrass prairie plant communities. *J. Veg. Sci.* 4: 157-162.

Goldberg, D. E. & Gross, K. L. 1988. Disturbance regimes of midsuccessional old-fields. *Ecology* 69: 1677-1688.

Grabherr, G., Gottfried, M. & Pauli, H. 1994. Climate effects on mountain plants. *Nature* 369: 448.

Grime, J. p. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344-347.

Grime, J. P. 1979. *Plant strategies and vegetation process.* Wiley, Chichester.

Hill, M. O. & Stevens, P. A. 1981. The density of viable seeds in soils of forest plantations in upland Britain. *J. Ecol.* 69: 693-709.

Ikeda, H. & Okutomi, K. 1992. Effects of species interactions on community organization along a trampling gradient. *J. Veg. Sci.* 3: 217-222.

Ingersoll, C. A. & Wilson, M. V. 1992. Buried propagule bank of a high subalpine site: microsite variation and comparisons with aboveground vegetation. *Can. J. Bot.* 71: 712-717.

Johnson, A. S., Ford, W. M., & Hale, P. E. 1993. The effects of clearcutting on herbaceous understories are still not fully known. *Conserv. Biol.* 7: 433-435.

Keddy, P. A. & Shipley, B. 1989. Competitive hierarchies in herbaceous plant communities. *Oikos* 54: 234-241.

Kellman, M. C. 1970. The viable seed content of some forest soil in coastal British Columbia. *Can. J. Bot.* 48: 1383-1385.

Klinkhamer, P. G. L. & De Jong, T. J. 1985. Shoot biomass and species richness in relation to some environmental factors in a coastal dune area in The Netherlands. *Vegetatio* 63: 129-132.

Kutiel, P & Danin, A. 1987. Annual species diversity and above-ground phytomass in relation to some soil properties in the sand dunes of the northern Sharon plains, Israel. *Vegetatio* 70: 45-49.

Lavassor, C., Ortega, M., & Peck, B. 1990. Seed bank dynamics of Mediterranean pastures subject to mechanical disturbance. *J. Veg. Sci.* 1: 339-344.

Major, J. & Pyott, W. T. 1966. Burial of viable seeds in two California bunch sites and their bearing on the definition of flora. *Vegetatio* 13: 253-282.

McGinley, A. M. & Tilman, D. 1993. Short term response of old-field plant communities to fire and disturbance. *Am. Midl. Nat.* 129: 409-413.

Milchunas, D. G., Lauenroth, W. K., Chapman, P. L. & Kazempour, M. K. 1990. Community attributes along a perturbation gradient in a shortgrass steppe. *J. Veg. Sci.* 1: 375-384.

Miller, T. M. 1994. Direct and indirect species interactions in an early old-field plant community. *Am. Nat.* 143: 1007-1025.

Moore, D. R. J. & Keddy, P. A. 1989. The relationship between species richness and standing crop in woodlands. The importance of the scale. *Vegetatio* 79: 90-106.

Montalvo, J., Casado, M. A., Lavassor, C. & Pineda, F. D. 1993. Species diversity patterns in Mediterranean grasslands. *J. Veg. Sci.* 4: 213-222.

Muller, W. H., Lorber, P. & Halley, B. 1968. Volatile growth inhibitors produced by *Salvia leuciphylla*: effect on seedling growth and respiration. *Bull. Torrey. Bot. Club.* 95: 415-422.

Newman, E. I., 1963. Factors controlling the germination rate of winter annuals. *J. Ecol.* 51: 625-639.

Nilsson, C. & Wilson, S. D. 1991. Convergence in plant community structure along desperate gradients: are lakeshores inverted mountainsides ?. *Am. Nat.* 137:

774-790.

Olff, H. & Bakker, J. P. 1991. Long term dynamics of standing crop and species composition after the cessation of fertilizer application to mown grassland. *J. Appl. Ecol.* 28: 1040-52.

Oomes, M. J. M., 1992. Yield and species density of grassland during restoration management. *J. Veg.* Sci. 3: 271-4.

Pacala, S. W. & Crawley, M. J. 1992. Herbivore and plant diversity. *Am. Nat.* 140: 243-260.

Peet, P. K.; Glenn-Lewin, D. C. & Wolf, J. W. 1983. Prediction of man's impact on plant species diversity, A challenge for vegetation science. in. Holzner, W.; Werger, M. J. A. & Ikusima,I. (eds.) *Man's impact on vegetation.* pp. 41-54. Junk. The Hague.

Peet, R. K. & Christensen, N. L. 1988. Changes in species diversity during secondary forest succession on the North Carolina Piedmont. pages 233-245. in During, H. J., Werger, M. J. A. & Willems, J. H. eds., *Diversity and patterns in plant communities.* Academic Publishing, The Hague, The Netherlands.

Platt, W. J. & Weis, T. M. 1985. An experimental study of competition among fugitive prairie plants. *Ecology* 66: 708-720.

Pratt, D. W.; Black, R. A. & Zamora, B. A. 1984. Buried viable seed in a ponderosa pine community. *Can. J. Bot.* 62: 272-277.

Putz, F. E & Appanah, S. 1987. Buried seeds, newly dispersed seeds, and the dynamics of a lowland forest in Malaysia. *Biotropica* 19: 326-33.

Rabinowitz, D.& Rapp, J. K. 1985. Colonization and establishment of Missouri prairie plants on artificial soil disturbances. III. species abundance, distributions, survivorship and rarity. *Am. J. Bot.* 72: 1618-1628.

Rampton, H. H. & Ching, T. H. 1970. Persistence of crop seeds in soil. *Agron. J.* 62: 272-277.

Reed, F. C. 1977. Plant species number, biomass accumulation and productivity of a differentially fertilized Michigan old-field. *Oecologia* 30: 43-53.

Root, T. L. & Schneider, S. H. 1993. Can large scale climatic models be linked with multiscale ecological studies ? *Conserv. Biol.* 7: 256-270.

Schafer, D. E. & Chilcote, D. O. 1970. Factors influencing persistence and depletion in buried seed populations. II. The effects of soil temperature and moisture. *Crop Sci.* 10: 342-345.

Schiffman and Johnson (1992) Sparse buried seed banks in a southern Appalachian oak forest: implication of succession. *Am. Midl. Nat.* 127: 258-267.

Schneider, R. L., & Sharitz, R. R. 1986. Seed bank dynamics in a southern riverine swamp. *Am. J. Bot. 73*: 1022-1030.

Silvertown, J. 1980. The dynamics of a grassland ecosystem: botanical equilibrium in the Park Grass Experiment. *J. Appl. Ecol.* 17: 491-504.

Specht, R. L. Groundy, R. I. & Specht, A. 1990. Species richness of plant communities: relationship with community growth and structure. *Isr. J. Bot.* 39: 465-480.

Ter Heerdt, G. N. J., Bakker, J. P. & De Leeuw, J. 1991. Seasonal and spatial variation in living and dead plant material in a grazed grassland as resulted to plant species diversity. *J. Appl. Ecol.* 28:120-127.

Thompson, K. & Grime, J. P. 1979. seasonal variation in the seed-banks of herbaceous species in ten contrasting habitats. *J. Ecol.* 67: 893-991.

Thompson, K. 1987. Seeds and seed banks. *New Phytol.* 106: 23-34.

Tilman, D. 1982. *Resource competition and community structure*, Princeton University Press, Princeton.

Tilman, D. & Olff, H. 1991. an experimental study of the effect of pH and nitrogen on grassland vegetation. *Acta Oecol.* 12: 427-441.

Tilman, D. 1993. Species richness of experimental productivity gradients: How important is colonization limitation ?. *Ecology* 74: 2179-2191.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2-16.

Unger, I. A. & Woodal, S. R. J. 1993. The relationship between the seed bank and species composition of plant communities in two British salt marshes. *J. Veg. Sci.* 4: 531-536.

Van Wieren, S. E. 1991. The management of populations of large mammals. in Spellerberg, I. F., Goldberg, F. B. & Morris, M. G. (eds). *The scientific management of temperate communities for conservation.* Blackwell Scientific, Oxford. pp. 103-128.

Vermeer, J. G. & Berendse, F. 1983. The relationship between nutrient availability , shoot biomass and species richness in grassland and wetland communities. *Vegetatio* 53: 121-126.

Vinton, M. A. & Hartnett, D. C. 1992. Effect of bison (*Bison bison*) grazing on *Andropogon gerardii* and *Panicum virgatum* in burned and unburned tallgrass prairies. *Oecologia* 90: 374-382.

Vinton, M. A. Hartnett, D. C. Fick, E. J. & Briggs, J. M. 1993. Interactive effect of fire, bison (*Bison bison*) grazing and plant community composition in Tallgrass prairie. *Am. Midl. Nat.* 129: 10-18.

Warr, S. J.; Thompson, K. & Kent, M. 1993. Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. *Prog. Physiol. Geog.* 17: 329-347.

Wheeler, B. D. 1988. Species richness, species rarity and conservation evaluation of rich fen vegetation in lowland England and Wales. *J. Appl. Ecol.* 25: 331-353.

Wheeler, B. D. & Giller, K. E. 1982. Species richness of herbaceous fen vegetation in Broadland, Norfolk in relation to the quantity of above ground plant material. *J. Ecol.* 70: 179-200.

Willems, J. H. 1983. species composition and above ground phytomass in chalk grassland with different management. *Vegetatio* 52: 171-80.

Willems, J. H.; Peet, R. K. & Bike, R. 1993. Changes in Chalk-grassland structure and species richness resulting from selective nutrient additions. *J. Veg. Sci.* 4: 203-212.

Wilson, S. D. & Keddy, P. A. 1988. Species richness and biomass accumulation along an experimental gradient. *Oikos* 53: 375-80.

Wilson, R. G. Kerr. E. D. & Nelson, L. A. 1985. Potential for using weed seed content in the soil to predict future weed problems. *Weed Sci.* 33: 171-175.

Wilson, S. D. & Shay, J. M. 1990. Competition, fire and nutrients in mixed grass prairie. *Ecology* 71: 1959-1967.

Wilson S. D. & Tilman, D. 1991. Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community. *Oecologia* 88: 61-71.

Yemm, E. W. & Willis, A. J. 1962. The effects of meleic hydrazide and 2, 4-dichlophenoxyacetic acid on roadside vegetation. *Weed Res.* 2: 24-40.

Young, K. R.; Ewel, J. J. & Brown, B. J. 1987. Seed dynamics using forest succession in Costa Rica. *Vegetatio* 71: 157-173.

Zeevalking, H. J. & Fresco, L. F. M. 1977. Rabbit grazing and species diversity in a dune area. *Vegetatio* 35: 193-196.

CHAPTER II

THE STRUCTURE OF PLANT MICRO-COMMUNITIES EMERGING FROM SOIL SEED BANKS: EFFECTS OF SOIL SOURCE AND DISTURBANCE

ABSTRACT: I undertook a greenhouse study to examine the effects of disturbance (clipping) on the structure of experimental plant micro-communities emerging from soil seed banks collected from four different sites (i. e. roadside, forest, prairie, and old field), all in Osage County, Oklahoma. Plant micro-communities emerging from the forest soil samples showed significantly higher mean biomass than all other treatments during the first two harvests, but in the third harvest plant micro-communities emerging from the old-field soil samples had maximum biomass. During the first two harvests, significantly higher species richness than all other treatments was observed for plant micro-communities emerging from the prairie soil samples and during the third harvest for those emerging from the old-field soil seed banks. Grasses dominated in terms of biomass and frequency during the first harvest, but in the second and third harvests, forbs had higher biomass than grasses. The relationship between species richness and biomass of experimental plant micro-communities manifested unimodal curves for all four sites during the first harvest and partially during the second and third harvests. The among-site differences in the relationship between species richness and biomass can be mainly attributed to the variation in soil fertility and seed banks. Similarly, among-harvest differences in the relationship between species richness and biomass may be assigned to disturbances, and the variation in the life cycles of plant species. In conclusion, these experimental plant micro-communities mimicked many natural plant communities in exhibiting unimodal curves for the relationship between species richness and biomass. Further studies on experimental plant micro-communities emerging from soil seed banks may prove helpful in evaluating different ecological models.

Keywords: Seed banks, disturbance, species richness-biomass relationship, species richness.

Nomenclature: Great Plains Flora Association 1986.

INTRODUCTION

Disturbances play a key role in shaping the relationship between species richness and biomass of herbaceous plant communities (Sousa 1984; Day et al. 1988; Puerto et al. 1990; Dudley & Lajtha 1993; Vinton et al. 1993). By removing high biomass accumulations, they decrease the dominating effects of competitively superior species (Willems 1983; Day et al. 1988; Ter Heerdt et al. 1991; Bobbink & Willems 1993; Glenn & Collins 1993; Willems et. al. 1993). After disturbance, the change in competitive hierarchy effectively counteracts the competitive exclusion process. The increased light penetration and provision of suitable moisture and temperature conditions for the soil seed banks in the patches created by disturbances, promote the germination and growth of some opportunistic ruderal species. After an episode of disturbance, the establishment of intermediate biomass levels favorable for the coexistence of some rare fugitive plant species along with competitively dominant plant species results in high species richness (Collins 1987; Glenn & Collins 1992; Keddy & Shipley 1989; Ellison & Farnsworth 1993; Montalvo et al. 1993).

Grime's model (1973, 1979) of the species richness and biomass relationship (hereafter, SRBR) predicts that the highest species richness in a plant community is related to intermediate levels of above ground biomass. Low species richness at low biomass is considered to result from some stress exerted by disturbances or low resource levels, while low species richness at higher biomass is attributed to extensive interspecific competition resulting in competition exclusion. The demonstration of unimodal curves for the species richness-biomass relationship from some plant (Al-Mufti et al. 1977; Kutiel & Danin 1987; Tilman 1993), ant (Anderson 1992) and rodent communities (Brown 1972) confirms Grime's model.

Contrary to Grime's model (1973, 1979) some findings (Wheeler and Giller 1982; Wisheu and Keddy 1989), reveal a negative correlation between species richness and biomass. In these models high biomass levels are always related to low species richness. Therefore, they have suggested further testing and refinement of the general model. One possible explanation for these controversial reports is that they might have recorded the high biomass levels only, which correspond to the right extreme of unimodal curve.

Hidden edaphic differences (i.e. soil depth, texture, fertility, moisture content of the soil, and seed banks) influence the above ground biomass and species richness of plant communities (Herben et al. 1993; Klinkhamer & de Jong 1985; Day et al. 1988; Belcher et al. 1992). Sites with enriched soils are characterized by high biomass levels but low species richness (Willems 1983; Kutiel & Danin 1987; Wheeler 1988). In contrast, site with impoverished soils support the establishment of a few early successional species (Olff & Bakker 1991). Belcher et al. (1992) used ordination and classification techniques to describe the vegetation among four alvar sites in Canada. They found that among site differences in species composition corresponded to differences in some soil characteristics. Therefore, if soil seed banks collected from various sites are allowed to germinate, the differences in the edaphic factor may cause among site variation in the structure of emerging plant micro-communities.

Plant species varying in their life form respond differently to seasonal environmental changes or meteorological patterns (Espigares & Peco 1993). The variable germination success and growth rates of different plant species in response to varying environmental conditions cause a dominance hierarchy in plant communities (Christie & Detling 1982; Becilieri et al. 1993). Owing to this gradual change in dominance hierarchy, plant communities exhibit temporal changes in the species richness and above ground biomass levels (Al-Mufti et al. 1977; Wheeler & Shaw 1991).

Studies on the SRBR of plant communities have been mainly confined to wetland, lakeshore, and grassland vegetation (Vermeer & Berendse 1983; Willems 1983; Klinkhamer & Jong 1985; Bakker 1987; Wilson & Keddy 1988; Puerto et al. 1990; Nilsson & Wilson 1991; Oomes 1992). Despite the fact that some findings (Major & Pyott 1966; Watkinson 1975) emphasize the importance of incorporating buried viable seeds in plant ecological studies for developing model experimental systems, little is known about the SRBR of experimental plant communities emerging from soil seed banks.

Soil seed banks are considered an integral part of a plant community. Depending upon the seed size (Thompson 1987), soil type (Hill & Stevens 1981; Granstrom 1988), and depth of burial (Rampton & Ching 1970), seed banks can retain their viability for several decades (Warr et al. 1993). However, when disturbed and exposed to suitable light and moisture conditions at soil surface, they show excellent germination and sometimes prove better colonizers than even freshly dispersed seeds (Putz & Appanah 1987; Young et al. 1987). They reflect the history of the existing vegetation, reveal among site differences in the species composition (Schiffman & Johnson 1992) and contribute tremendously during secondary succession (Fenner 1985; Ingersol & Wilson 1992; del Moral & Wood 1993; Warr et al. 1993).

Additionally, plant micro-communities emerging from soil seed banks are very easy to manipulate and replicate. They can potentially become a model system for testing existing models, and developing the new ones relating to the SRBR. The purpose of this study is to determine whether a unimodal relationship exists between species richness and biomass of plant micro-communities emerging from soil seed banks, and if so, whether this relationship varies among different sites and among harvests following disturbances. I predict that the plant micro-communities emerging from soil seed banks will exhibit unimodal curves for the SRBR.

MATERIALS AND METHODS

Study sites

I selected four study sites (i.e., roadside, forest, prairie, and old field) located within the Nature Conservancy's Tallgrass Prairie Preserve, Osage County, Oklahoma. These sites were selected to study soil seed banks from different environmental conditions, but not necessarily required to typify specific habitat types. Soil seed banks of these sites were expected to vary greatly due to variation in soil fertility and different histories of past disturbances. Results from chemical analysis (details on soil collection are given in the next section) are presented in Table 1. The roadside site is located along a gravel county road (Range 8 E, Township 28 N, Section 35 NW 1/4) between a tall-grass prairie and a drainage ditch . Apparently this soil has been extensively eroded by wind and water. Chemical analysis of the soil samples from this site indicates that it is very infertile, presumably because of extensive leaching and loss of organic matter. Soil seed banks of this site were expected to contain a large number of ruderal species especially annuals which characteristically invade infertile and disturbed sites. The forest site is a bottom-land forest dominated by *Juglans nigra* and *Celtis sp.* It is located between a tall grass prairie and a creek (Range 8 E, Township 28 N, Section 35 NW 1/4) where occasional flooding results in sedimentation of alluvial soils. Therefore, its soil is very rich in organic matter and other nutrient contents. Shade tolerant and moisture loving understory species were expected to be in abundance in its soil seed banks. The prairie site was chosen

Table 1. Chemical analysis and some physical attributes of soil samples collected from different sites. S. D.= Standard deviation. CEC = Cation exchange capacity.

		Roadside		Forest		Prairie		Old-field		Mixed	
Characteristic	Units	Mean	S. D.	Mean	S. D.	Mean	S. D.	Mean	S. D.	Mean	S. D.
Nitrogen release	p.p.m.	47.750	1.521	56.250	1.677	53.000	1.620	60.000	0.612	53.625	0.650
Phosphorus											
Easily extractable	p.p.m.	8.750	0.829	38.750	2.278	10.250	0.433	41.500	0.866	21.500	1.118
Bray II	p.p.m.	11.000	1.732	79.000	3.536	10.750	1.299	75.500	2.500	44.500	2.179
Potassium	p.p.m.	309.000	7.176	371.750	12.173	212.250	6.869	357.750	3.345	324.000	10.198
Organic matter	%	4.550	0.304	7.325	0.630	6.075	0.680	8.875	0.228	6.3000	0.274
Calcium	p.p.m.	5857.500	125.492	4272.250	264.489	2280.500	99.741	3431.750	38.590	4504.000	165.640
Soluble sulfur	p.p.m.	24.000	0.707	24.250	0.829	16.500	0.500	21.000	0.000	23.000	0.707
Magnesium	p.p.m.	452.750	13.274	315.000	8.544	220.000	9.539	314.250	3.419	339.500	8.411
Sodium	p.p.m.	29.250	1.299	16.250	0.829	13.000	1.871	15.000	0.707	19.500	0.866
Minor nutrients											
Boron	p.p.m.	1.238	0.019	1.725	0.047	0.783	0.033	1.095	0.025	1.158	0.024
Iron	p.p.m.	86.250	2.278	104.500	3.202	177.000	6.595	124.000	1.871	126.000	5.788
Manganese	p.p.m.	136.500	2.693	210.750	7.013	89.500	2.693	92.250	1.090	134.250	3.631
Copper	p.p.m.	2.260	0.068	2.785	0.100	1.473	0.052	2.160	0.032	2.198	0.064
Aluminum	p.p.m.	364.750	32.599	238.250	65.419	371.750	11.670	332.000	12.145	307.250	63.136
Zinc	p.p.m.	4.100	0.245	8.325	0.426	8.675	0.249	7.775	0.205	7.225	0.640
CEC	M.E./100	35.285	0.737	26.070	1.437	15.375	0.713	21.685	0.235	27.793	0.961
pH	H_2O 1:1	7.700	0.071	7.325	0.109	6.650	0.050	7.125	0.043	7.275	0.043

inside a tallgrass prairie (Range 8 E, Township 28 N, Section 35 NW 1/4) which has remained under moderate grazing by livestock and experienced occasional burns for several decades. Its soil is very low in organic matter and N-P-K content. Soil seed banks at this site were expected to contain a large number of perennial grassland species. The old-field site located between a gravel county road and a creek (Range 8 E, Township 28 N, Section 35 NW 1/4) was under cultivation for some time. Its soil is characteristically alluvial. Due to at least six years of abandonment, soil seed banks of this site were expected to be rich in species that preferably invade fertile soils. A mixture of soil seed banks from all four sites was hypothesized to result in higher species richness than the component seed banks in the emerging plant micro-communities.

Soil processing

To collect soil samples I established a 3 m * 300 m plot along roadside and 30 m * 30 m plots at forest, prairie, and old-field sites on May 14, 1992. From each site I collected 50 (20 cm * 20 cm * 3 cm) randomly located soil samples. Soil samples were transported to the laboratory in black polythene bags and processed using the methods adopted by Thompson and Grime (1979) and Lavassor et al. (1990). After spreading the soil samples on metal trays I placed them in the dark until dry. When dry, I gently broke soil clumps and passed the samples through 1 cm^2 mesh to remove stones and large plant fragments. I thoroughly mixed the soil samples for each site and again placed them in the dark at room temperature for one month to break dormancy (Newman 1963; Schneider and Sharitz 1986).

For each site I filled soil in 40 (10 cm * 10 cm * 5 cm) plastic pots, from a total of 200 pots. An additional lot of 40 pots was filled with soil thoroughly mixed from all four habitats. I sent ten well-mixed soil samples for each site to Brookside Laboratories, Inc., Ohio, for chemical analysis. The results are presented in Table 1.

Greenhouse experiment

I placed all soil filled pots under natural sunlight in a greenhouse on June 14, 1992, and kept their surface moist throughout the study period. The above-ground vegetation was harvested on August 14, October 14, and December 14, 1992. After drying in an oven at 55.6 °C, I determined biomass for each species in each pot.

Data analysis

The species composition of experimental plant micro-communities was evaluated in terms of frequency (percentage of pots having a plant species). Change in percentage biomass proportion of forbs, grasses and sedges of plant micro-communities emerging from different soil seed banks was also determined.

To examine the patterns in species composition among different sites and harvests, I performed canonical correspondence analysis (CCA) (ter Braak 1986). The square root transformation of biomass, elimination of pots with zero biomass, down-weighing of rare species, and passiveness of unidentified species was considered necessary to dampen the effects of noise.

I used the SYSTAT statistical package (Walkinson, 1990) to analyze the biomass and species richness data by two-way analysis of variance, to examine the differences among sites and harvests. I applied a second order orthogonal polynomial regression equation (Steel & Torrie 1980) to estimate the SRBR:

$$\text{Species Richness} = \beta_0 + \beta_1 X + \beta_2 X^2 + \varepsilon$$

β_0, β_1 and β_2, are the regression coefficients estimated by b_0, b_1 and b_2 respectively. X represents biomass, X^2 is biomass squared and ε indicates the unexplained variability in the model. The significance of β_1 (linear coefficient) only, indicates that species richness responds linearly to biomass. A significant quadratic coefficient (β_2) indicates that a parabolic curve better fits the relationship between species richness and biomass. From a positive sign (+) for the quadratic coefficient (β_2) it would be inferred that the unimodal curve is upwardly concave, and a negative sign (-) for quadratic coefficient (β_2) will indicate a downwardly concave curve. I predict that the SRBR of experimental plant micro-communities emerging from soil seed banks with a significantly ($p < 0.05$) negative quadratic coefficient (β_2) will exhibit downwardly concave unimodal curves.

RESULTS

Biomass

During harvests 1 & 2, plant micro-communities emerging from the forest soil seed banks had significantly higher mean biomass than all other treatments (Table 2). In harvest 3, plant micro-communities emerging from the old-field soil seed banks had maximum biomass, but it differed significantly from roadside treatment only, which due to low soil fertility showed minimum biomass levels during the all three harvests. Perhaps due to depletion of nutrients by the harvested plant material, biomass for all treatments declined in the successive harvests. The interaction term between sites and harvests for biomass was also highly significant (Table 4).

Species richness

The species richness exhibited significant differences among sites (Table 3). In harvest 1, plant micro-communities from the prairie site seed banks had the maximum species richness, which was significantly higher than all other treatments. The prairie site

Table 2. Biomass (dry weight in grams per 0.01 m2) of plant micro-communities emerging from soil soil seed banks. Duncan's New Multiple Range Test is used to make pairwise comparisons. Torrie 1980). Treatment means sharing the same letters are not statistically sinificant at $p < 0.05$, S. D. = Standard deviation.

	Harvest 1		Harvest 2		Harvest 3	
Sites	Mean	S. D.	Mean	S. D.	Mean	S. D.
Roadside	1.646 a	0.893	0.509 a	0.545	0.279 a	0.564
Forest	5.654 d	2.364	3.688 d	1.951	1.109 b	0.668
Prairie	2.184 b	0.857	1.842 b	1.391	0.909 b	0.837
Old field	3.921 c	1.472	2.680 c	1.188	1.391 b	0.520
Mixed	3.473 c	1.403	2.205 bc	1.716	0.885 b	0.803

Table 3. Species richness (number of species in 0.01 m2) of plant microcommunities emerging from soil seed banks. Duncan's New Multiple Range Test used to make pairwise comparisons (Steel & Torrie 1980). Treatment means sharing the same letters are not statistically different at $p < 0.05$, S. D. = Standard deviation.

	Harvest 1		Harvest 2		Harvest 3	
Sites	Mean	S. D.	Mean	S. D.	Mean	S. D.
Roadside	2.450 a	1.182	2.300 a	1.005	1.400 a	1.200
Forest	2.975 a	1.405	2.575 ab	0.972	2.350 ab	0.792
Prairie	4.500 c	1.817	3.525 c	1.500	2.025 ab	1.060
Old field	4.225 b	1.620	3.200 bc	1.166	2.950 c	1.117
Mixed	3.875 b	1.676	3.375 c	1.713	2.325 ab	1.506

Table 4. Analysis of variance table (F ratio) for biomass and species richness of plant micro-communities emerging from soil seed banks.

Treatment	Biomass	Species richness
Sites	74.673**	22.268**
Harvests	184.345**	52.375**
Sites * Harvests	11.371**	3.288**

$p < 0.001$

seed banks showed maximum species richness in harvest 2, as well, but it differed significantly from mean species richness for roadside and forest treatments only. In harvest 3, plant micro-communities from the old-field soil samples exhibited significantly higher mean species richness than all other treatments. Like biomass, the minimum species richness in all three harvests was shown by roadside soil seed banks that had very low soil fertility. Species richness also showed a declining trend in all treatments in the subsequent harvests. The interaction term between sites and harvests for species richness was also highly significant ($P<0.001$)(Table 4).

Species composition

Among-site differences

Species composition of plant micro-communities emerging from soil seed banks revealed high among-sites heterogeneity (Table 5). During harvest 1, plant micro-communities from roadside seed banks comprised 17 different species. Among these *Euphorbia stictospora, Setaria glauca* and *Solanum rostratum* had the highest frequency. *Muhlenbergia schreberi* emerged as an abundant species from forest, old-field, and mixed soil seed banks. From the prairie site seed banks *Dichanthelium acuminatum* emerged with the highest frequency. The majority of species in all five plant microcommunities were infrequent.

In harvest 2, *Muhlenbergia schreberi* emerged as an abundant species from the forest, old field, and the mixed soil samples and *Euphorbia stictospora* emerged as an abundant species from the roadside and prairie site seed banks. With a few exceptions, the other species in this harvest were infrequent.

During harvest 3, *Muhlenbergia schreberi* and *Stellaria media* from the forest seed banks emerged in abundance. Plant micro-communities emerging from the old-field soil seed banks abounded in *Muhlenbergia schreberi* and *Rumex crispus.* From the mixed soil seed banks only *Muhlenbergia schreberi* emerged with high frequency of occurrence. The remaining species from all seed banks during this harvest emerged infrequently.

Among-harvest differences

Species composition of plant micro-communities emerging from different soil seed banks exhibits very clear among-harvest differences (Table 5). The frequency of occurrence of some dominant species especially grasses (i.e. *Muhlenbergia schreberi* and *Setaria glauca*) declined gradually. In contrast, some forbs (i.e. *Rumex crispus* and *Stellaria media*) showed a gradual increase in their frequency of occurrence after the first and second disturbance. Similar trends were observed in the percentage biomass of forbs, grasses and sedges. Plant micro-communities emerging from the roadside, prairie, and old field soil samples had a higher proportion of grasses than forbs during harvest 1 (Fig. 1, 3, & 4). Thereafter, forbs comprised higher proportion of biomass than grasses and sedges in the harvests 2 & 3. Proportion of grass species emerging from the forest seed banks was higher than forbs during harvests 1 and 2, but in harvest 3, biomass proportions of both grasses and forbs were approximately equal (Fig. 3). Grasses emerging from mixed soil samples also had higher biomass than forbs during harvest 1 & 2, but later on during harvest 3, forbs gained higher biomass proportion than grasses (Fig. 5). If present, sedges showed a gradual decline in their percentage biomass proportion in the subsequent harvests.

Overall the maximum number of species (species encountered from all replicates) emerged from the mixed soil seed banks during harvests 1 & 2, and minimum either from the roadside (harvest 1) or from the forest (harvest 2) soil seed banks (Table 6). A gradual decline in the total species list was observed for all seed bank in the successive harvests. As such, in harvest 3, plant micro-communities emerging from all seed banks

Table 5. Frequency (percentage of pots in which a plant species was found) of plant species emerging from different soil seed banks.

	Harvest 1					Harvest 2					Harvest 3				
Species name	Roadside	Forest	Prairie	Old field	Mixed	Roadside	Forest	Prairie	Old field	Mixed	Roadside	Forest	Prairie	Old field	Mixed
Acalypha virginica	*	15.0	5.0	5.0	*	*	*	*	*	*	*	*	*	*	*
Ambrosia psilostachya	*	*	*	*	*	*	*	*	*	*	*	2.5	*	*	*
Ambrosia trifida	*	15.0	*	*	*	2.5	15.0	*	*	5.0	5.0	17.5	*	2.5	5.0
Ammania coccinea	*	*	*	*	*	*	*	7.5	2.5	*	*	*	*	*	*
Aristida oligantha	*	*	*	*	*	2.5	*	*	*	*	7.5	*	17.5	*	*
Bothriochloa saccharoides	*	*	*	*	5.0	*	*	*	10.0	2.5	*	*	*	*	*
Bromus japonicus	*	2.5	*	5.0	2.5	12.5	*	12.5	7.5	*	5.0	*	7.5	7.5	2.5
Chaerophyllum procumbens	*	*	*	*	*	*	2.5	*	*	*	12.5	*	5.0	*	*
Chloris verticillata	*	*	*	5.0	2.5	*	2.5	*	*	*	*	*	*	*	*
Cirsium sp.	*	*	2.5	*	*	*	*	*	*	*	*	2.5	*	2.5	*
Croton capitatus	*	*	5.0	2.5	*	*	*	*	*	*	*	*	*	*	*
Croton monanthogynus	2.5	*	*	12.5	2.5	*	*	*	*	*	*	*	*	*	*
Cyperus acuminatus	*	*	37.5	*	*	*	*	2.5	*	*	*	*	*	*	*
Cyperus filiculmis	*	2.5	2.5	*	*	*	2.5	*	*	*	*	*	*	*	*
Cyperus ovularis	*	*	67.5	*	35.0	*	*	50.0	*	17.5	*	*	20.0	*	17.5
Cyperus sp.	*	*	*	*	*	5.0	2.5	*	2.5	*	*	*	12.5	2.5	*
Cyperus strigosus	*	12.5	15.0	*	*	*	*	*	*	5.0	*	*	*	*	*
Dichanthelium acuminatum	2.5	7.5	87.5	12.5	25.0	5.0	*	32.5	*	12.5	2.5	2.5	27.5	*	5.0
Digitaria sanguinalis	*	35.0	*	2.5	2.5	*	*	*	15.0	2.5	*	*	*	*	*
Elephantopus carolinianus	*	*	*	*	*	*	*	*	*	2.5	*	*	*	*	*
Eleusine indica	10.0	*	22.5	5.0	17.5	*	*	*	*	5.0	*	*	*	2.5	*
Eragrostis cilianensis	7.5	*	2.5	5.0	2.5	2.5	*	*	2.5	5.0	*	*	*	*	*
Eragrostis hirsuta	2.5	*	5.0	*	5.0	2.5	*	10.0	*	2.5	*	*	*	*	*
Eragrostis intermedia	*	*	*	*	*	7.5	*	*	*	*	*	*	*	*	*
Eragrostis spectabilis	*	*	2.5	*	2.5	*	*	*	*	2.5	*	*	*	*	*
Erigeron sp.	*	*	*	7.5	5.0	2.5	*	*	5.0	7.5	*	*	*	10.0	*
Erigeron strigosus	*	*	2.5	5.0	*	*	*	12.5	12.5	5.0	*	*	*	*	*
Eupatorium rugosum	*	12.5	12.5	*	5.0	*	*	*	*	2.5	2.5	*	*	*	*
Euphorbia nutans	2.5	5.0	10.0	30.0	10.0	*	7.5	*	*	2.5	*	*	*	*	*
Euphorbia stictospora	70.0	20.0	22.5	65.0	55.0	82.5	30.0	67.5	55.0	56.0	37.5	2.5	*	10.0	7.5
Hieracium gronovii	*	*	*	*	*	*	*	2.5	*	*	*	*	*	10.0	*
Leucospora multifida	*	22.5	*	*	5.0	*	*	*	*	5.0	*	*	*	*	*

Table 5. continued.

	Harvest 1					Harvest 2					Harvest 3				
Species name	Roadside	Forest	Prairie	Old field	Mixed	Roadside	Forest	Prairie	Old field	Mixed	Roadside	Forest	Prairie	Old field	Mixed
Melilotus officinalis	15.0	*	*	5.0	2.5	7.5	*	5.0	2.5	*	2.5	5.0	5.0	*	*
Mollugo verticillata	2.5	17.5	*	5.0	2.5	*	*	2.5	*	*	*	2.5	*	*	*
Muhlenbergia schreberi	5.0	90.0	2.5	92.5	82.5	12.5	97.5	10.0	90.0	77.5	10.0	85.0	7.5	70.0	52.5
Oenothera biennis	5.0	5.0	27.5	25.0	10.0	2.5	*	*	20.0	2.5	*	*	*	12.5	12.5
Oenothera laciniata	*	*	*	2.5	5.0	*	*	*	*	*	*	2.5	2.5	27.5	22.5
Oxalis corniculata	*	*	15.0	*	*	25.0	10.0	37.5	5.0	17.5	10.0	12.5	35.0	12.5	17.5
Panicum anceps	*	*	*	*	*	2.5	*	2.5	*	10.0	*	*	*	*	*
Panicum dichotomiflorum	*	*	*	*	*	2.5	*	*	*	*	*	*	*	*	*
Paspalum setaceum	2.5	2.5	52.5	2.5	15.0	27.5	*	15.0	5.0	17.5	10.0	*	5.0	20.0	2.5
Physalis longifolia	*	5.0	*	*	*	*	*	*	*	*	*	2.5	*	*	*
Phytolacca americana	*	2.5	*	*	*	*	2.5	*	*	*	*	*	*	*	*
Plantago virginica	*	*	*	*	*	*	2.5	*	*	*	5.0	*	2.5	*	2.5
Polygonum ramosissimum	*	*	*	*	*	*	2.5	*	*	*	*	*	*	*	*
Rumex crispus	*	*	32.5	47.5	10.0	*	5.0	35.0	75.0	37.5	5.0	7.5	40.0	80.0	30.0
Setaria glauca	50.0	2.5	17.5	25.0	30.0	*	*	10.0	2.5	*	10.0	*	2.5	*	5.0
Sida spinosa	*	*	7.5	27.5	2.5	*	*	*	*	*	*	*	*	*	2.5
Solanum carolinense	*	10.0	*	*	2.5	*	5.0	*	*	2.5	*	*	*	*	*
Solanum nigrum	2.5	7.5	*	5.0	5.0	*	7.5	*	5.0	7.5	*	2.5	*	*	*
Solanum rostratum	57.5	2.5	*	2.5	22.5	*	5.0	2.5	*	2.5	*	*	*	*	*
Sporobolus asper	*	*	*	*	*	*	*	5.0	*	5.0	*	*	*	*	*
Stellaria media	*	*	*	*	*	15.0	50.0	20.0	2.5	10.0	15.0	87.5	12.5	25.0	32.5
Strophostyles leiosperma	*	*	5.0	*	*	*	*	*	*	*	*	*	*	*	*
Taraxacum officinale	*	*	*	*	*	2.5	*	*	*	*	*	*	*	*	*
Tridens flavus	2.5	*	*	*	7.5	2.5	*	*	*	*	*	*	*	*	*
Trifolium campestre	5.0	*	7.5	20.0	2.5	*	*	*	*	*	*	*	*	*	*
Trifolium repens	*	*	7.5	*	*	*	*	*	*	*	*	*	*	*	*
Verbena bracteata	*	*	2.5	*	*	2.5	*	*	*	*	*	*	*	*	*
Vicia villosa	*	2.5	*	*	*	*	*	*	*	*	*	*	*	*	*

* : Species absent

Table 6. Number of plant species encountered in all replicates of a given treatment.

Treatment	Harvest 1	Harvest 2	Harvest 3
Roadside	17	21	15
Forest	22	17	14
Prairie	27	20	15
Old-field	25	18	15
Mixed	30	28	15

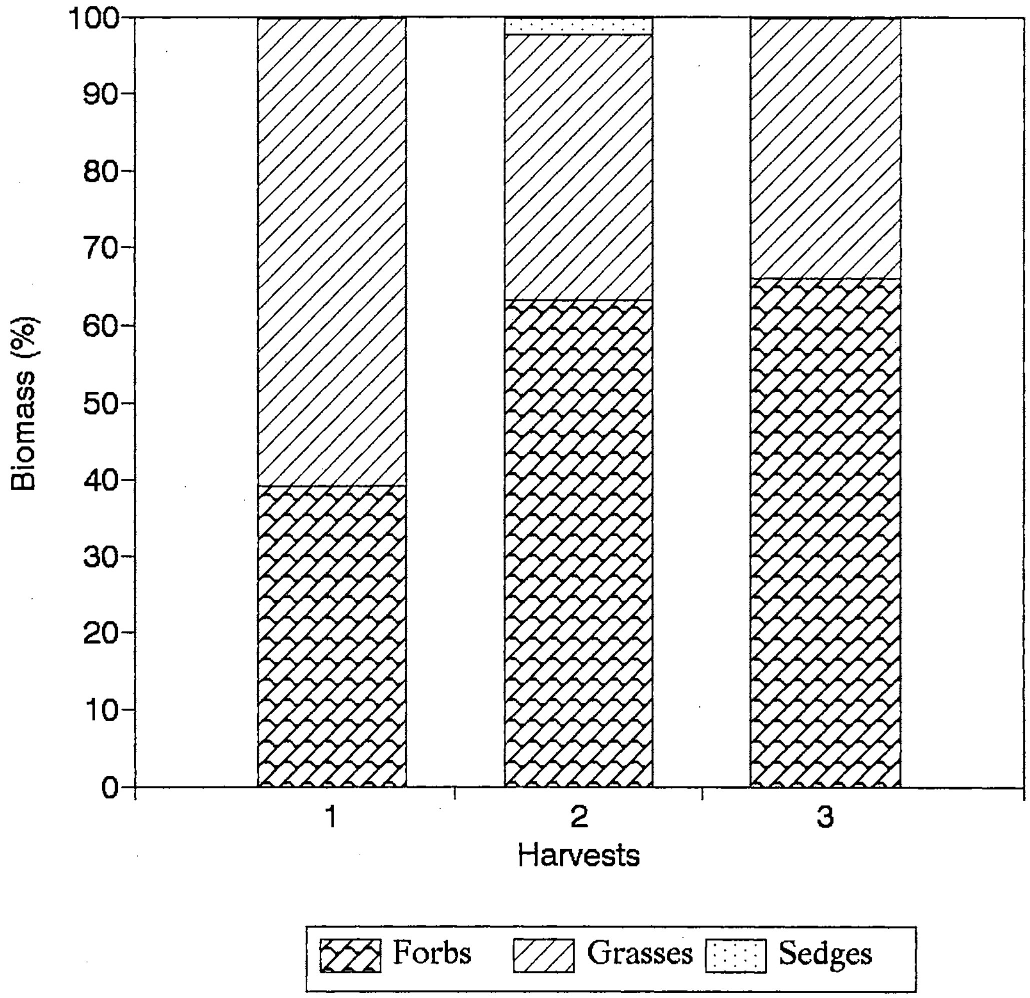

Fig. 1. Biomass proportion (%) of forbs, grasses and sedges in the plant micro-communities emerging from the Roadside soil seed banks.

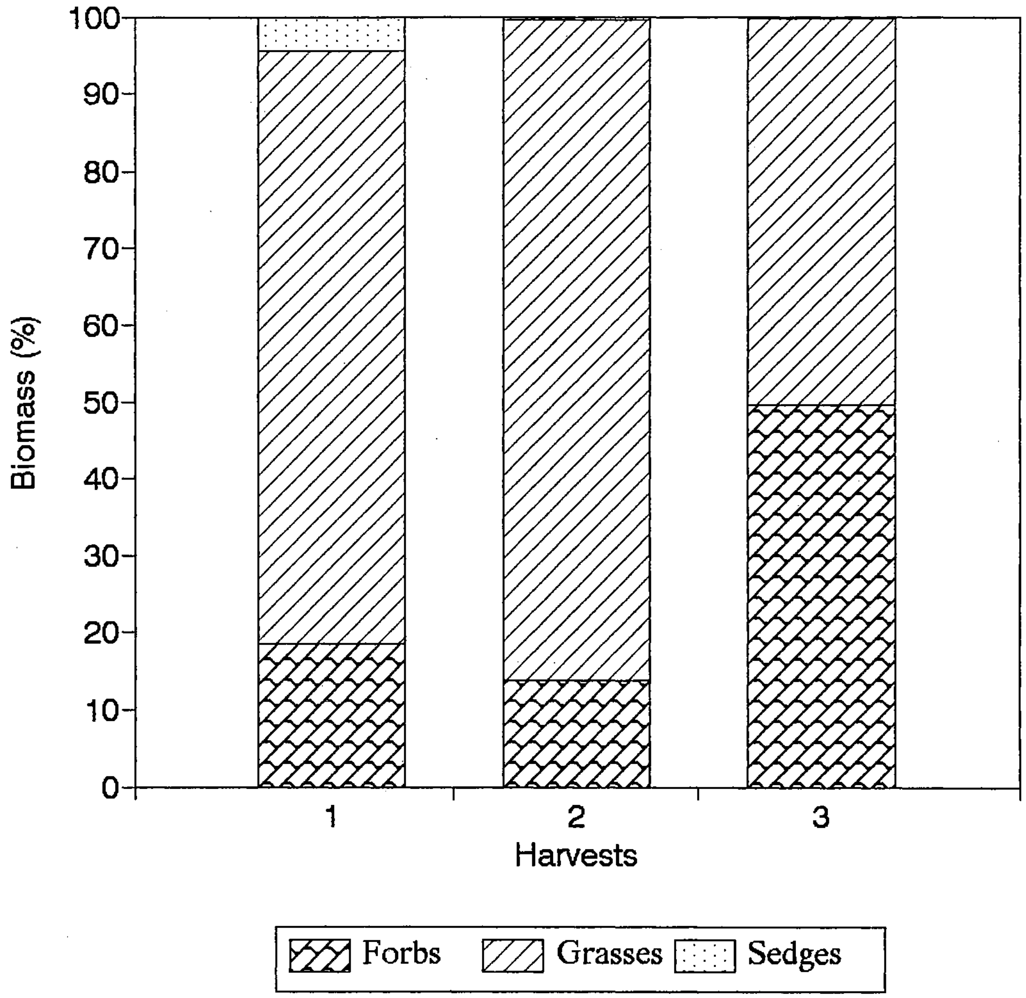

Fig. 2. Biomass proportion (%) of forbs, grasses, and sedges in the plant micro-communities emerging from the Forest site soil seed banks.

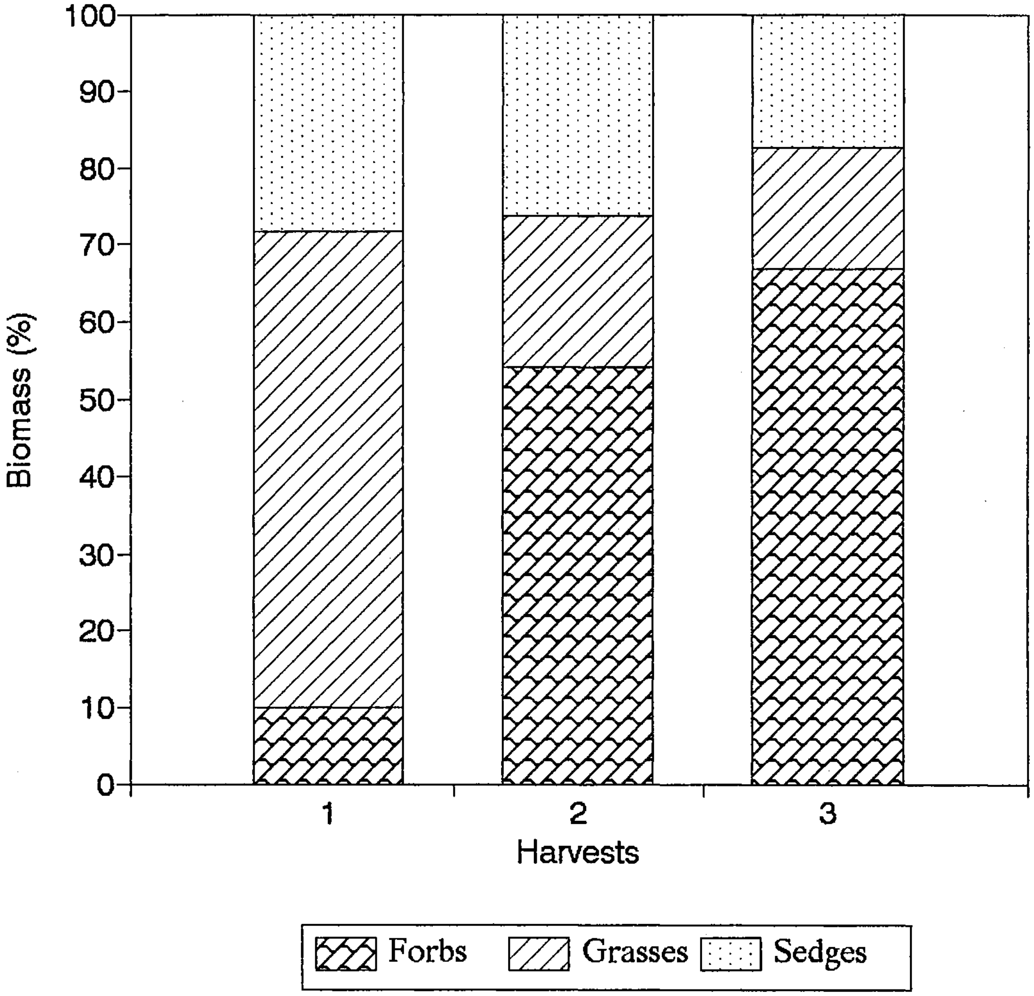

Fig. 3. Biomass proportion (%) of forbs, grasses and sedges in the plant micro-communities emerging from the Prairie soil seed banks.

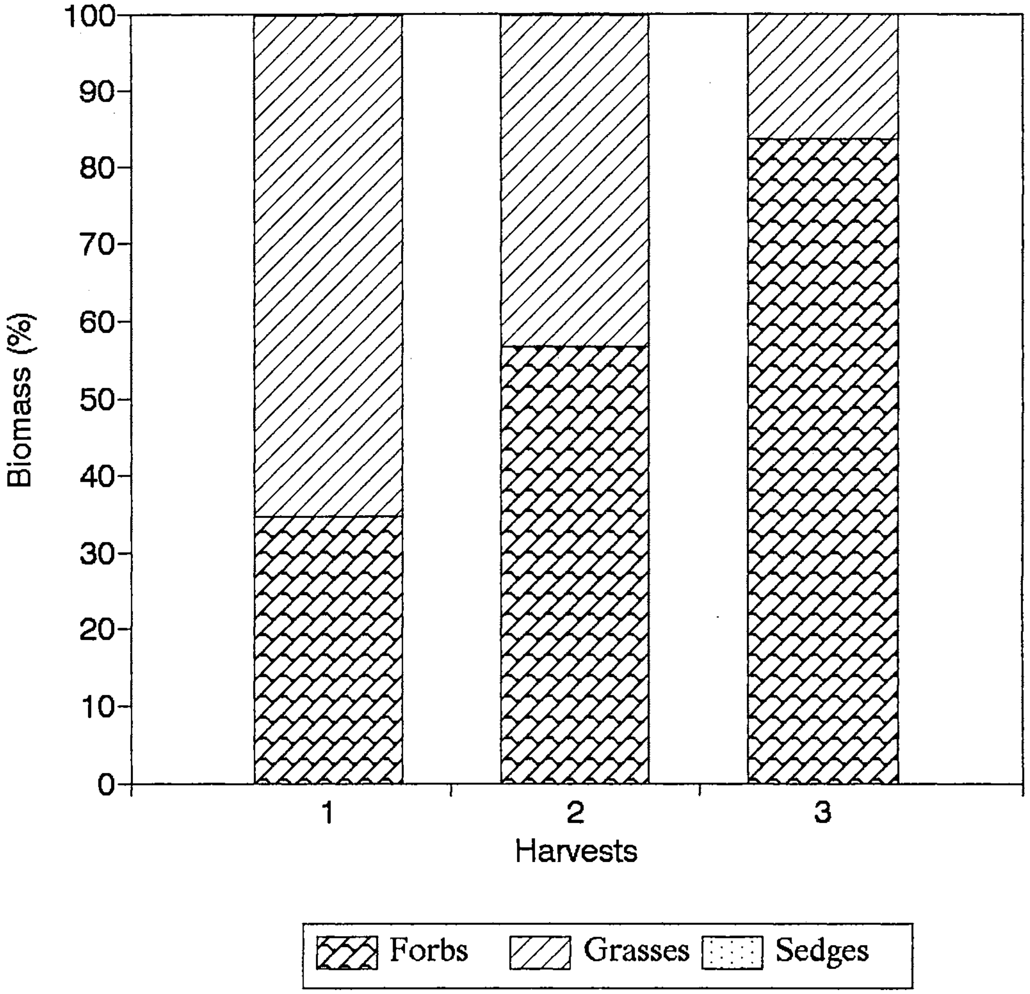

Fig. 4. Biomass proportion (%) of forbs, grasses and sedges in the plant micro-communities emerging from the Old field soil seed banks.

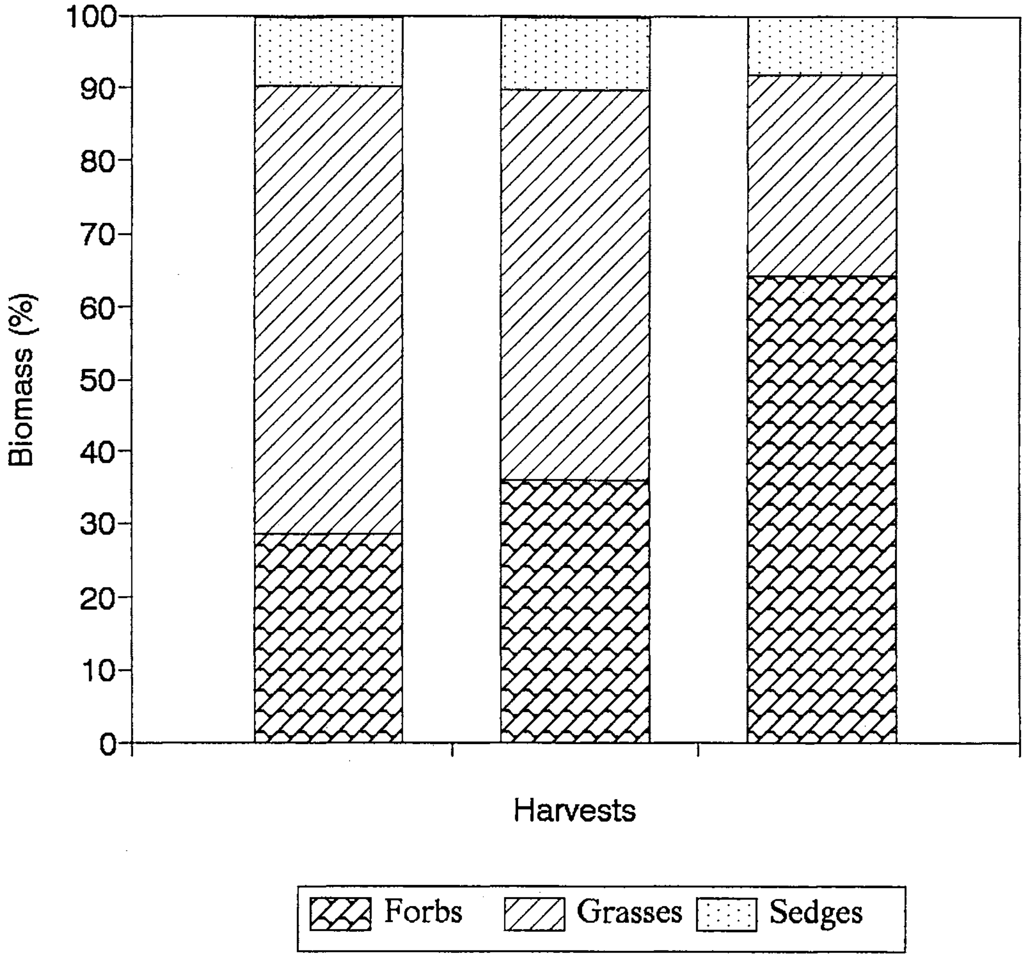

Fig. 5. Biomass proportion (%) of forbs, grasses, and sedges in the plant micro-communities emerging from the Mixed soil seed banks.

had almost the same potential species richness.

Canonical Correspondence Analysis (CCA)

The first most important gradient in the canonical correspondence analysis (CCA) is along axis 1, which reveals the among sites differences in the species composition (Fig. 6). The forest site plant micro-communities are abundant in *Digitaria sanguinalis, Mollugo verticilata, Solanum nigrum,* and *Muhlenbergia schreberi.* They occupy the top left corner along axis 1, and seem different from all other sites in their species composition. Species composition of plant micro-communities emerging from the old field soil seed banks shows close resemblance with the species composition of plant micro-communities from the mixed soil seed banks. They indicate high abundance of *spectabilis, Oenothera biennis,* and *Stellaria media.* The roadside plant micro-communities, are very different from the forest site plant micro-communities in their species composition. They are abundant in some annual weeds like *Solanum rostratum, Setaria glauca, Eleusine indica* and *Eragrostis hirsuta.* The prairie site plant micro-communities are abundant in *Oxalis corniculata* and *Cyperus ovularis.* Their species composition shows close resemblance to that for the roadside plant micro-communities. Plant micro-communities from the mixed soil seed banks are located almost in the middle. Their species composition is intermediate between that for plant micro-communities from all four seed banks.

The second most important gradient is along axis 2, that depicts the among harvests differences in species composition. It also reflects the gradient between roadside and old-field or prairie. During harvest 1, species composition shows close resemblance to the species composition of plant micro-communities from the roadside seed banks, but through time it becomes more similar to the species composition for old field plant micro-communities. Furthermore, during harvest 1, some grasses (i. e., *Eleusine indica,*

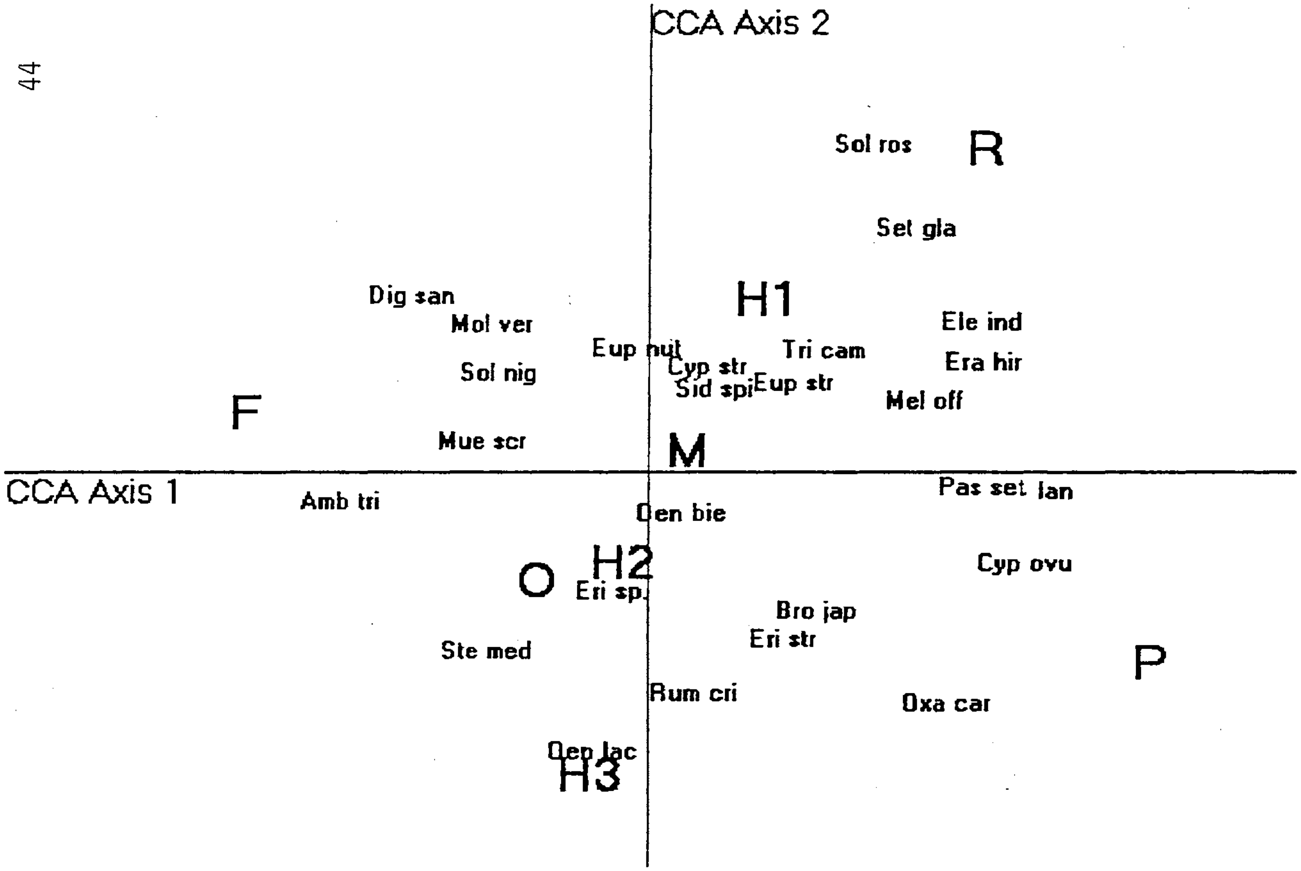

Fig. 6. Canonical Correspondence Analysis of plant micro-communities emerging from soil seed banks. Large letters indicate centroids of sample scores. Species codes are the first three letters of the generic and species' name, see Appendix 1, for complete list of the species encountered. F = Forest site, M = Mixed soil samples, O = Old-field site, P = prairie site, R = Roadside site, H1 = Harvest 1, H2 = Harvest 2, H3 = Harvest 3.

Eragrostis hirsuta, Digitaria sanguinalis, and *Muhlenbergia schreberi*) occur more abundantly than forbs, but during harvest 3, forbs (i. e., *Stellaria media, Rumex crispus, Oxalis corniculata* and *Oenothera laciniata*) show high abundance.

Species richness and biomass relationship (SRBR)

Among-site differences

In harvest 1, the species richness and biomass relationships (SRBR) of plant micro-communities emerging from soil seed banks for all four sites had highly significant ($p < 0.001$) linear as well as quadratic coefficients and exhibited unimodal curves (Table 7, Fig. 7). For plant micro-communities from the mixed soil samples, only the linear component for SRBR was highly significant.

The prairie site plant micro-communities had both linear as well as quadratic components for SRBR highly significant during harvest 2 (Table 7, Fig. 8). The linear coefficient for SRBR in the old field treatment was also highly significant. In all other treatments during this harvest neither linear nor quadratic relationship was significant.

During harvest 3, plant micro-communities from the old field and mixed soil seed banks had only the linear component for the SRBR highly significant. Plant micro-communities emerging from the roadside, forest, and prairie site seed banks had the linear as well as quadratic component for SRBR highly significant (Table 7, Fig. 9). The multiple r^2 values indicate that during harvest 3, biomass could explain up to 36.3 % variation in species richness as compared to the 47.5 % variation in species richness explained by biomass during harvest 1.

Table 7. Regression model for the relationship between species richness and biomass of plant micro-communities emerging from soil seed banks.

Harvest	Site	Model fitted	p value	r^2
1	Roadside	$0.585 + 2.218\ B^{****} - 0.509B^{2****}$	0.000	0.454
1	Forest	$0.343 + 0.934B^{***} - 0.071B^{2****}$	0.001	0.330
1	Prairie	$0.085 + 2.714B^{****} - 0.275B^{2***}$	0.000	0.418
1	Old field	$0.445 + 1.722B^{****} - 0.169B^{2****}$	0.000	0.475
1	Mixed	$1.391 + 0.920B^{**} - 0.051B^{2NS}$	0.014	0.207
2	Roadside	$1.723 + 1.655B^{NS} - 0.476B^{2NS}$	0.023	0.184
2	Forest	$2.466 + 0.206B^{NS} - 0.037B^{2NS}$	0.472	0.040
2	Prairie	$1.807 + 1.876B^{****} - 0.326B^{2***}$	0.000	0.377
2	Old field	$1.781 + 0.840B^{*} - 0.097B^{2NS}$	0.079	0.128
2	Mixed	$2.377 + 0.387B^{NS} + 0.018B^{2NS}$	0.004	0.261
3	Roadside	$0.870 + 3.134B^{****} - 0.867B^{2**}$	0.000	0.363
3	Forest	$1.375 + 1.532B^{**} - 0.432B^{2*}$	0.023	0.184
3	Prairie	$1.459 + 1.669B^{**} - 0.623B^{2**}$	0.056	0.145
3	Old field	$0.807 + 2.413B^{*} - 0.550B^{2NS}$	0.014	0.206
3	Mixed	$1.043 + 2.089B^{***} - 0.396B^{2NS}$	0.000	0.354

$*: p < 0.10$, $**: p < 0.05$, $***: p < 0.01$, $****: p < 0.005$

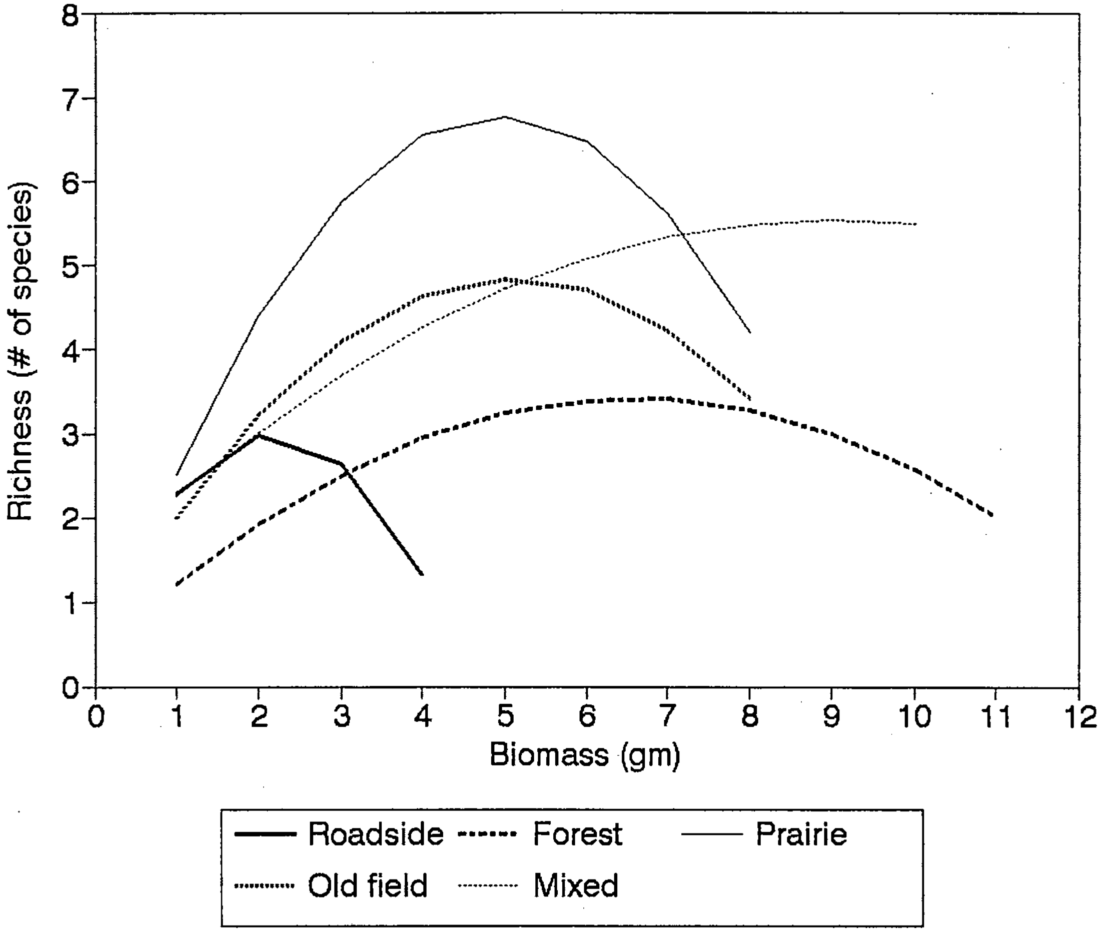

Fig. 7. The relationship between species richness and biomass of experimental plant micro-communities emerging from soil seed banks during Harvest 1. These are not original data, but regression equations (see table 7).

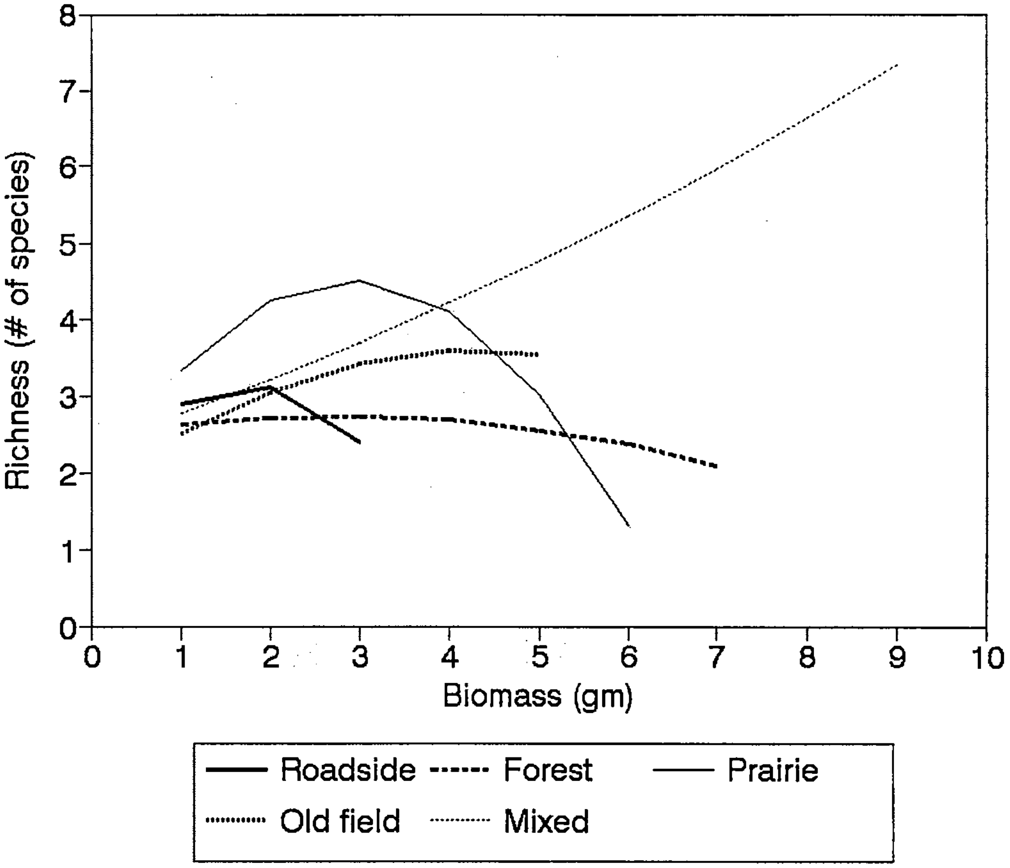

Fig. 8. The relationship between species richness and biomass of plant microcommunities emerging from soil seed banks during Harvest 2. Not original data, but obtained by regression equation (see Table 7). Biomass scale different from Fig. 7.

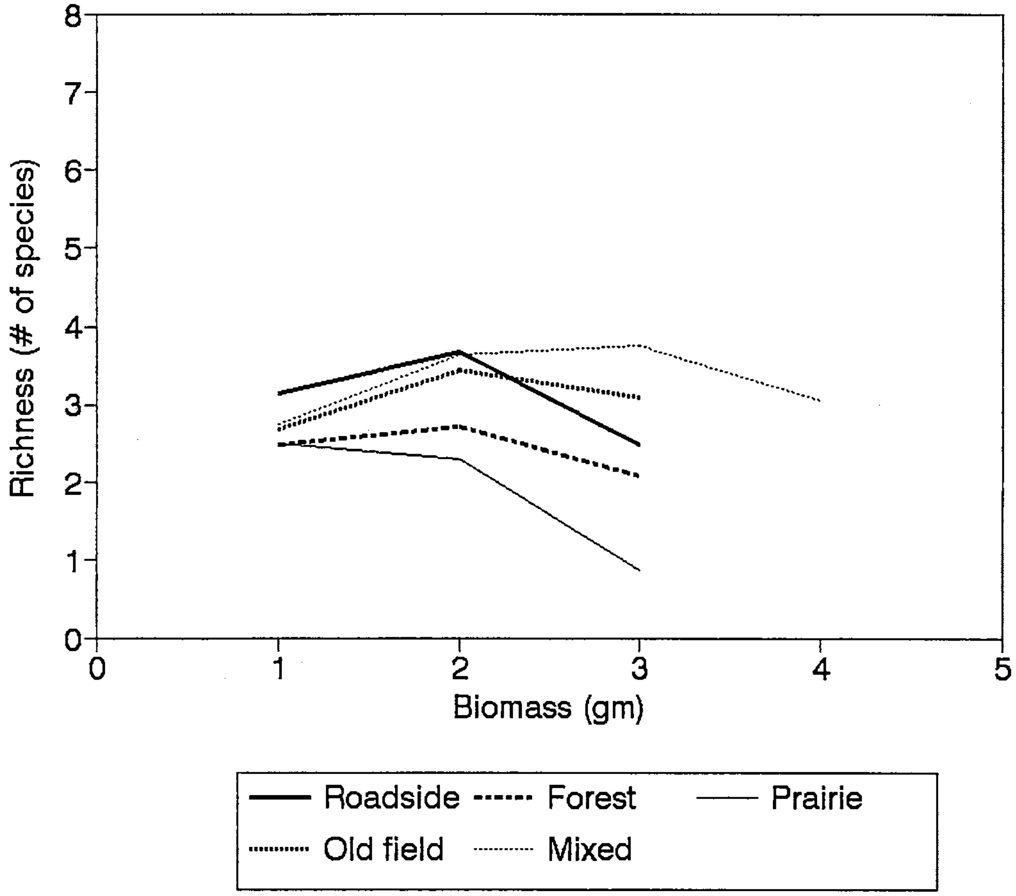

Fig. 9. The relationship between species richness and biomass of plant micro-communities emerging from soil seed banks during Harvest 3. Not original data, obtained by regression equations (see Table 7). Biomass scale different from Fig. 7 & 8.

Among-harvest differences

Plant micro-communities emerging from soil seed banks revealed clear differences among harvests for the SRBR (Table 5, Fig. 10-12). The roadside and forest treatments showed similar trends for the SRBR. Both treatments have significant linear as well as quadratic components for the SRBR, and exhibit unimodal curves during the first and third harvests.

The prairie treatment had both linear and quadratic coefficients for the SRBR highly significant during the all three harvests. The SRBR of plant micro-communities emerging from the old field soil samples also had the linear as well as quadratic coefficients highly significant, and exhibited unimodal curves during harvest 1, but in the harvests 2 and 3, only the linear component for the SRBR was observed significant in this treatment. The SRBR of plant micro-communities emerging from the mixed soil samples also had only the linear component highly significant during harvests 1 and 3.

DISCUSSION

The above-ground biomass, species richness, species composition and the SRBR of experimental plant micro-communities emerging from soil seed banks exhibited significant among-site and among-harvest differences. As the experiment was conducted under controlled environmental conditions in a greenhouse, a random variation in the soil seed banks, differences in soil fertility, variation in the life histories of emerging species and change in growing season, may be considered the main factors causing among-site variation.

Seed banks from the roadside site with the least soil fertility resulted in low biomass levels, as well as low species richness. In contrast, seed banks from the old field and forest sites with high soil fertility yielded in high biomass levels but low species richness. The prairie soil seed banks with intermediate fertility resulted in intermediate biomass levels, and had the highest species richness during the first two harvests. As such plant microcommunities emerging from prairie site seed banks confirm both Tilman's (1982) resource model that predicts high species richness at intermediate resource levels as well as Grime's (1973, 1979) model that relates high species richness to intermediate biomass levels. Similar results have been achieved during ecological surveys of some natural plant communities (Klinkhamer & Jong 1985; Kutiel & Danin 1987; Day et al. 1988).

The low biomass levels and low species richness from the infertile roadside soil are in agreement with Grime's (1973, 1979) stress strategy. Similarly high biomass levels but low species richness corresponding to the forest and old field site seed banks which had high soil fertility also seem in agreement with Grime's (1973, 1979) competitive exclusion process. The intentional experimental fertilization of impoverished sites (Tilman 1993) has also confirmed that high fertility levels through competitive exclusion process lead to low species richness.

Day et al. (1988) in a *Typha latifolia* dominated riverine marsh vegetation, and Bobbink & Willems (1993) in a *Brachypodium pinnatum* dominated chalk grassland observed that the dominance of a single species caused dramatic decrease in the species richness. In this study also low species richness of plant microcommunities emerging from the forest and old field seed banks may be attributed to the negative effects of abundantly occurring *Muhlenbergia schreberi.*

Plant microcommunities from the mixed soil seed banks perhaps due to the dominating effects of *Muhlenbergia schreberi,* did not yield in significantly higher species richness than other treatments, so they contradicted my prediction. The species richness of all pots emerging from mixed soil samples was higher than any other treatment, but there is no appropriate statistical method to test its significance.

By removing biomass accumulations disturbances can cause substantial reduction in the soil fertility of the disturbed plant communities (Bakker 1987; Bobbink & Willems 1993). This reduction in soil fertility subsequently not only affects the growth rates and seed germination of different plant species, but also influences the biomass as well as species richness of future plant communities It seems in this study as well, two intense disturbances had reduced the soil fertility that might have gradually hampered the growth rates in the subsequent harvests. The significant interaction between sites and harvests for the biomass and species richness in this study may therefore be attributed to the gradual reduction in soil fertility caused by two disturbances. Wilson & Tilman (1991) examined the interactive effects of fertilization and disturbance on the community structure in an old-field community in Minnesota, and reached the same conclusion. The heterogeneity in the soil seed banks and their differential germination response following two disturbances may be considered another factor responsible for these significant interaction effects between sites and harvests.

Differences in the life cycle and regenerative abilities of plant species can cause drastic changes in the species composition of plant communities (Fagerstom & Agren 1979; Shmida & Elner 1984; Belsky 1986; Belsky 1992; van der Maarel & Sykes 1993). During the first two harvests in this study, grasses had higher biomass than forbs, but afterwards forb surpassed grasses. Perhaps following second disturbance, the low regenerative capability of abundantly occurring grasses (*Dichanthelium acuminatum, Muhlenbergia schreberi,* and *Setaria glauca*) and a sedge (*Cyperus ovularis*), but rapid growth and germination of some opportunistic forbs (*Rumex crispus, Stellaria media, Oenothera laciniata* and *Oxalis corniculata*) resulted in high forb biomass. Therefore, among-harvests significant differences in the species composition of plant micro-communities might result from variation in the life histories of plant species influenced by two intense disturbances. Similar temporal changes have been reported by Wheeler & Giller (1982), Ter Heerdt et al. (1991) and Bobbink & Willems (1993) for some natural plant communities.

Canonical correspondence analysis orders the plant micro-communities in to two main groups along the first most important axis. Species composition of plant micro-communities emerging from the forest, old-field, and mixed soil seed banks that had high soil fertility show close resemblance with one another and comprise the first category. The second category seems to be composed of the roadside and prairie site plant micro-communities. Soil samples from these both sites had low fertility. The species composition of plant micro-communities belonging to these sites also shows close resemblance with each other and seems much different from the other plant micro-communities emerging from soil seed banks. Therefore the differences in the species composition of experimental plant micro-communities may be attributed to the random differences in seed source and soil fertility.

As predicted the SRBR of plant micro-communities for all four sites during the first harvest, and partially during the second and third harvests exhibited unimodal curves as in Grime's (1973,1979) model. However the r^2 values indicate that biomass determined at most 47.5 % of the variability in species richness. The remaining unexplained variability in the model might have occurred due to some other factors like within site chance variation in the seed pool and differences in the life cycles of emerging plant species. Similar results have been reported by Gough et al. 1994. They also observed a very weak correlation ($R^2 = 0.02$) between the species richness and community biomass of 36 marsh communities. They related up to 89 % variability in the species richness to the environmental conditions.

In conclusion, differences in the soil fertility and species composition of seed banks influencing the competitive exclusion process seem responsible for these among-site differences in the SRBR of experimental plant microcommunities. Similarly, among-harvest differences in the structure of plant micro-communities may be attributed to the intense and frequent disturbances and the variability in the life cycles of different species. Plant microcommunities emerging from soil seed banks were very easily manipulated.

They mimicked some natural plant communities in response to disturbances. They can prove a very effective tool for examining the existing models, and may eventually lead to an improved understanding of coexistence in species-rich ecosystems.

References

Al-Mufti, M. M., Syeds, C. L., Furness, C. L., Grime, J. P., & Band, S. R. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *J. Ecol.* 65: 759-791.

Anderson, A. N. 1992. Regulation of "momentary" diversity by dominant species in exceptionally rich ant communities in the Australian seasonal tropics. *Am. Nat.* 140: 401-420.

Bacilieri, R., Bouchet, M. A., Bran, D., Grandjanny, M., Maistre, M., Parret, P. & Romane, F. 1993. Germination and regeneration mechanisms in Mediterranean degenerate forests. *J. Veg. Sci.* 4: 241-246.

Bakker, J. P. 1987. Grazing as a management tool in the restoration of species rich grasslands. *Proceedings of the Koniklijke van Watenschappen Series C.* 90: 404-429.

Belcher, J. W., Keddy, P. A. & Catling , P. M. 1992. Alvar vegetation in Canada: a multivariate description of two scales. *Can. J. Bot.* 70: 1279-1291.

Belsky, A. J. 1986. Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania. I. Colonization of grazed and ungrazed plots. *J. Ecol.* 74: 419-438.

Belsky, J. 1992. Effect of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *J. Veg. Sci.* 3: 187-200.

Bobbink, R. & Willems, J. H. 1993. Restoration management of abandoned chalk grasslands in the Netherlands. *Biodiv. and Conserv.* 2: 616-626.

Christie, E. K. & Detling, J. K. 1982. Analysis of interference between C_3 and C_4 grasses in relation to temperature and soil nitrogen Supply. *Ecology* 63: 1277-1284.

Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. *Ecology* 68: 1243-1250.

Day, R. T., Keddy, P. A. & McNeill, J. 1988. Fertility and disturbance gradients: a summary model for riverine marsh vegetation. *Ecology* 69: 1044-1054.

del Moral, R. & Wood, D. M. 1993. Early primary succession on a barren volcanic plain at Mount St. Helens, Washington. Am. *J. Bot.* 80: 981-991.

Dudley, L. J. & Lajtha, K. 1993. The effects of prescribed burning on nutrient availability and primary production in Sandplain grasslands. *Am. Midl. Nat.* 130: 286-298.

Ellison, A. M. & Farnsworth, E. J. 1993. Seedling survivorship growth, and response to disturbance in Belizean mangal. *Am. J. Bot.* 80: 1137-1145.

Epigares, T. & Peco, B. 1993. Mediterranean pasture dynamics: the role of germination. *J. Veg. Sci.* 4: 189-194.

Fagerström, T. & Ågren, G. I. 1979. Theory for coexistence of species differing in regeneration properties. *Oikos* 33: 1-10.

Fenner, M. 1985. *Seed Biology*. Chapman and Hall, London.

Glenn, S. M. & Collins, S. L. 1992. Effects of scale and disturbance on rates of immigration and extinction of species in prairies. *Oikos* 63: 273-280.

Glenn, S. M. & Collins, S. L. 1993. Experimental analysis of patch dynamics in tall-grass prairie plant communities. *J. Veg Sci.* 4: 157-162.

Gough, L., Grace, J. B. & Taylor, K. L. 1994. The relationship between species richness and community biomass: the importance of environmental variables. *Oikos* 70: 271-279

Granström, A. 1988. Seed banks at six open and afforested heathland sites in southern

Sweden. *J. Appl. Ecol.* 25: 297-306.

Great Plains Flora Association. 1986. *Flora of the Great Plains.* University Press of Kansas. Lawrence, Kansas.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344-347.

Grime, J. P. 1979. *Plant strategies and vegetation processes.* Chichester. Wiley & Sons, New York.

Herben, T., Krahulec, F., Hadincova, V. & Skalova, H. 1993. Small scale spatial dynamics of plant species in a grassland community over six years. J. Veg. Sci. 4: 163-170.

Hill, M. O. & Stevens, P. A. 1981. The density of viable seeds in soils of forest plantations in upland Britain. *J. Ecol.* 69: 693-709.

Ingersoll, C. A. & Wilson, M. V. 1992. Buried propagule bank of a high subalpine site: microsite variation and comparisons with aboveground vegetation. *Can. J. Bot.* 71: 712-717.

Keddy, P. A. & Shipley, B. 1989. Competitive hierarchies in herbaceous plant communities. *Oikos* 54: 234-241.

Klinkhamer, P. G. L. & de Jong, T. J. 1985. Shoot biomass and species richness in relation to some environmental factors in a coastal dune area in the Netherlands. *Vegetatio* 63: 129-32.

Kutiel, P & Danin, A. 1987. Annual species diversity and above ground phytomass in relation to some soil properties in the sand dunes of the northern Sharon plains, Israel. *Vegetatio* 70: 45-49.

Lavassor, C., Ortega, M., & Peck, B. 1990. Seed bank dynamics of Mediterranean pastures subject to mechanical disturbance. *J. Veg. Sci.* 1: 339-344.

Major, J. & Pyott, W. T. 1966. Burial of viable seeds in two California bunchgrass sites and their bearing on the definition of flora. *Vegetatio* 13: 253-282.

Montalvo, J., Casado, M. A., Lavassor, C. & Pineda, F. D. 1993. Species diversity patterns in Mediterranean grasslands. *J. Veg. Sci.* 4: 213-222.

Newman, E. I., 1963. Factors controlling the germination rate of winter annuals. *J. Ecol.* 51: 625-639.

Nilsson, C. & Wilson, S. D. 1991. Convergence in plant community structure along disparate gradients: are lakeshores inverted mountainsides? *Am. Nat.* 137: 774-790.

Olff, H. & Bakker, J. P. 1991. Long term dynamics of standing crop and species composition after the cessation of fertilizer application to mown grassland. *J. Appl. Ecol.* 28: 1040-52.

Oomes, M. J. M., 1992. Yield and species density of grassland during restoration management. *J. Veg. Sci.* 3: 271-274.

Puerto, A., Rico, M., Matías, M. D., & García, J. A. 1990. Variation in structure and diversity in Mediterranean grassland related to trophic status and grazing intensity. *J. Veg. Sci.* 1: 445-53.

Putz, F. E. & Appanah, S. 1987. Buried seeds, newly dispersed seeds, and the dynamics of a lowland forest in Malaysia. *Biotropica* 19: 326-33.

Rampton, H. H. & Ching, T. H. 1970. Persistence of crop seed in soils. *Agron. J.* 62: 272-277.

Schiffman, P. M. & Johnson, W. C. 1992. Sparse buried seed bank in a southern Appalachian oak forest: implications for succession. *Am. Midl. Nat.* 127: 258-267.

Schmida, A. & Ellner, S. 1984. Coexistence of plant species with similar niches. *Vegetatio* 58: 29-55.

Schneider, R. L., & Sharitz, R. R. 1986. Seed bank dynamics in a southern riverine Swamp. *Am. J. Bot.* 73: 1022-1030.

Sousa, W. P. 1984. The role of disturbances in natural communities. *Annu. Rev. Ecol. Syst.* 5: 353-391.

Steel, R. G. D. & Torrie, J. H. 1980. *Principles and procedures of statistics.* McGraw-Hill Publishing Company, Oklahoma city.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.

Ter Heerdt, G. N. J., Bakker, J. P. & De Leeuw, J. 1991. Seasonal and spatial variation in living and dead plant material in a grazed grassland as resulted to plant species diversity. *J. Appl. Ecol.* 28: 120-127.

Thompson, K. 1987. Seed and seed banks. *New Phytol.* 106: 23-34.

Thompson, K. & Grime, J. P. 1979. seasonal variation in the seed-banks of herbaceous species in ten contrasting habitats. *J. Ecol.* 67: 893-991.

Tilman, D. 1982. *Resource competition and community structure*, Princeton University Press, Princeton.

Tilman, D. 1993. Species richness of experimental productivity gradients: How important is colonization limitation? *Ecology* 74: 2179-2191.

van der Maarel, E. & Sykes, M. T. 1993. Small scale species turnover in a limestone grassland: the carousal model and some comments on the niche concept. *J. Veg. Sci.* 4: 179-188.

Vermeer, J. G. & Berendse, F. 1983. The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities. *Vegetatio* 53: 121-126.

Vinton, M. A.; Hartnett, D. C.; Fick, E. J. & Brigs, J. M. 1993. Interactive effect of fire, bison (*Bison bison*) grazing and plant community composition in Tallgrass prairie. *Am. Midl. Nat.* 129: 10-18.

Walkinson, L. 1990. *SYSTAT. The system of statistics.* Evanston, IL. SYSTAT. Inc.

Watkinson, A. R. 1975. the population biology of a due annual, *Vulpia membranacea.* Ph. D. thesis. University of Wales. In: Moore, P. D. & Chapman, S. B. 1986. (Ed.) *Methods in plant ecology,* The Academic Press, Osney Mead, Oxford.

Warr, S. J., Thompson, K. & Kent, M. 1993. Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. *Prog. Phys. Geog.* 17: 329-347.

Wheeler, B. D. & Giller, K. E. 1982. Species richness of herbaceous fen vegetation in Broadland, Norfolk in relation to the quantity of above ground plant material. *J. Ecol.* 70: 179-200.

Wheeler, B. D. 1988. Species richness, species rarity and conservation evaluation of rich fen vegetation in lowland England and Wales. *J. Appl. Ecol.* 25: 331-353.

Wheeler, B. D. & Shaw, S. C. 1991. Above-ground crop mass and species richness of the principal types of herbaceous rich-fen vegetation of lowland England and Wales. *J. Ecol.* 79: 285-301.

Willems, J. H. 1983. species composition and above ground phytomass in chalk grassland with different management. *Vegetatio* 52: 171-80.

Willems, J. H., Peet, R. K. & Bike, L. 1993. Changes in chalk grassland structure and species richness resulting from selective nutrient additions. *J. Veg. Sci.* 4: 203-212.

Wilson, S. D. & Keddy, P. A. 1988. Species richness and biomass accumulation along an experimental gradient. *Oikos* 53: 375-80.

Wilson, S. D. & Tilman, D. 1991. Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community. *Oecologia* 88: 61-71.

Wisheu, I. C. & Keddy, P. A. 1989. Species richness-standing crop relationships along four gradients: constraint on the general model. *Can. J. Bot.* 67: 1609-1617.

Young, K. R. Ewel, J. J. & Brown, B. J. 1987. Seed dynamics using forest succession in Costa Rica. *Vegetatio* 71: 157-173.

CHAPTER III

RESPONSE OF PLANT MICRO-COMMUNITIES EMERGING FROM SOIL SEED BANKS TO FERTILIZATION AND DISTURBANCE

ABSTRACT: Fertilization and disturbance play a major role in structuring natural plant communities. In a greenhouse study, I examined the influence of disturbance and fertilization on the relationship between species richness and biomass and other attributes of experimental plant micro-communities emerging from soil seed banks. The above-ground mean biomass was significantly influenced by both fertilization and disturbance as well as by their interactive effects, whereas species richness was significantly influenced by fertilization only. The Fertilized & Not Disturbed plant micro-communities showed maximum mean biomass but low species richness. In contrast, the Not Fertilized & Disturbed plant micro-communities had the highest mean species richness but lowest mean biomass. Canonical Correspondence Analysis revealed that species composition was strongly related to both fertility and disturbance. Plant species belonging to fertilized plant micro-communities showed higher average biomass than those experiencing disturbance. The relationship between species richness and biomass of Not fertilized & Disturbed plant micro-communities displayed unimodal curves. The F&D (Fertilized & Disturbed) as well as, F&ND plant micro-communities also had concave-down but not unimodal curves; this perhaps due to low biomass levels.

Plant micro-communities emerging from soil seed banks simulated some natural plant communities in displaying unimodal curves for the relationship between species richness and biomass. A significant decrease in the species richness corresponding to high biomass levels in Fertilized & Not Disturbed plant micro-communities, and the highest species richness relating to low biomass levels in Not Fertilized & Disturbed plant communities is also consistent with field data on species richness and biomass.

Keywords: Seed banks, species richness, unimodal curve, species richness and biomass relationship.

Nomenclature: Great Plains Flora Association, 1986.

Abbreviations: SRBR = Species richness and biomass relationship, F&D = Fertilized & Disturbed, F&ND = Fertilized & Not Disturbed, NF&D = Not Fertilized & Disturbed, NF&ND = Not Fertilized & Not Disturbed.

INTRODUCTION

The species richness of plant communities is significantly influenced by soil fertility and disturbances (White 1979; Armesto & Pickett 1985; Belsky 1986; Bakker 1987; Carson & Barrett 1988; Day et al. 1988). If not disturbed, accumulations of dead above-ground biomass occupy considerable space and hinder light penetration, and therefore have negative effects on the growth and germination of opportunistic species (Bobbink & Willems 1993). Under these adverse environmental conditions, poor seed germination (Tilman 1993) and competitive exclusion of some shade intolerant species by shrubs and trees (Adams et al. 1982; Gehring & Bragg 1992) results in low species richness (Wheeler & Giller 1982; Willems 1983; Bobbink & Willems 1987; Collins & Glenn 1988; Wilson 1993). Following a disturbance, the reduction in the negative effects of competitively superior canopy species and improved germination and establishment of competitively inferior species (del Moral & Wood 1993; Ellison & Farnsworth 1993) result in high species richness.

The intensity and frequency of disturbance influence the relationship between species richness and biomass of plant communities. Some experiments (Bakker 1987; Collins 1990; Bobbink & Willems 1993) indicate that low disturbance levels prove ineffective in reducing the vigorous growth of dominant species. After frequent and intense disturbances as well, many species fail to regenerate (Collins & Glenn 1988). Therefore, both high and low levels of disturbance prevent the achievement of high species richness. Intermediate levels of disturbance, however, prove very effective in maintaining the suitable biomass levels that relate to high species richness (Grime 1973, 1979;

Al-Mufti et al. 1977; Connell 1978; Armesto & Pickett 1985).

Soil fertility also influences the species composition of plant communities (Reed 1977; Tilman 1982; Vermeer & Berendse 1983; Wisheu & Keddy 1989; Puerto et al. 1990; Nilsson & Wilson 1991). Impoverished soils are usually invaded by early successional species (Olff & Bakker 1991). The invading species due to low nutrient supply do not grow vigorously and therefore do not competitively exclude each other. Nutritionally poor sites have often been observed to be very rich in species (Tilman 1986; Bakker 1987; Carson & Barrett 1988; Day et al 1988; Willems et al. 1993). Alternatively, in habitats with high soil fertility, only a few dominant species control the resources (Tilman & Olff 1991). Because of vigorous growth, they occupy more space, and extract more nutrients and moisture from the soil than their competitively inferior neighbor species. As a result of interspecific interactions, competitively inferior species are not only deprived of necessary resources and show tremendous reduction in their biomass, but also may become excluded from the site (Ellison & Farnsworth 1993). Such habitats have high biomass levels and low species richness.

At productive sites, frequent and intense disturbances overcome the monopoly of dominant species for space, light, moisture and nutrients. The improved germination and growth of some fugitive species reshapes the relationship between species richness and biomass under these altered conditions. Extensive work has been conducted to determine the role of disturbances and fertility, in reshaping the relationship between species richness and biomass of some natural plant communities (Wilson & Tilman 1991; Bobbink 1991; Belsky 1993; Bobbink & Willems 1993). This relationship has not yet been studied for experimental plant micro-communities emerging from soil seed banks, despite the fact that they are very easy to grow and manipulate.

The objective of this study is to apply fertilization and disturbance to plant micro-communities emerging from soil seed banks, and examine how the species composition and the relationship between species richness and biomass of these experimental plant micro-communities are influenced by these treatments.

I hypothesize that plant micro-communities emerging from soil seed banks will exhibit unimodal curves. I also hypothesize that fertilized plant micro-communities will have high biomass and result in lower species richness as a result of competitive exclusion process as compared to not fertilized and disturbed plant communities.

MATERIALS AND METHODS

On May 14, 1993, I selected four different sites -- roadside, forest, prairie, and old field-- in the Nature Conservancy's Tallgrass Prairie Preserve, Osage County, Oklahoma, for collection of the soil seed bank in each. Information about the study sites and the methods for collecting and processing the soil samples are presented in chapter II.

On June 14, 1993, I filled 80 plastic pots measuring 10 cm *10 cm * 5 cm with the mixed soil samples for each of the following four treatments:

Treatment No.	Treatment	Abbreviation
1	Fertilized & Disturbed	F&D
2	Fertilized & Not Disturbed	F&ND
3	Not Fertilized & Disturbed	NF&D
4	Not Fertilized & Not disturbed	NF&ND

I placed all the pots on greenhouse tables under natural sunlight in a completely randomized design. I kept the soil surface of all pots moist throughout the study period. On July 14, 1993, I clipped the plant communities at a 1 cm height above soil surface to create the disturbance treatment. The same day, I incorporated Osmacote controlled release fertilizer, manufactured by Sierra, Yosmate DR. 1001 Milpitas, Ca. U. S. A., @ 4 mg cm^{-1}, as a fertilization treatment. On August 14, 1993, I harvested the above-ground vegetation from all pots near the soil surface and placed in an oven at 55.5 °C to dry. I sorted the oven dried phytomass for each species in each pot and weighed each species.

Soil from all pots for each treatment was again separately well-mixed and ten randomly selected soil samples from each treatment were sent to Brookside Laboratories, Inc, Ohio, for chemical analysis (Table 1).

Data analysis

The species composition of experimental plant communities was evaluated in terms of frequency (percentage of pots having a plant species), and average biomass for each

Table 1. Chemical and physical attributes of soil samples after harvesting the plant micro-communities emerging from soil seed banks. S. D. = Standard deviation. F&D = Fertilized & Disturbed, F&ND = Fertilized & Not Disturbed, NF& D = Not Fertilized & Disturbed, NF&ND = Not Fertilized & Not Disturbed. CEC = Cation exchange capacity.

		F&D		F&ND		NF&D		NF&ND	
Characteristic	Units	Mean	S. D.	Mean	S. D.	Mean	S. D.	Mean	S. D.
Nitrogen release	p.p.m.	55.900	1.393	56.200	2.052	55.900	1.319	55.400	1.356
Phosphorus									
Easily extractable	p.p.m.	352.400	94.375	310.700	85.020	25.800	3.600	23.500	2.500
Bray II	p.p.m.	193.000	7.603	193.300	5.604	61.900	6.139	57.600	6.037
Potassium	p.p.m.	875.400	232.274	796.600	225.936	236.600	21.115	244.300	31.292
Organic matter	%	7.220	0.538	7.340	0.806	7.230	0.516	7.010	0.541
Calcium	p.p.m.	4608.800	308.389	4736.500	208.218	3258.600	116.516	3196.000	88.455
Magnesium	p.p.m.	291.000	13.289	304.700	23.694	321.900	10.464	326.400	17.839
Soluble sulphur	p.p.m.	332.800	104.234	315.500	12.342	37.100	6.268	38.600	5.953
Sodium	p.p.m.	149.500	33.140	165.700	44.304	142.500	19.971	155.100	25.465
Minor nutrients									
Boron	p.p.m.	1.147	0.083	1.158	0.101	1.248	0.288	1.147	0.082
Iron	p.p.m.	145.300	21.322	133.900	8.549	111.700	10.771	112.300	9.504
Manganese	p.p.m.	116.300	9.849	100.020	34.422	116.000	7.113	118.700	14.304
Copper	p.p.m.	1.953	0.097	1.934	0.107	2.080	0.102	2.043	0.093
Aluminum	p.p.m.	245.200	34.008	247.000	44.315	187.400	46.399	174.300	48.908
Zinc	p.p.m.	5.870	0.283	5.970	0.355	5.810	0.345	5.810	0.362
CEC	M.E./100	32.271	3.344	32.614	2.395	21.012	0.660	20.804	0.579
pH	H_2O 1:1	6.550	0.258	6.590	0.187	7.530	0.046	7.530	0.110

species. Canonical Correspondence Analysis (CCA) was performed to examine the differences in species composition among different treatments (ter Braak 1986). To diminish the effect of statistical noise, square root transformation of biomass, elimination of pots with zero biomass, down-weighting of rare species, and passively ordinating unidentified species was considered appropriate.

All the regressions were performed by using the SYSTAT statistical package (Walkinson, 1990). Two way analysis of variance test was performed to analyze the data pertaining to biomass and species richness. A second order orthogonal polynomial regression equation (Steel & Torrie 1980) was applied to examine the relationship between species richness and biomass:

$$\text{Species richness} = \beta 0 + \beta_1 X + \beta_2 X^2 + \varepsilon$$

β_0, β_1, and β_2 are the regression coefficients estimated by b_0, b_1 and b_2 respectively. X represents biomass, X^2 is biomass squared and ε indicates the unexplained variability (or error) in the model. A significant β_1 indicates that species richness responds linearly to biomass and a significant β_2 indicates that a parabolic curve better fits the relationship between species richness and biomass. A positive sign (+) for the quadratic coefficient (β_2) will indicate an upwardly concave parabolic curve, while a negative sign (-) for the quadratic coefficient (β_2) will represent a downwardly concave (or unimodal) parabolic curve. I hypothesized that the SRBR of plant micro-communities emerging from soil seed banks, will have a significantly negative ($p < 0.05$) quadratic coefficient (β_2).

RESULTS

Biomass

Both fertilization and disturbance as well as their interactive effects had a significant influence on the biomass of the experimental plant micro-communities (Table 2). The maximum biomass was recorded for the F& ND plant micro-communities and the minimum biomass for NF&D plant micro-communities (Table 3). The second highest biomass was recorded for the F&D plant micro-communities. The significance of these results must be interpreted cautiously because of the non-homogeneity of variances (Walkinson 1990). A square root transformation did not substantially reduce the heterogeneity of variances. A logarithmic transformation was impossible because of some data entries with zero values.

Species richness

Only fertilization significantly influenced the species richness of the plant micro-communities emerging from the soil seed banks (Table 2). In contrast to biomass, the highest species richness was observed for the NF&D plant micro-communities (Table 3). The minimum species richness was recorded for F&D plant micro-communities.

Species composition

The species composition of experimental plant micro-communities in terms of frequency (percentage of pots in which a species occurred) of each species showed slight variation among treatments (Table 4). In terms of average biomass, the majority of species showed a sequential declining trend (F&ND→F&D and NF&ND→NF&D). The overall maximum number of species (from all replicates) was recorded for the NF&D plant micro-communities and the overall minimum species richness for the NF& ND (control) plant micro-communities (Table 5), but there is no proper statistical test to examine its significance.

The overall ordination of species composition of plant micro-communities emerging from soil seed banks as determined by Canonical Correspondence Analysis (Fig. 1) was highly significant ($p < 0.01$). The first most important axis as assessed by Monte Carlo test (ter Braak 1986) is also highly significant ($p < 0.01$). Axis 2, appears to be a disturbance gradient. *Eragrostis cilianensis, Solanum carolinense, Mollugo verticillata* and *Eupatorium rugosum* show comparatively high importance in the disturbed conditions. Similarly, *Eragrostis intermedia, Solanum nigrum, Panicum dichotomiflorum* and *Setaria glauca* seem to be high fertility indicator species. *Eragrostis spectabilis, Euphorbia nutans* and *Solanum rostratum* did not appear in disturbed

Table 2. Analysis of variance table for biomass (dry weight in grams per 0.01 m^2) and species richness (number of species in 0.01 m^2) of experimental plant micro-communities emerging from soil seed banks

	Biomass		Species richness	
Variables	F ratio	p value	F ratio	p value
Fertilization	374.391	< 0.001	5.470	< 0.05
Disturbance	40.413	< 0.001	1.130	> 0.1
Fertilization * Disturbance	15.106	< 0.001	2.657	> 0.1

Table 3. Mean and standard deviation (S. D.) of biomass (dry weight in grams per 0.01 m^2) and species richness (number of species in 0.01 m^2) of experimental plant micro-communities emerging from soil seed banks, S. D. = Standard deviation.

	Biomass		Species richness	
Treatment	Mean	S. D.	Mean	S. D.
Fertilized & Disturbed (F&D)	13.505	6.287	3.413	1.429
Fertilized & Not Disturbed (F&ND)	19.215	6.912	3.888	1.500
Not Fertilized & Disturbed (NF&D)	4.884	2.104	4.113	1.796
Not Fertilized & Not Disturbed (NF&ND)	6.262	2.547	4.013	1.521

Table 4. Frequency and mean biomass (in grams) and the standard deviation (S. D.) ofbiomass of plant species in micro-communities emerging from soil seed banks.

	Fertilized & Disturbed			Fertilized & not Disturbed			Not Fertilized & Disturbed			Not Fertilized Not Disturbed		
Species name	% Frequency	Mean biom.	S. D.	% Frequency	Mean biom.	S. D.	% Frequency	Mean biom.	S. D.	% Frequency	Mean biom.	S. D.
Acalypha virginica	1.25	0.017	0.150	2.50	0.055	0.469	1.25	0.006	0.050	3.75	0.072	0.406
Ambrosia psilostachya	1.25	0.001	0.010	*	*	*	2.50	0.014	0.121	*	*	*
Ambrosia trifida	1.25	0.002	0.013	8.75	0.226	1.092	10.00	0.028	0.139	6.50	0.035	0.196
Aster simplex	*	*	*	*	*	*	1.25	0.001	0.011	*	*	*
Bothriochloa saccharoides	*	*	*	1.25	0.053	0.467	*	*	*	*	*	*
Bouteloua curtipendula	1.25	0.007	0.062	1.25	0.009	0.077	*	*	*	*	*	*
Bromus japonicus	*	*	*	*	*	*	*	*	*	*	*	*
Cenchrus pauciflorus	1.25	0.040	0.358	2.50	0.251	1.805	*	*	*	*	*	*
Chenopodium album	*	*	*	*	*	*	*	*	*	1.25	0.021	0.184
Chloris verticillata	1.25	0.021	0.188	1.25	0.009	0.077	3.75	0.018	0.098	3.75	0.018	0.097
Cirsium undulatum	*	*	*	*	*	*	*	*	*	1.25	0.012	0.110
Commelina erecta	1.25	0.011	0.094	*	*	*	*	*	*	*	*	*
Croton capitatus	*	*	*	1.25	*	0.003	1.25	0.007	0.063	2.50	0.008	0.048
Cynodon dactylon	*	*	*	1.25	0.010	0.087	*	*	*	*	*	*
Cyperus acuminatus	7.50	0.046	0.181	2.50	0.036	0.229	13.75	0.118	0.397	7.50	0.032	0.162
Cyperus filiculmis	*	*	*	2.50	0.094	0.823	1.25	0.022	0.192	*	*	*
Cyperus ovularis	2.50	0.014	0.113	3.75	0.084	0.452	7.50	0.159	0.696	10.00	0.105	0.489
Dichanthelium acuminatum	1.25	0.001	0.011	2.50	0.461	3.069	2.50	0.088	0.632	1.25	0.008	0.072
Digitaria sanguinalis	7.50	0.372	1.803	12.50	1.065	3.439	26.25	0.453	1.096	21.25	0.345	0.787
Eleusine indica	6.25	0.205	1.406	12.50	0.496	3.114	13.75	0.181	0.817	13.75	0.149	0.567
Eragrostis cilianensis	3.75	0.583	3.165	*	*	*	6.25	0.123	0.724	7.50	0.205	1.065
Eragrostis hirsuta	21.25	0.351	0.891	21.50	0.694	1.764	37.50	0.481	0.908	32.50	0.462	0.826
Eragrostis intermedia	16.25	1.638	4.834	17.50	1.711	4.945	8.75	0.146	0.523	3.75	0.072	0.452
Eragrostis pilosa	*	*	*	1.25	0.043	0.381	*	*	*	*	*	*
Eragrostis spectabilis	1.25	0.043	0.384	3.75	0.192	1.041	1.25	0.012	0.110	1.25	0.139	1.232
Erigeron strigosus	3.75	0.009	0.049	7.50	0.023	0.096	12.50	0.043	0.154	10.00	0.028	0.121
Eupatorium rugosum	6.25	0.012	0.057	2.50	0.012	0.088	2.50	0.004	0.026	*	*	*
Euphorbia dentata	*	*	*	*	*	*	*	*	*	1.25	0.028	0.249
Euphorbia nutans	3.75	0.243	1.288	27.50	1.540	3.128	6.75	0.183	0.993	12.50	0.330	1.136
Euphorbia strictospora	48.75	0.698	1.396	46.25	0.769	1.682	45.00	0.475	0.763	43.75	0.376	0.665
Euphorbia supina	1.25	0.012	0.108	1.25	0.032	0.282	1.25	0.014	0.087	*	*	*

Tab. 4. continued

	Fertilized & Disturbed			Fertilized & Not Disturbed			Not Fertilized & Disturbed			Not Fertilized Not Disturbed		
Species name	% Frequency	Mean biom.	S. D.	% Frequency	Mean biom.	S. D.	% Frequency	Mean biom.	S. D.	% Frequency	Mean biom.	S. D.
Leucospora multifida	16.25	0.048	0.153	18.75	0.072	0.218	21.25	0.109	0.281	20.00	0.051	0.178
Melilotus officinalis	1.25	*	0.003	*	*	*	2.50	0.002	0.011	*	*	*
Mollugo verticillata	17.50	0.394	1.358	5.00	0.097	0.548	12.50	0.092	0.294	13.75	0.145	0.446
Muhlenbergia schreberi	68.75	5.236	5.765	60.00	3.901	4.992	56.25	0.843	1.139	50.00	1.143	1.897
Oenothera biennis	5.00	0.058	0.318	5.00	0.170	0.942	5.00	0.051	0.271	7.50	0.084	0.364
Oenothera laciniata	1.25	0.001	0.004	2.50	0.009	0.070	*	*	*	2.50	0.005	0.037
Oxalis corniculata	*	*	*	1.25	0.003	0.023	*	*	*	*	*	*
Panicum anceps	12.50	0.279	1.121	11.25	0.522	2.302	11.25	0.133	0.626	6.75	0.102	0.619
Panicum capillare	3.75	0.181	1.341	1.25	0.013	0.117	3.75	0.074	0.524	7.50	0.311	1.333
Panicum dichotomiflorum	3.75	0.360	2.251	7.50	0.712	3.014	6.25	0.095	0.595	3.75	0.092	0.659
Paspalum setaceum	5.00	0.284	1.894	8.75	0.622	2.651	7.75	0.123	0.483	10.00	0.409	1.503
Physalis longifolia	1.25	0.151	1.340	1.25	0.049	0.431	*	*	*	*	*	*
Physalis virginiana	1.25	*	*	*	*	*	3.75	0.069	0.434	1.25	0.002	0.017
Phytolacca americana	*	*	*	1.25	0.018	0.159	1.25	0.010	0.084	2.50	0.027	0.175
Plantago major	*	*	*	*	*	*	1.25	0.007	0.061	*	*	*
Polygonum ramosissimum	*	*	*	*	*	*	1.25	0.001	0.008	*	*	*
Rumex crispus	13.75	0.101	0.348	11.25	0.151	0.548	20.00	0.094	0.233	12.50	0.076	0.236
Setaria glauca	8.75	1.040	3.987	11.25	2.209	6.556	2.50	0.097	0.605	5.00	0.321	1.420
Sida spinosa	1.25	0.102	0.907	1.25	0.110	0.973	5.00	0.150	0.665	1.25	0.022	0.191
Solanum carolinense	6.25	0.169	0.783	1.25	0.070	0.621	2.50	0.027	0.197	5.00	0.029	0.166
Solanum nigrum	5.00	0.271	1.357	6.25	0.174	0.772	2.50	0.008	0.048	5.00	0.028	0.157
Solanum rostratum	6.25	0.065	0.276	30.00	1.841	3.348	8.75	0.053	0.246	28.75	0.694	1.525
Sporobolus asper	*	*	*	1.25	0.002	0.019	6.25	0.044	0.228	7.50	0.055	0.267
Strophostyles helvola	*	*	*	*	*	*	1.25	0.032	0.282	*	*	*
Strophostyles leiosperma	2.50	0.032	0.267	1.25	0.001	0.007	1.25	0.001	0.006	*	*	*
Tridens flavus	13.75	0.375	1.269	13.75	0.605	2.141	16.25	0.190	0.566	17.50	0.148	0.435
Trifolium campestre	3.75	0.011	0.062	2.50	0.005	0.032	1.25	0.001	0.011	5.00	0.056	0.287
Trifolium repens	1.25	0.004	0.033	*	*	*	*	*	*	1.25	0.001	0.009
Verbena bracteata	*	*	*	*	*	*	*	*	*	2.50	0.022	0.159
Verbena canadensis	1.25	0.002	0.016	*	*	*	1.25	0.006	0.053	*	*	*

* Species absent or zero value

Table 5. Number of plant species encountered in all replicates of a given treatment.

Treatment	Number of species
Fertilized & Disturbed (F&D)	44
Fertilized & Not Disturbed (F&ND)	45
Not Fertilized & Not Disturbed (NF&D)	46
Not fertilized & Not Disturbed (NF&ND)	41

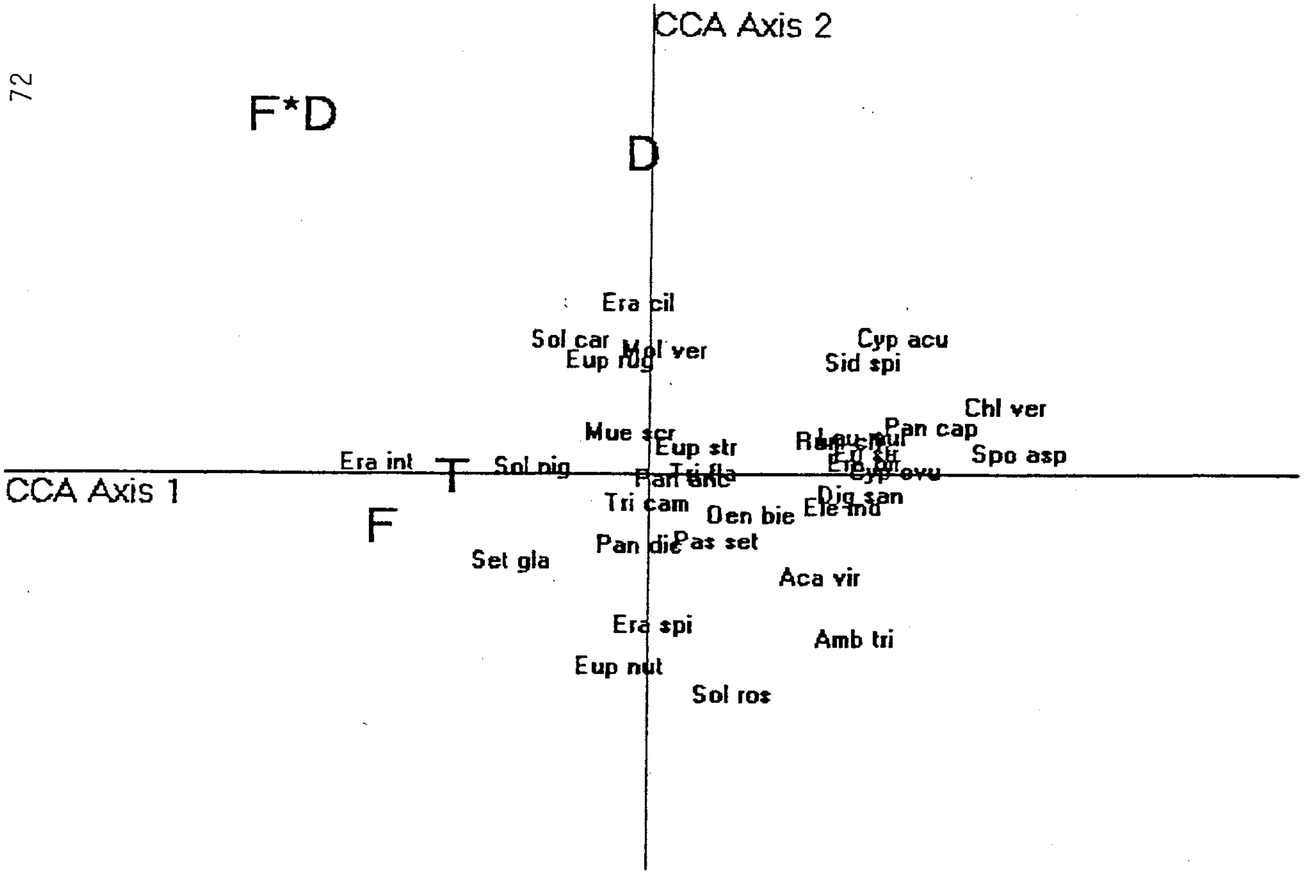

Fig. 1. Canonical Correspondence Analysis of plant micro-communities emerging from soil seed banks. Large letters indicate centroids of sample scores. Species codes are the first three letters of the generic and species' name, see Appendix 1, for complete list of the species encountered. F = Fertilization, D = Disturbance, F*D = Fertilization by Disturbance interaction, T = Table 2 (in contrast to greenhouse Table 1).

conditions. In the infertile and undisturbed (NF&ND) conditions *Acalypha virginica, Ambrosia trifida* and *Solanum rostratum* show high importance. Most of the species show high importance at the intermediate position where the indices of disturbance and fertilization coincide or join each other. The effect of experimental Table 2 used for placing the pots in the greenhouse is similar to that of fertilization, but the magnitude of the effect is small.

Species richness and biomass relationship (SRBR)

The SRBR of the NF&D plant micro-communities exhibited unimodal curve (Table 6, Fig. 2) with significant linear as well as the quadratic term. In the F&D and F&ND plant micro-communities, both the linear and the quadratic components for the SRBR were highly significant, but they did not exhibit true unimodal curves. Neither the linear nor the quadratic coefficients for the SRBR were highly significant for the NF&ND plant micro-communities. They therefore did not reveal significant unimodal curve for the SRBR.

DISCUSSION

The above-ground biomass of plant micro-communities emerging from soil seed banks was significantly influenced by both fertilization and disturbance as well as by their interactive effects. Plant micro-communities having access to high soil fertility without any disturbance (F&ND) showed maximum biomass, and the disturbed plant communities with low soil fertility (NF&D) gained minimum biomass. Similar results have been reported by Wilson and Tilman (1991). They also examined the interactive effects of fertilization and disturbance on the community structure in an old-field study and found that biomass increased with fertilization, but decreased with disturbance.

The species richness of plant micro-communities was significantly influenced by fertilization only. Fertilized plant micro-communities without disturbance with high soil fertility (F& ND) yielded low species richness. In contrast, disturbed plant micro-communities growing at comparatively infertile soil (NF&D) maintained high species richness. Willems, et al. (1993) conducted a series of fertilization experiments in a chalk

Table 6. Regression model for species richness as a function of biomass in experimental plant micro-communities emerging from soil seed banks, the column of p values is for the overall model.

Treatments	Model fitted	p value	r^2
Fertilized & Disturbed (F&D)	$1.654^{****} + 0.261B^{***} - 0.008B2^{**}$	0.006	0.119
Fertilized & Not Disturbed (F&ND)	$0.933^{NS} + 0.260B^{**} - 0.005B2^{*}$	0.002	0.139
Not Fertilized & Disturbed (NF&D)	$0.463^{NS} + 1.348B^{****} - 0.104B^{2****}$	0.000	0.291
Not Fertilized & Not Disturbed (NF&ND)	$2.600^{****} + 0.364B^{NS} - 0.019B^{2NS}$	0.125	0.053

NS : $p > 0.10$, * : $p < 0.10$, ** : $p < 0.05$, *** : $p < 0.01$, **** , $p < 0.005$

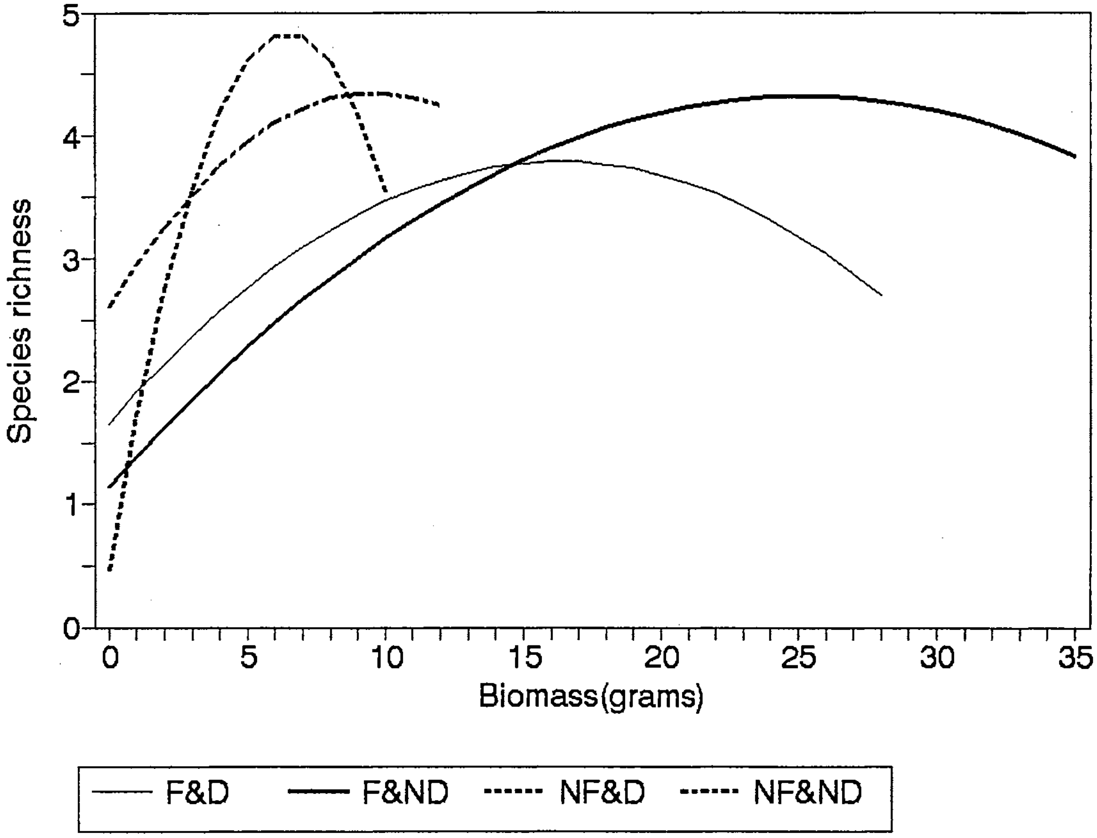

Fig. 2. Relationship between species richness and biomass of plant micro-communities emerging from soil seed banks. The curves are based on regression equations (Table. 6); data points not shown. F&D = Fertilized & Disturbed, F&ND = Fertilized & Not Disturbed, NF&D = Fertilized & Not Disturbed.

grassland in the Netherlands and reached the same conclusion. They observed that fertilization doubled the above-ground production, but simultaneously decreased species richness. Day et al. (1988) analyzed a riverine marsh vegetation in Canada, and reported that high species richness corresponded to low fertility levels. The paradox of enrichment (Peet et al. 1983), the long run Park Grass Experiment at Rothamsted England initiated in 1857 (Silvertown 1980), and several other experiments (Tilman 1987; Wheeler 1988; Milchunas et al. 1990; Bobbink 1991; Tilman & Olff 1991; Wilson & Tilman 1991) indicate that the high biomass levels acquired as a result of artificial fertilization trigger the competitive exclusion process and consequently yield low species richness. Low species richness corresponding to high biomass levels in the F&ND plant micro-communities in this study may be attributed to the competitive exclusion process.

Nutritionally poor habitats are usually invaded by stress-tolerant plant species (Day et al. 1988; Olff & Bakker 1991) which neither can grow fast nor gain high biomass that pose negative effects on the neighbor species. Therefore, weak interspecific interactions among the competing species prove ineffective to competitively exclude each other, and yield high species richness at infertile sites. As an alternative strategy, the use of manipulated disturbances has proved very effective in creating the nutrient poor conditions and counteracting the competitive exclusion process to achieve high species richness in the Netherlands (Bakker 1987; Bobbink & Willems 1993). The high species richness corresponding to low biomass levels in the NF&D plant micro-communities may be associated with disturbance and low soil fertility that might have counteracted the competitive exclusion process.

The interactive effects between disturbance and fertilization are considered of specific important in plant communities (Wilson & Tilman 1991). Fertilization generally yields high biomass levels by promoting the growth rates of plant species. In contrast, disturbances check the fast growth and result in low biomass (Wilson & Shay 1990). In this study, the F&D plant micro-communities showed rapid regeneration following disturbance and resulted in high biomass because of high soil fertility. In contrast, the NF&D plant micro-communities could not regenerate rapidly following disturbance and yielded the lowest biomass. Therefore, the significant interactive effects between fertilization and disturbance for biomass in this study may be attributed to the variation in soil fertility that influenced differently the regenerative abilities and growth rates of plant species in different plant micro-communities.

Species composition of the plant micro-communities was significantly influenced by the fertilization and disturbance treatments. Perhaps due to the uniformity of the seed banks, the frequency of abundant species like *Muhlenbergia schreberi* and *Euphorbia stictospora,* as well as some infrequent species was observed to be more or less similar in all treatments. The among treatment differences in the mean biomass of different species however, may be attributed to the variation in soil fertility.

The SRBR for the all treated (F&D, F&ND & NF&D) plant micro-communities had significant linear and quadratic coefficients and showed unimodal curves more or less similar to Grime's unimodal curve (1973; 1979). Similar results have been reported for some natural plant communities (Al-Mufti, et al. 1977; Huston 1978; Klinkhamer & De Jong 1985; Kutiel & Danin 1987; Olff & Bakker 1991). A common feature of all these studies is that they relate high species richness to intermediate biomass levels as was observed in this experiment.

The r^2 values indicate that at most, less than 30 % of the variability in the species richness can be explained by a quadratic function of biomass levels. As the experiment was conducted in a greenhouse, the remaining variability may be attributed to the random variation in the soil seed banks. The short time lag following disturbance is another possible reason for low explained variance. It is worth considering that the maximum r^2 for the SRBR was recorded for the NF&D plant micro-communities that experienced some sort of stress due to low fertility and perturbation. As such these results seem consistent with both the intermediate disturbance hypothesis (Connell 1978) as well as Tilman's (1982) resource model.

In conclusion, experimental plant micro-communities emerging from soil seed banks simulated natural plant communities in their responses to fertilization and disturbance. The results achieved during this study encourage further experimentation on plant micro-communities emerging from soil seed banks, and the generalization of different models dealing with the SRBR.

References

Adams, D. E.; Anderson, R. C. & Collins, S. C. 1982. Differential response of woody and herbaceous species to summer and winter burning in an Oklahoma grassland. *Southwest. Nat.* 27:55-61.

Al-Mufti, M. M., Syeds, C. L., Furness, C. L., Grime, J. P., & Band, S. R. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *J. Ecol.* 65: 759-791.

Armesto, J. J. & Pickett, S. T. A. 1985. Experimental disturbance in Old-field plant communities: impact on species richness and abundance. *Ecology* 66:230-240.

Bakker, J. P. 1987. Grazing as a management tool in the restoration of species rich grasslands. Proceedings of the Koniklijke van Watenschappen Series C., 90: 404-429.

Belsky, J. 1986. Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania. I. Colonization of grazed and ungrazed plots. *J. Ecol.* 74: 419-438.

Belsky, J. 1993. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *J. Veg. Sci.* 3:187-200.

Bobbink, R. 1991. Effects of nutrient enrichment in Dutch grasslands. *J. Appl. Ecol.* 28: 28-41.

Bobbink, R. & Willems, J. H. 1987. Increasing dominance of *Brachypodium pinnatum* (L.) Beauv. in Chalk grasslands: a threat to a species-rich ecosystem. *Biol. Conserv.* 56:1-21.

Bobbink, R. & Willems, J. H. 1993. Restoration management of abandoned chalk grasslands in the Netherlands. *Biodiv. & Conserv.* 2: 616-626.

Carson, W. P. & Barrett, G. W. 1988. Succession in old-field communities: Effects of contrasting types of nutrient enrichment. *Ecology* 69:984-994.

Collins, S. L. 1990. Patterns of community structure during succession in tallgrass prairie. *Bull. Torrey. Bot. Club* 117:397-408.

Collins, S. L. & Glenn, S. M. 1988. Disturbance and community structure in North American prairies, pp. 131-143. In: During H. J.; Werger, M. J. A. & Willems J. H. (eds.),. *Diversity and pattern in plant communities.* SPB Academic Publishers, The Hague, The Netherlands.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.

Day, R. T., Keddy, P. A.; McNeil, J. & Carleton, T. 1988. Fertility and disturbance gradients: a summary model for riverine marsh vegetation. *Ecology* 69: 1044-1054.

del Moral, R. & Wood, D. M. 1993. Early primary succession on a barren volcanic plain at Mount St. Helens, Washington. *Am. J. Bot.* 80: 981-991.

Ellison, A. M. & Farnsworth, E. J. 1993. Seedling survivorship growth, and response to disturbance in Belizean mangal. *Am. J. Bot.* 80: 1137-1145.

Gehring, J. L. & Bragg, T. B. 1992. Changes in prairie vegetation under Eastern Red Cedar (*Juniperus virginiana* L.) in an eastern Nebraska Bluestem prairie. *Am. Midl. Nat.* 128:209-217.

Great Plains Flora Association.1986. *Flora of the great plains.* University Press of Kansas, Lawrense, Kansas.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* (London) 242:344-347.

Grime, J. P. 1979. *Plant strategies and vegetation process.* Wiley, Chichester.

Huston, M. 1979. A general hypothesis of species diversity. *Am. Nat.* 113: 81-101.

Keddy, P. A. & Shipley, B. 1989. Competitive hierarchies in herbaceous plant communities. *Oikos* 54: 234-241.

Klinkhamer, P. G. L. & De Jong, T. J. 1985. Shoot biomass and species richness in relation to some environmental factors in a coastal dune area in the Netherlands. *Vegetatio*. 63: 129-32.

Kutiel, P & Danin, A. 1987. Annual species diversity and above ground phytomass in relation to some soil properties in the sand dunes of the northern Sharon plains, Israel. *Vegetatio.* 70: 45-49.

Milchunas, D. G., Lauenroth, W. K., Chapman, P. L. & Kazempour, M. K. 1993. Community attributes along a perturbation gradient in a shortgrass steppe. *J. Veg. Sci.* 1: 375-384.

Nilsson, C. & Wilson, S. D. 1991. Convergence in plant community structure along desperate gradients: are lakeshores inverted mountainsides ?. *Am. Nat.* 137: 774-790.

Olff, H. & Bakker, J. P. 1991. Long term dynamics of standing crop and species composition after the cessation of fertilizer application to mown grassland. *J. Appl. Ecol.* 28: 1040-52.

Peet, P. K.; Glenn-Lewin, D. C. & Wolf, J. W. 1983. Prediction of man's impact on plant species diversity, A challenge for vegetation science. in. Holzner,W., Werger, M. J. A. & Ikusima,I. (eds.) *Man's impact on vegetation.* pp. 41-54. Junk The Hague.

Puerto, A, Rico, M., Matías, M. D., & García, J. A. 1990. Variation in structure and diversity in mediterranean grassland related to trophic status and grazing intensity. *J. Veg. Sci.* 1: 445-453.

Reed, F. C. 1977. Plant species number, biomass accumulation and productivity of a differentially fertilized Michigan old-field. *Oecologia* 30: 43-53.

Steel, R. G. D. & Torrie, J. H. 1980. *Principles and Procedures of Statistics: A Biometrical Approach.* Mcgraw-Hill Publishing Company, New York.

Silvertown, J. 1980. The dynamics of a grassland ecosystem: botanical equilibrium in the Park Grass Experiment. *J. Appl. Ecol.* 17: 491-504.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.

Tilman, D. 1982. *Resource composition and community structure.* Princeton University press, Princeton.

Tilman, D. 1986. Nitrogen-limited growth in plants from different successional stages. *Ecology* 67: 555-563.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along an experimental nitrogen gradient. *Ecol. Monog.* 57: 189-214.

Tilman, D. 1993. Species richness of experimental productivity gradients: How important is colonization limitation ?. *Ecology* 74: 2179-2191.

Tilman, D. & Olff, H. 1991. an experimental study of the effect of pH and nitrogen on grassland vegetation. *Acta Oec.* 12: 427-441.

Vermeer, J. G. & Berendse, F. 1983. The relationship between nutrient availability , shoot biomass and species richness in grassland and wetland communities. *Vegetatio* 53: 121-126.

Walkinson, L. 1990. *SYSTAT. The system of statistics.* SYSTAT. Inc., Evanston, IL.

Wheeler, B. D. 1988. Species richness, species rarity and conservation evaluation of rich fen vegetation in lowland England and Wales. *J. Appl. Ecol.* 25: 331-353.

Wheeler, B. D. & Giller, K. E. 1982. Species richness of herbaceous fen vegetation in Broadland, Norfolk in relation to the quantity of above ground plant material. *J. Ecol.* 70: 179-200.

White, P. S. 1979. Pattern, process and natural disturbance in vegetation. *Bot. Rev.* 45: 229-299.

Willems, J. H. 1983. species composition and above ground phytomass in chalk grassland with different management. *Vegetatio* 52: 171-80.

Willems, J. H.; Peet, R. K. & Bike, R. 1993. Changes in Chalk-grassland structure and species richness resulting from selective nutrient additions. *J. Veg. Sci.* 4:203-212.

Wilson, S. D. 1993. Competition and resource availability in heath and grassland in the Snowy mountains of Australia. *J. Ecol.* 81:441-451.

Wilson, S. D. & Shay, J. M. 1990. Competition, fire and nutrients in mixed grass prairie. *Ecology* 71: 1959-1967.

Wilson, S. D. & Tilman, D. 1991. Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community. *Oecologia* 88: 61-71.

Wisheu, I. C. & Keddy, P. A. 1989. Species richness- standing crop relationships along four lakeshore gradients: constraint on the general model. *Can. J. Bot.* 67: 1609-1617.

Chapter IV

THE STRUCTURE OF PLANT MICRO-COMMUNITIES EMERGING FROM SOIL SEED BANKS: IMPLICATIONS ROR NATURAL PLANT COMMUNITIES

Anthropogenic disturbance has caused a drastic reduction in natural plant communities worldwide (Bock & Bock 1993; Hannah et al. 1994; Turner et al. 1994). The species richness of the remaining plant communities is also threatened because of deteriorating climatic conditions (Root & Schneider 1993; Grabherr et al. 1994; Pyšek 1994; Turner et al. 1994). In efforts to conserve the species richness of endangered plant communities, ecologists have made substantial advances in the past few years. Ecological surveys of a variety of plant communities and extensive experimentation have elucidated key factors responsible for the coexistence of species. Among these the function of above-ground biomass, disturbances, seasonal environmental changes, soil fertility, and soil seed banks have been found to be of specific importance (Coffin & Lauenroth 1994; Dean et al. 1994). Consequently, several models emphasizing the role of different ecological factors in plant communities have come forth. Among them, Grime's (1973, 1979) unimodal model dealing with the relationship between the species richness and biomass, Connell's (1978) intermediate disturbance hypothesis, and Tilman's (1982) resource competition model particularly have become the foci of ecological theory.

Grime (1973, 1979) proposed a unimodal relationship between species richness and biomass of herbaceous plant communities. He attributed low species richness at the lower extreme to some sort of stress exerted by disturbances or low soil fertility.

Similarly, he explained low species richness at the upper extreme to the competitive exclusion process. Al-Mufti et al. (1977) further refined the model after analyzing the herbaceous vegetation of thirteen sites in the Sheffield region of England. They found the highest species richness at a specific biomass range (350-750 g m^{-2}). Grime's (1973,1979) model subsequently has been found applicable to a variety of plant (Klinkhamer & De Jong 1985; Kutiel & Danin 1987; Moore & Keddy 1989; Belcher et al. 1992), ant (Anderson 1992), and rodent (Brown 1972) communities. Some ecological studies however, relate the highest species richness to low biomass levels and challenge the generality of this model (Wisheu & Keddy 1989). One possible resolution to this contradiction is that Wisheu & Keddy may have sampled only low biomass levels that relate to the left extreme in Grime's model.

In Connell's (1978) intermediate disturbance hypothesis, maximum species richness is predicted at intermediate disturbance levels. According to this model, infrequent and low disturbance levels prove ineffective in reducing the diversity-suppressing effects of dominant species. Following intense and frequent disturbances as well, the failure of some species to regenerate produces low species richness (Young et al. 1987). However, intermediate disturbance levels in some plant communities have proved helpful in enhancing the species richness (Bakker 1987; Specht et al. 1990; Ter Heerdt et al. 1991; Bobbink & Willems 1993). The selection of a suitable disturbance factor and the maintenance of appropriate disturbance levels still remains an unsolved issue (Glenn & Collins 1992).

Tilman's (1982) model predicts high species richness at intermediate resource levels. It predicts that very low resource levels hamper plant growth and result in low species richness. The fast growth of dominant species due to high resource levels also results in low species richness because of competitive exclusion. Yemm & Willis (1962) had already demonstrated that the competitive exclusion process could be controlled if by some means the fast growth of dominant species is checked. During an experiment following the application of a growth retardant, they observed that the reduction in biomass resulted in an increased species richness. Ecological surveys of some natural plant communities have revealed that sites with enriched soil usually yield high biomass levels, but low species richness when compared to impoverished sites (Vermeer & Berendse 1983; Day et al. 1988). In accordance with the paradox of enrichment (Peet et al. 1983), artificial fertilization of some plant communities has also yielded low species richness probably because of the competitive exclusion process. Consistent with Grime's model (1973, 1979) in certain circumstances, the enrichment of infertile habitats also has initially resulted in high species richness (Carson & Barrett 1988; Milchunas et al. 1990). Therefore, the problem still seems unsolved.

Soil seed banks can contribute tremendously to secondary succession. Depending upon soil fertility and history of past disturbances (Young et al. 1987; Warr et al. 1993; Coffin & Lauenroth 1994; Dean et al. 1994; Zammit & Zedler 1994), they manifest interesting among-site differences (Beatty 1991; Dessaint et al. 1991). Sometimes they show close resemblance to the above-ground vegetation (Beatty 1991; Unger & Woodall 1993). Plant micro-communities emerging from soil seed banks also can be easily manipulated under controlled greenhouse conditions where stochastic changes in environmental factors cannot influence the results.

I conducted two greenhouse experiments to examine the influence of manipulated disturbances (clipping near soil surface) and fertilization in structuring the plant micro-communities emerging from soil seed banks. A secondary objective of this study was to determine whether these micro-communities could be model systems for experimentation in community ecology, and to make recommendations for their practical implementation in natural plant communities.

I collected soil seed banks from four different sites - roadside, forest, prairie and old-field - located in The Nature Conservancy's Tallgrass Prairie Preserve, near Pawhuska, Oklahoma for both experiments. During the first experiment, I determined the role of disturbance (clipping near soil surface) and soil source on the structure of plant micro-communities emerging from soil seed banks. Plant micro-communities emerging from soil seed banks were clipped thrice at two-month intervals. The harvested plant material was oven dried, weighed, and statistically analyzed.

Plant micro-communities revealed significant among-site and among-harvest differences in the above-ground biomass, species richness, and species composition. Variation in the seed banks and soil fertility seem to be the main factors controlling among-site differences. Plant micro-communities emerging from the forest, old-field and mixed (mixture of all four seed banks) soil seed banks had high biomass and low species richness, probably caused by high soil fertility. These results are similar to those obtained in the long-term Park Grass Experiment (Silvertown 1980). In contrast, plant micro-communities emerging from prairie site seed banks with slightly low soil fertility maintained high species richness with intermediate biomass levels. The roadside soil samples were very poor in soil fertility. Therefore, they not only resulted in the least biomass levels, but also in the least species richness.

Plant micro-communities exhibited significant among harvest (temporal) differences in the species richness and biomass levels. Similar temporal changes in species richness and standing biomass have been reported by Oomes (1992) for grassland communities in the Netherlands. These differences can be attributed to a number of factors. The stress imposed by two intense disturbances deteriorating the regenerative abilities of plant species seems the main factor responsible for this variation (Young et al. 1987; Coffin & Lauenroth 1994; Jones et al 1994). A gradual depletion of soil fertility by disturbances through harvested plant litter (Bakker 1987; Bobbink & Willems 1993) may be considered the second most important factor leading to a gradual decline in the above-ground biomass. The change in the growing season and the variation in the life history traits of the plant species (Coffin & Lauenroth 1994) also may have caused among-harvest differences.

The interactive effects of sites by harvests on the biomass and species richness were highly significant. It seems that two intense disturbances and soil fertility interacted synergistically on the biomass and the species richness of plant micro-communities. Two intense disturbances might have further depleted the seed banks already varying in their fertility and therefore resulted in significant site by harvest interactive effects on the species richness and biomass. Similar results have been reported by Wilson & Tilman (1991).

Canonical Correspondence Analysis (CCA) of species composition also revealed a sequential arrangement of plant micro-communities emerging from soil seed banks along a fertility gradient. The forest and old-field site plant micro-communities with almost the same soil fertility showed close resemblance in their species composition. In contrast, the roadside and prairie soil samples had low soil fertility. The species composition of plant micro-communities emerging from them also exhibited close resemblance to each other, but differed greatly from the species composition of the remaining plant micro-communities emerging from relatively fertile soil samples. Not surprisingly, the mixed soil samples had intermediate fertility. Species composition of plant micro-communities emerging from them also occupied the intermediate position. In a recent study, Olff et al. (1993) examined the species dynamics and nutrient accumulation during early primary succession in some coastal sand dunes in the Netherlands. They observed that the edaphic factor was the most important determinant causing the differences in species composition. In another study, Olff et al. (1994) related successional changes in the species composition of grasslands to the germination attributes of different species.

Initially grasses had higher frequency than forbs in the first harvest, but subsequently forbs gained higher frequency than grasses. Similar temporal fluctuations in the frequency of occurrence of many short-lived species have been reported by Armesto & Pickett (1985) and Olff et al. (1994) . They considered the change in soil fertility solely responsible for these fluctuations. However, Ohtsuka & Ohsava (1994) associated the transition in the frequency of annual and perennial species to the variable intensity and frequency of disturbances. They observed that infrequent disturbances promoted the dominance of perennial grasses but inhibited the invasion of forbs. In contrast, frequent disturbances supported the invasion of annuals mostly forbs (e. g., *Stellaria media*, *Veronica* sp., *Oxalis corniculata* and *Rumex* sp.) through time. I observed similar results in this study. Such results also have been observed following disturbance during some field studies (Collins 1987; Ellison & Farnsworth 1993; Pysek 1994).

The relationship between species richness and biomass exhibited unimodal curves for the plant micro-communities emerging from soil seed banks of all four sites during the first harvest. During the subsequent harvests, the SRBR for some plant micro-communities also displayed unimodal curves like Grime's (1973; 1979) model. The r^2 values gradually decreased in the successive harvests. It seems owing to change in the growing season some species had lost their regenerative ability. As a result their low biomass accumulations might have influenced the species richness very meagerly (low r^2).

In the second experiment, I examined the effects of disturbance and fertilization on the community structure of plant micro-communities emerging from soil seed banks. In many respects, the nature of the experimental plant micro-communities confirmed the results of the first experiment. The among-treatment differences in the above-ground biomass, species richness, as well as in the relationship between species richness and biomass were similar to the among-site differences in the first experiment. The fertilized plant micro-communities, either disturbed or not disturbed showed maximum biomass that resulted in low species richness. This is probably a result of competitive exclusion (Day et al. 1988; Wheeler & Giller 1982; Williams 1983; Wheeler 1988; Bobbink 1991; Olff et al. 1993; Tilman 1993). In contrast, unfertilized plant micro-communities, especially the disturbed one, had high species richness in accordance with Tilman's resource model (1982) which predicts the coexistence of maximum number of species at low resource levels. Many experimental demonstrations (Tilman 1987; Carson & Barrett 1988; Wilson

& Shay 1990) as well as field observations (Vermeer & Berendse 1983; Day et al. 1988; Bobbink 1991; Olff & Bakker 1991) also relate the highest species richness to low soil fertility.

It seems in the unfertilized plant micro-communities, that disturbance effectively removed the canopy cover as observed by Armesto & Pickett (1985) and Ellison & Farnsworth (1993), and maintained the intermediate biomass levels that relate to the highest species richness in accordance with Grime's model (1973, 1979). In contrast, the fertilized and disturbed plant micro-communities regenerated very quickly and soon gained high biomass. Thase high biomass accumulations were expected to quickly reduce species richness through competitive exclusion. However, perhaps due to short time period following disturbance the influence of biomass on the species richness remained very meager (low r^2 values). The relationship between species richness and biomass of fertilized and disturbed plant micro-communities therefore, did not reveal true unimodal curves.

In conclusion, experimental plant micro-communities emerging from soil seed banks simulated natural plant communities in many aspects during both experiments. They displayed unimodal curves for the relationship between species richness and biomass as predicted by Grime's model (1973, 1979). They resembled natural plant communities in their response to disturbance and fertilization. The results achieved during this study support Tilman's resource model (1982) as well as Connell's (1978) intermediate disturbance hypothesis.

Four important ecological processes seem involved in regulating the structure of experimental plant micro-communities emerging from soil seed banks.

First, the competitive exclusion process triggered by soil fertility resulted in low species richness for plant micro-communities from sites/treatments with high soil fertility. Second, disturbances reduced the vigor of dominant species, counteracted the competitive exclusion process and therefore produced high species richness. Third, disturbances gradually depleted the fertility level through harvested plant litter, and therefore, resulted in significant among-harvest differences in species richness, above-ground biomass and species composition. Finally, disturbances played a detrimental role in maintaining the intermediate biomass levels and displaying unimodal curves for the relationship between species richness and biomass.

Implication for the conservation of natural plant communities:

Although the focus of this study was to test different ecological models, the results have implications for the conservation of biodiversity in natural plant communities. I found many plant species emerging from soil seed banks collected from different sites, during the two greenhouse experiments. This regenerative ability of soil seed banks may prove helpful in the conservation of natural plant communities. I also observed that disturbances removed biomass accumulations of experimental plant micro-communities very effectivly and resulted in high species richness. In natural plant communities, disturbance can be employed to increase species richness by reducing the negative influences of dominant species. Plant micro-communities emerging from soil seed banks may prove a promising tool for testing different ecological models before their generalization and implementation in natural plant communities.

References

Al-Mufti, M. M., Syeds, C. L., Furness, C. L., Grime, J. P., & Band, S. R. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *J. Ecol.* 65: 759-791.

Anderson, A. N. 1992. Regulation of "momentary" diversity by dominant species in exceptionally rich ant communities in the Australian seasonal tropics. *Am. Nat.* 140:401-420.

Armesto, J. J. & Pickett, S. T. A. 1985. Experimental disturbance in Old-field plant communities: impact on species richness and abundance. *Ecology* 66:230-240.

Bakker, J. P. 1987. Grazing as a management tool in the restoration of species rich grasslands. Proceedings of the Koniklijke van Watenschappen Series C., 90: 404-429.

Beatty, S. W. 1991. Colonization dynamics in a mosaic landscape: the buried seed pool. *J. Biogeog.* 18:553-563.

Belcher, J. W., Keddy, P. A. & Catling, P. M. 1992. Alvar vegetation in Canada: a multivariate description at two scales. *Can. J. Bot.* 70: 1279-1291.

Bobbink, R. 1991. Effects of nutrient enrichment in Dutch grasslands. *J. Appl. Ecol.* 28: 28-41.

Bobbink, R. & Willems, J. H. 1993. Restoration management of abandoned chalk grasslands in the Netherlands. *Biodiv. & Conserv.* 2: 616-626.

Bock, C. E. & Bock, J. H. 1993. Cover of perennial grasses in southeastern Arizona in relation to livestock grazing. *Conserv. Biol.* 7: 371-377.

Brown, J. H. 1972. Species diversity of seed eating desert rodents in sand dune habitats. *Ecology* 54: 775-784.

Carson, W. P. & Barrett, G. W. 1988. Succession in old-field communities: effects of contrasting types of nutrient enrichment. *Ecology* 69: 984-994.

Coffin, D. P. & Lauenroth, W. K. 1994. Successional dynamics of a semiarid grassland: effects of soil texture and disturbance size. *Vegetatio* 110: 67-82.

Collins, S. L. 1987. Interaction of disturbance in tallgrass prairie: a field experiment. *Ecology* 68: 1243-1250.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.

Day, R. T., Keddy, P. A.; McNeil, J. & Carleton, T. 1988. Fertility and disturbance gradients: a summary model for riverine marsh vegetation. *Ecology* 69: 1044-1054.

Dean, W. R. J., Milton, S. J. Ryan, P. G. & Moloney, C. L. 1994. The role of disturbance in the establishment of indigenous and alien plants at Inaccessible and Nightingale Islands in the South Atlantic Ocean. *Vegetatio* 113: 13-23.

Dessaint, F., Chadoeuf, R. & Barralis, G. P. 1991. Spatial analysis of weed seeds in the cultivated soil seed bank. *J. Appl. Ecol.* 28: 721-730.

Ellison, A. M. & Farnsworth, E. J. 1993. Seedling survivorship growth, and response to disturbance in Belizean mangal. *Am. J. Bot.* 80: 1137-1145.

Glenn, S. M. & Collins, S. L. 1992. Effects of scale and disturbance on rates of immigration and extinction of species in prairies. *Oikos* 63: 273-280.

Glenn, S. M. & Collins, S. L. 1993. Experimental analysis of patch dynamics in tallgrass prairie plant communities. *J. Veg. Sci.* 4: 157-162.

Grabherr, G., Gottfried, M. & Pauli, H. 1994. Climate effects on mountain plants. *Nature* 369: 448.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344-347.

Grime, J. P. 1979. *Plant strategies and vegetation process.* Chichester, England: Wiley.

Hannah, L., Lohse, D., Hutchinson, C., Carr, J. L. & Lankerani, A. 1994. A preliminary inventory of human disturbance of world ecosystems. *Ambio* 23: 246-250.

Jones, R. H., Sharitz, R. R., Dixon, P. M., Segal, D. S. & Schneider, R. L. 1994. Woody plant regeneration in four flood-plain forests. *Ecol. Monog.* 63: 345-367.

Klinkhamer, P. G. L. & De Jong, T. J. 1985. Shoot biomass and species richness in relation to some environmental factors in a coastal dune area in the Netherlands. *Vegetatio* 63: 129-32.

Kutiel, P & Danin, A. 1987. Annual species diversity and above ground phytomass in relation to some soil properties in the sand dunes of the northern Sharon Plains, Israel. *Vegetatio* 70: 45-49.

Milchunas, D. G., Lauenroth, W. K., Chapman, P. L. & Kazempour, M. K. 1993. Community attributes along a perturbation gradient in a shortgrass steppe. *J. Veg. Sci.* 1: 375-384.

Moore, D. R. J. & Keddy, P. A. 1989. The relationship between species richness and standing crop in woodlands: the importance of the scale. *Vegetatio* 79: 90-106.

Ohtsuka, T. & Ohsawa, M. 1994. Accumulation of buried seeds and establishment of ruderal therophytic communities in disturbed habitat, central Japan. *Vegetatio* 110: 83-96.

Olff, H. & Bakker, J. P. 1991. Long term dynamics of standing crop and species composition after the cessation of fertilizer application to mown grassland. *J. Appl. Ecol.* 28: 1040-52.

Olff, H., Huisman, J. & Van Tooren, B. F. 1993. Species dynamics and nutrient accumulation during primary succession in coastal sand dunes. *J. Ecol.* 81: 693-706.

Olff, H., Pegtel, D. M., van Groenendael, J. M. & Bakker, J. B. 1994. Germination strategies during grassland succession. *J. Ecol.* 82: 69-77.

Oomes, M. J. M., 1992. Yield and species density of grassland during restoration management. *J. Veg.* Sci. 3: 271-4.

Peet, P. K.; Glenn-Lewin, D. C. & Wolf, J. W. 1983. Prediction of man's impact on plant species diversity, A challenge for vegetation science. in. Holzner,W., Werger, M. J. A. & Ikusima, I. (eds.) *Man's impact on vegetation.* pp. 41-54. Junk, The Hague.

Pyšek, P. 1994. Patterns of species dominance and factors affecting community composition in areas deforested due to air pollution. *Vegetatio* 112: 45-56.

Root, T. L. & Schneider, S. H. 1993. Can large scale climatic models be linked with multiscale ecological studies ? *Conserv. Biol.* 7: 256-270.

Silvertown, J. 1980. The dynamics of a grassland ecosystem: botanical equilibrium in the Park Grass Experiment. *J. Appl. Ecol.* 17: 491-504.

Specht, R. L. Groundy, R. I. & Specht, A. 1990. Species richness of plant communities: relationship with community growth and structure. *Isr. J. Bot.* 39: 465-480

Ter Heerdt, G. N. J., Bakker, J. P. & De Leeuw J. 1991. Seasonal and spatial variation in living and dead plant material in a grassland as related to plant species diversity. *J. Appl. Ecol.* 28: 120-127.

Tilman, D. 1982. *Resource competition and community structure.* Princeton University Press, Princeton.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along an experimental nitrogen gradient. *Ecol. Monog.* 57: 189-214.

Tilman, D. 1993. Species richness of experimental productivity gradients: How important is colonization limitation ?. *Ecology* 74: 2179-2191.

Turner II, B. L., Meyer, W. B. & D. L. Skole. 1994. Global land-use/land-cover change: towards an integrated study. *Ambio* 23: 91-95.

Unger, I. A. & Woodal, S. R. J. 1993. The relationship between the seed bank and species composition of plant communities in two British salt marshes. *J. Veg. Sci.* 4: 531-536.

Vermeer, J. G. & Berendse, F. 1983. The relationship between nutrient availability , shoot biomass and species richness in grassland and wetland communities. *Vegetatio* 53: 121-126.

Warr, S. J.; Thompson, K. & Kent, M. 1993. Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. *Prog. Physiol. Geog.* 17: 329-347.

Wheeler, B. D. 1988. Species richness, species rarity and conservation evaluation of rich fen vegetation in lowland England and Wales. *J. Appl. Ecol.* 25: 331-353.

Wheeler, B. D. & Giller, K. E. 1982. Species richness of herbaceous fen vegetation in Broadland, Norfolk in relation to the quantity of above ground plant material. *J. Ecol.* 70: 179-200.

Willems, J. H. 1983. species composition and above ground phytomass in chalk grassland with different management. *Vegetatio* 52: 171-80.

Wilson, S. D. & Shay, J. M. 1990. Competition, fire and nutrients in mixed grass prairie. *Ecology* 71: 1959-1967.

Wilson, S. D. & Tilman, D. 1991. Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community. *Oecologia* 88: 61-71.

Wisheu, I. C. & Keddy, P. A. 1989. Species richness- standing crop relationships along four lakeshore gradients: constraints on the general model. *Can. J. Bot.* 67: 1609-1617.

Yemm, E. W. & Willis, A. J. 1962. The effects of meleic hydrazide and 2, 4-dichlophenoxyacetic acid on roadside vegetation. *Weed Res.* 2: 24-40.

Young, K. R.; Ewel, J. J. & Brown, B. J. 1987. Seed dynamics using forest succession in Costa Rica. *Vegetatio* 71: 157-173.

Zammit, C. & Zedler, P. H. 1994. Organization of the soil seed bank in mixed chaparral. *Vegetatio* 111: 1-16.

APPENDIX 1

List of taxa emerging from soil seed banks collected from different sites in the Nature Conservancy's Tallgrass Prairie Preserve, near Pawhuska, Osage County, Oklahoma. Letters following the species name and authority are the sites and treatments in which a species occurred: In experiment 1, F = Forest site, M = Mixed soil seed banks, O = Old-field site, P = Prairie site, R = Roadside site. In experiment 2, F&D = Fertilized & Disturbed, F&ND = Fertilized & Not Disturbed, NF&D = Not Fertilized & Disturbed, NF&ND = Not Fertilized & Not Disturbed.

APIACEAE

Chaerophylum procumbens (L.) Crantz. - F, P, R, NF&ND

ASTERACEAE

Ambrosia psilostachya DC. - F, F&D, NF&D

Ambrosia trifida L. - F, M, O, R, F&D, F&ND, NF&D, NF&ND

Aster simplex Willd. - NF&D

Cirsium sp. - F, O, P

Cirsium undulatum (Nutt.) Sreng. - NF&ND

Elephantopus carolinianus Raeusch - M

Erigeron sp. - M, O, R

Erigeron strigosus Muhl. ex Willd. - M, O, P, F&D, F&ND, NF&D, NF&ND

Eupatorium rugosum Houtt. - F, M, P, R, F&D, F&ND, NF&D

Hieracium gronovii L. - O, P

Taraxacum officinale Weber. - R

CARYOPHYLLACEAE

Stellaria media (L.) Syr. - F, M, O, P, R

COMMELINACEAE

Commelina erecta L. - F&D

CYPERACEAE

Cyperus acuminatus Torr. & Hook. - P, F&D, F&ND, NF&D, NF&ND

Cyperus filiculmis Vahl. - F, P, F&ND, NF&D

Cyperus ovularis (Michx.) Torr. - M, P, F&D, F&ND, NF&D, NF&ND

Cyperus strigosus Torr. & Hook. - F, M, P

Cyperus sp. - F, O, P, R

EUPHORBIACEAE

Acalypha virgniana L. - F, P, O, F&D, F&ND, NF&D, NF&ND

Croton capitatus Michx. - O, P, F&D, NF&D, NF&ND

Croton monanthogynos Michx. - M, O, R

Euphorbia dentata Michx. - NF&ND

Euphorbia nutans Lag. - F, M, O, P, R, F&D, F&ND, NF&D, NF&ND

Euphorbia stictospora Engelm. - F, M, O, P, R, F&D, F&ND, NF&D, NF&ND

Euphorbia supina Raf. - F&D, F&ND, NF&D

FABACEAE

Melilotus officinalis (L.) Pall. - F, M, O, P, R, F&D, NF&D

Strophostyles helvola (L.) Ell. - NF&D

Strophostyles leiosperma (T. & G.) Piper. - P, F&D, F&ND, NF&D, NF&ND

Trifolium campestre Schreb. - M, O, P, R, F&D, F&ND, NF&D, NF&ND

Trifolium repens L. - P, F&D, NF&ND

Vicia villosa Roth.-F

LYTHRACEAE

Ammania coccinea Rottb. - O, P

MALVACEAE

Sida spinosa L. - M, O, P, F&D, F&ND, NF&D, NF&ND

MOLLUGINACEAE

Mollugo verticillata L. - F, M, O, P, R, F&D, F&ND, NF&D, NF&ND

ONAGRACEAE

Oenothera biennis L. - F, M, O, P, R, F&D, F&ND, NF&D, NF&ND

Oenothera laciniata Hill. - F, M, O, P, F&D, F&ND, NF&ND

OXALIDACEAE

Oxalis corniculata L. - F, M, O, P, R, F&ND

PHYTOLACCACEAE

Phytolacca americana L. - F, F&ND, NF&ND, NF&ND

PLANTAGINACEAE

Plantago major L. - NF&D

Plantago virginica L. - F, M, P, R

POACEAE

Bothrichloa saccharoides (Sw.) Rydb. - M, O, F&ND

Bromus japonicus Thunb. ex Murr. - F, M, O, P, R

Cenchrus pauciflorus Benth. - F&D, F&ND

Chloris verticillata Nutt. - F, M, O, F&D, F&ND, NF&D, NF&ND

Cynodon dactylon (L.) Pers. - F&ND

Dichanthelium acuminatum (Sw.) Gould & Clark. - F, M, O, P, R, F&D, F&ND, NF&D, NF&ND

Digitaria sanguinalis (L.) Scop. - F, M, O, F&D, F&ND, NF&D, NF&ND

Eleusine indica (L.) Gaertn. - M, O, P, R, F&D, F&ND, NF&D, NF&ND

Eragrostis cilianensis (All.) E. Mosher - M, O, P, R, F&D, NF&D, NF&ND

Eragrostis hirsuta (Michx.) Nees. - M, P, R, F&D, F&ND, NF&D, NF&ND

Eragrostis intermedia Hitchc. - R, F&D, F&ND, NF&D, NF&ND

Eragrostis pilosa (L.) Beauv. - F&ND

Eragrostis spectabilis (Pursh) Steud. - M, P, F&D, F&ND, NF&D, NF&ND

Muhlenbergia schreberi J. F. Gmel. - F, M, O, P, R, F&D, F&ND, NF&D, NF&ND

Sporobolus asper (Michx.) Kunth. - M, P, F&ND, NF&D, NF&ND

Panicum anceps Michx. - M, P, R, F&D, F&ND, NF&D, NF&ND

Panicum capillare L. - F&D, F&ND, NF&D, NF&ND

Panicum dichotomiflorum Michx. - R, F&D, F&ND, NF&D, NF&ND

Paspalum setaceum Michx. - F, M, O, P, R, F&D, F&ND, NF&D, NF&ND

Setaria glauca (L.) Beauv. - F, M, O, P, R, F&D, F&ND, NF&D, NF&ND

Tridens flavus (L.) Hitchc. - M, R, F&D, F&ND, NF&D, NF&ND

POLYGONACEAE

Polygonum ramosissimum Michx. - F, NF&D

Rumex crispus L. - F, M, O, P, R, F&D, F&ND, NF&D, NF&ND

SCROPHULARIACEAE

Leucospora multifida (Michx.) Nutt. - F, M, F&D, F&ND, NF&D, NF&ND

SOLANACEAE

Physalis longifolia Nutt. - F, F&D, F&ND

Physalis virginiana P. Mill. - F&D, NF&D, NF&ND

Solanum carolinense L. - F,M, F&D, F&ND, NF&D, NF&ND

Solanum nigrum L. - F, M, O, R, F&D, F&ND, NF&D, NF&ND

Solanum rostratum Dun. - F, M, O, R, F&D, F&ND, NF&D, NF&ND

VERBENACEAE

Verbena bracteata Lag. & Rodr. - P, R, NF&ND

Verbena canadensis (L.) Britt. - F&D, NF&D

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