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Diversity, productivity, and stability in perennial polycultures used for grain, forage, and biomass production

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**Diversity, productivity, and stability in perennial polycultures
used for grain, forage, and biomass production**

by

Valentín Daniel Picasso Risso

A dissertation submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Sustainable Agriculture

Program of Study Committee:
E. Charles Brummer, Co-major Professor
Matt Liebman, Co-major Professor
Philip Dixon
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To Lucia,

Mati and Santi,

and all the children of this planet.

Ad Maiorem Dei Gloriam

Om Mani Padme Hum

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ABSTRACT

The objective of this dissertation was to determine to what extent plant species diversity affects biomass and seed productivity, weed invasion, and stability in perennial herbaceous polycultures across three years, two harvest management regimes, and two locations in central Iowa, USA. Average biomass productivity consistently increased in polycultures with increasing species richness across all environment-years. In most situations, polycultures were more productive than the average of monocultures, but not more productive than the best adapted species in monoculture for each environment. Polyculture overyielding was due to complementarity among species in the community rather than to selection effects of individual species at all richness levels across environments and was likely explained by legume-grass facilitation. Polycultures with high richness had lower variability in yield (i.e., greater stability) than the highest yielding monocultures. Seeds of two perennial grain species were harvested; intermediate wheatgrass produced up to 65.8 ± 6.5 g m^{-2} of seed and Illinois bundleflower up to 55.0 ± 8.1 g m^{-2}. Plant breeding and better agronomic management are needed to increase these yields in the near future to be practical for production situations. The mixture comprising both perennial grains produced as much seed as the best yielding monoculture each year. Polycultures of Illinois bundleflower with C4 grasses and polycultures of intermediate wheatgrass with legumes produced as much seed as the monocultures. Weed biomass decreased exponentially with seeded species richness in all environments. Most polycultures exerted greater weed suppression than perennial grain monocultures but also they had reduced seed yields. Breeding and management of crop mixtures to optimize the trade-off between seed yield and weed suppression is a central challenge for the development of perennial polyculture systems. The dialogue between Ecology and Agriculture provides a basis for designing sustainable production systems.

RESUMEN (ABSTRACT IN SPANISH)

El objetivo de esta tesis doctoral fue determinar el efecto de la diversidad de especies de plantas en la productividad de biomasa total y semilla, la invasión de malezas, y la estabilidad de la producción en policultivos herbáceos perennes durante tres años, dos sistemas de manejo, y dos localidades en Iowa, Estados Unidos. La productividad promedio de biomasa se incrementó consistentemente en policultivos con mayor riqueza de especies en todos los años y ambientes. En la mayoría de los casos, los policultivos fueron más productivos que el promedio de los monocultivos, pero no más productivos que el monocultivo de la especie más adaptada a cada ambiente. La ventaja en rendimiento de los policultivos fue causada por la complementariedad entre las especies de la comunidad y no por efectos de selección de especies individuales para todos los niveles de riqueza de especies en todos los ambientes, y fue probablemente explicada por facilitación entre leguminosas y gramíneas. Los policultivos con mayor riqueza de especies tuvieron menor variabilidad en rendimiento (mayor estabilidad de producción) que los monocultivos de mayor rendimiento. Se cosechó semilla de dos especies perennes para grano; *Thinopyron intermedium* produjo hasta 65.8 ± 6.5 g m^{-2} de semilla y *Desmanthus illinoensis* hasta 55.0 ± 8.1 g m^{-2}. Si bien estos rendimientos no son viables para la producción comercial, a través del mejoramiento genético y la utilización de mejores prácticas agronómicas, se pueden incrementar estos rendimientos en el corto plazo. La producción de semilla de la mezcla de ambas especies no fue diferente del monocultivo más productivo cada año. Algunos policultivos (*D. illinoensis* con gramíneas C4 y *T. intermedium* con leguminosas) produjeron tanta semilla como los monocultivos respectivos. La biomasa de malezas se redujo exponencialmente al incrementar la riqueza sembrada de especies en todos los ambientes. La mayoría de los policultivos suprimieron más a las malezas que los monocultivos, pero tuvieron menor rendimiento de semilla. Mejoramiento genético e investigación en manejo agronómico de mezclas de especies que optimicen el compromiso entre producción de semilla y supresión de malezas es un desafío central para el diseño de sistemas de policultivos perennes. El diálogo entre Ecología y Agricultura es la base para desarrollar sistemas de producción sustentables.

CHAPTER I. INTRODUCTION

These are challenging times for humanity: climate change, wars, hunger and obesity epidemics, biodiversity loss, pollution and coastal dead zones, prospects of an energy crisis, poverty in rural and urban communities… These are exciting times for creative alternatives in the field of agriculture, when the passion for working towards sustainability is combined with the systematic method of scientific inquiry. A central challenge to scholars and practitioners of sustainable agriculture is to acknowledge the scientific and technological paradigms in which our work is embedded, which provide both foundations and limitations to our work. This dissertation follows a holistic scientific paradigm, which considers ecosystems as wholes with properties not reducible to the sum of their component parts. It is immersed in the Sustainable Agriculture tradition which seeks food systems at the same time socially fair, environmentally friendly, and economically viable. Also it is inspired by a technological paradigm in agriculture that seeks to mimic the structure of natural ecosystems to develop agroecosystems that run on sunlight and minimal external inputs, minimize ecological degradation, are efficient, stable, and support vibrant rural communities, i.e., Natural Systems Agriculture (Jackson, 1985). As such, it seeks to solve the 10,000 years old problem of agriculture based on annual crop monocultures by investigating the potential of diverse perennial polycultures as a more sustainable alternative production system.

Agro-biodiversity has many dimensions: temporal, spatial (at field, farm, and landscape scales), species, and genotypes, among others. Agro-biodiversity has been proposed as a key feature of sustainable agroecosystems. In Ecology, the role of biodiversity in various ecosystem functions has been a fertile field of research in the recent years. This dissertation draws insight from ecological and agroecological literature, applying it to perennial herbaceous polycultures. The objective of this dissertation is to determine to what extent plant species diversity affects biomass and seed productivity, weed invasion, and stability in perennial herbaceous polyculture communities across years, management regimes, and environments in central Iowa, USA.

The role of diversity in productivity and stability of ecosystems has been subject of an intense debate. I introduce the history of this debate in Chapter II of this dissertation,

providing an overview of the early diversity-stability debate in ecology, the biodiversity-ecosystem functioning debate, and some implications for the dialogue between Ecology and Agriculture.

In the following three chapters I report results from an extensive well replicated field experiment conducted over 4 years at two locations in central Iowa, USA, in which plots varying in perennial herbaceous plant species and in monocultures and polycultures were measured for biomass productivity, seed yield, and weed invasion.

In Chapter III we test the hypotheses that during the first two years of the experiment: 1) crop biomass productivity increases with increasing species richness; 2) weed biomass is reduced with increasing species richness; 3) the presence or absence of certain species changes the slope of the regression of biomass production on species richness; and 4) harvest management changes the slope of the regression of biomass production on species richness.

In Chapter IV, we test three hypotheses: 1) that the observed relationship between richness and biomass productivity is due to complementarity among species and not to a selection effect; 2) that the richness—productivity relationship remains the same across two harvest management regimes at each of two locations across three years; and 3) that diverse polycultures are more stable across environments than monocultures.

In Chapter V, we consider a subset of the experiment to explore issues of perennial forage and seed production and competitive ability of two dual purpose perennial crops (Illinois bundleflower and intermediate wheatgrass), testing four hypotheses: 1) the binary mixture of bundleflower and wheatgrass outperforms the constituent monocultures in terms of seed, forage, and protein yields and competitive ability with weeds; 2) companion species from different functional groups enhance production of the mixture compared to companion species from the same functional group; (3) bundleflower and wheatgrass exhibit good competitive ability in polycultures with other perennial companions by producing as much or more seed and forage than expected based on their proportion in the mixture; and 4) perennial polycultures including highly competitive companion species increase weed suppression without reducing yield compared to monocultures.

Finally, Chapter VI summarizes the main conclusions of the dissertation and suggests some future research questions to pursue.

CHAPTER II. HISTORY AND PHILOSOPHY OF THE BIODIVERSITY–ECOSYSTEM FUNCTIONING DEBATE IN ECOLOGY

A modified version of this paper will be submitted as a chapter in

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Valentin Picasso[1] and Kevin de Laplante[2]

INTRODUCTION

Population/community ecology and ecosystem ecology present very different perspectives on ecological phenomena. Over the course of the history of ecology there has been relatively little interaction between the two fields at a theoretical level, despite general acknowledgment that many ecosystem processes are both influenced by and constrain population- and community-level phenomena. However, recent years have seen a growing interest in theoretical models and experimental studies aimed at investigating the relationship between biological diversity and higher-level community and ecosystem properties, such as invasibility and productivity. This research on biodiversity and ecosystem functioning has spawned a large and growing literature that holds great promise for productive engagement between community ecology and ecosystem ecology. Indeed, the synthetic viewpoints developing out of this research may represent a genuine "paradigm shift" in ecology (Naeem, 2002).

However, this research has also generated heated debate among ecologists over experimental methodology and interpretation of research results. The debate burst into the public sphere in 2000 when a group of critics of the biodiversity-ecosystem functioning experiments accused proponents of misrepresenting the scientific debate to the public for political purposes. One media source described it as a "full war among ecologists" (Kaiser, 2000). Recent writings have been more conciliatory in tone, but this incident points to a

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broader socio-political context that has played an important role in both motivating and enabling research on biodiversity-ecosystem functioning relationships: the context of conservation science and environmental policy. A comprehensive overview of this debate needs to take account of this socio-political context.

Young ecologists are often unaware of the intellectual history of their field, or the relevance of this history for understanding the scientific and socio-political environment within which their work is situated. The primary aim of this paper is to provide an historical and conceptual overview of the biodiversity-ecosystem functioning debate that will help to illuminate research that is currently being conducted in this field. The paper also serves as an overview of the relevant philosophical literature on foundational concepts in ecology, and consequently may be of interest to historians and philosophers of ecology.

The biodiversity-ecosystem functioning debate is best viewed against the background of the diversity-stability debate in ecology, which we introduce first in this paper. Because the concepts of "biodiversity" and "function" are themselves subjects of considerable debate in ecology and philosophy of ecology we then critically assess the status of these concepts as they are used in ecology generally and in the biodiversity-ecosystem functioning literature in particular. Next we provide a historical account of the biodiversity-ecosystem functioning debate focusing in the development of the research program, the critical response, the public "war among ecologists" and the synthesis framework that arose in 2000. A brief review of the research during recent years concludes the historical account. Finally, we discuss some interpretations of this debate focusing on the connections to environmental policy, philosophy of ecology, and agriculture.

BACKGROUND: THE DIVERSITY-STABILITY DEBATE

The long-standing debate in ecology over the relationship between the diversity and stability of ecological systems is commonly divided in three historical periods. Each period is characterized by a particular theoretical and empirical perspective on diversity-stability relationships, with the third period identified with a shift toward what we now call biodiversity-ecosystem functioning relationships (Ives, 2005; McCann, 2005).

The history of the diversity-stability debate has important lessons for contemporary research on biodiversity-ecosystem functioning. Central among these lessons is the

importance of distinguishing between (a) genuinely competing ecological hypotheses that share the same operational definitions of diversity and stability, and (b) different ecological hypotheses that employ different definitions of diversity and stability, and that hence may not be in genuine conflict.

The 1950s and 1960s

The view that diversity is positively correlated with stability was endorsed by a number of prominent ecologists in the 1950s and 1960s, including Eugene Odum, Robert MacArthur, and Charles Elton.

Odum (1953) related the notions of diversity and stability to the flow of energy through the trophic links in an ecological network. A system with greater redundancy in energetic pathways will be more stable than one with lesser redundancy. For Odum, diversity is interpreted as diversity of network connections, and stability as stability of energetic throughput and organizational structure – the more stable system is the one that suffers the least change in energy flow with the removal of a random species. However, these ecosystem concepts have a rough correspondence to population and community concepts via the identification of network nodes with species populations and network connections with trophic links.

MacArthur (1955) follows Odum in understanding stability as a measure of "the amount of choice which the energy has in following the paths up through the food web". He sketched a series of food webs and described the ramifications of energy partitioning for stability using information theory. Formally, MacArthur's notion of stability is a measure of the response of a community to a perturbation that influences the density of at least one of the species. MacArthur gives a semi-formal argument that recapitulates Odum's conclusion – in general, more diverse communities will be more stable than less diverse communities.

Elton's (1958) arguments draw on a wider range of theoretical and empirical evidence, but he agrees that diversity and stability are positively correlated. Elton noted that both simple Lotka-Volterra models and simple laboratory microcosms suffered from instability, and argued that simpler food webs are more vulnerable to invaders. Elton's definitions of stability vacillate within his discussion, but they reflect his general interest in dynamic instabilities that drive destructive oscillations and population explosions in food webs.

Elton's work on stability was based on plant species invasions and plant diseases in ecosystems, and therefore he is cited as the father of the diversity-invasibility hypothesis: species rich communities are more resistant to invasions by exotic species, because there are fewer resources available for new species in diverse communities. The diversity-invasibility debate would become one important dimension of the biodiversity-ecosystem functioning debate, because of the concerns with invasive species in natural ecosystems and weeds in agroecosystems.

To sum up, the broad consensus during this period was that stability of ecological systems is positively correlated with diversity, and indeed that diversity is a causal factor in generating stability.

The 1970s and 1980s

This consensus did not survive the next two decades. By the end of the 1980s the general consensus was that diversity is not, in general, positively correlated with stability. How did this shift in attitudes come about?

In the early 1970s mathematical ecologists began to systematically study diversity-stability relationships in model communities (Gardner and Ashby, 1970; May, 1973; Pimm, 1980). The conclusion of these studies undermined the conventional wisdom about diversity and stability.

The most influential work of this period was Robert May's seminal 1973 book *Stability and Complexity in Model Ecosystems*. May argued that diversity actually begets instability. More specifically, he showed that the chances of a randomly constructed Lotka-Volterra community being stable decreases with both the number of species in the community and the connectance among species, where connectance is measured by the probability that a pair of species interacts.

May's argument employed a very specific definition of stability: it is the probability that the population size of every species in the community would return to equilibrium if there were an arbitrarily small perturbation in the population size(s) of one of the species. It is important to note that this so-called "neighborhood stability" (or "Lyapunov stability") is an all-or-nothing property; for a given perturbation, either every population returns to equilibrium or it doesn't. May presents his results in terms of the probability that a

community, randomly selected from a certain hypothetical population of communities, is neighborhood-stable.

Stuart Pimm (1980) came to a similar conclusion in his influential analysis of stability properties of food webs. However, Pimm's analysis employs a different definition of stability. He questioned the ecological relevance of May's "arbitrarily small perturbations" and chose to model instead the effects of a more significant perturbation, the permanent removal of one of the species in the community. This "species-deletion stability" is defined as follows: it is the probability that the removal of one species will not lead to any further local extinctions. Pimm's analysis showed that, indeed, communities with more species were less "species-deletion stable" than communities with fewer species.

These theoretical results were taken to have broad significance for ecology and lead to a general rejection of the diversity-stability hypothesis among ecologists. The significance of these results can be challenged, however.

Consider, for example, that a negative diversity-stability relationship *is an immediate statistical consequence of the definitions of stability used by both May and Pimm.* If every species population must return to equilibrium after a perturbation (May), or if every species population must survive the permanent deletion of one species (Pimm), then the criteria for stability *necessarily* becomes more and more strict as you add more species to the community. The conclusion is independent of any particular feature of ecological communities; indeed, it can be viewed as an artifact of probability theory.

This fact can be viewed as undermining the empirical significance of the conclusions; the stability definitions that are employed in the analysis turn what ought to be an empirical hypothesis into a probabilistic *tautology* in idealized systems that are unlikely to be realized in nature anyway (Mikkelson, 1997). Moreover, it can be argued that these strict, population-level concepts of stability don't faithfully capture the original notions of stability expressed in the writings of Odum, MacArthur and Elton, which more often referred to functional properties of whole communities or ecosystems.

It is this intuition – that a proper test of the diversity-stability hypothesis should focus on functional properties of communities and ecosystems – that motivates more recent work on diversity-stability relations.

The 1990s

The 1990s saw a revival of the diversity-stability hypothesis in experimental studies that indicated a positive relationship between diversity and the stability of various functionally defined properties of communities and ecosystems. The leading figure in this revival was David Tilman (Tilman and Downing, 1994; Tilman et al., 1996), though many researchers have since contributed to research in this field.

The general conclusion of these more recent studies is that increasing species diversity may well decrease the stability of individual plant populations, but it may simultaneously *increase* the stability of higher-level community and ecosystem properties. This is because the increased fluctuations in population size induced by increased diversity aren't in phase across all populations – while some populations are decreasing, others may be increasing. Within a more diverse community there is a greater chance that downward fluctuations will be balanced by upward swings elsewhere in the community, resulting in greater stability of community and ecosystem properties that are averaged over individual population sizes.

These studies typically employ one of two measures of stability*: resistance to invasion* by new species, or *temporal stability* of an ecosystem property like biomass or productivity. Here, "temporal stability" is the mean value of a variable divided by its standard deviation, both calculated over time; it is a measure of the degree of variability of a property over time. These concepts of stability self-consciously reflect the concerns with resistance to invasion and temporal variability that dominated pre-1970s thinking about diversity-stability relationships. Note that this shift in stability measures inspired a corresponding shift in terminology, from talking about the stability of *population sizes* to the stability of *ecosystem functions*.

Another feature of the recent literature on diversity-stability relations is a recognition that "diversity" itself has many possible measures other than species richness. There is considerable interest, for example, in studying relationships between the *functional diversity* of a community and the stability of ecosystem functions (see section 3.1.2). Consequently, recent work has moved toward a broader investigation of relationships between different measures of *biodiversity* and the stability properties of *ecosystem functions*. Thus we arrive at the contemporary biodiversity-ecosystem functioning studies.

Diversity-stability relationships and environmental policy

Diversity-stability hypotheses do have implications for environmental policy, and this fact may be relevant in evaluating how ecologists interpret and report research findings. Consider, for example, (1) increasing concern over loss of biodiversity induced by environmental deterioration and loss of habitat, and (2) the growing perception that human impacts on the biosphere may significantly alter the behavior of ecosystems and threaten vital ecosystem services. Diversity-stability hypotheses are relevant to environmentalist arguments in both areas of concern by linking issues in one area to issues in the other. If you believe that certain types or levels of biological diversity are necessary to maintain the stability of ecosystems and correlated ecosystem services, then you can easily develop an argument for placing a high instrumental value on biodiversity, and thereby motivate environmental policies that promote the conservation and restoration of biodiversity.

This observation highlights an important fact: ecological research on diversity-stability relationships is conducted in a socio-political environment that favors certain outcomes over others. People who endorse environmental protection policies often look to ecology for scientific support for their agendas. Indeed, ecologists themselves may be motivated for similar reasons to look for evidence that supports a positive diversity-stability relationship.

In the 1970s and 1980s the majority view among ecologists was broadly skeptical of diversity-stability hypotheses. It was easy to regard ecologists who continued to defend a positive relationship between diversity and stability in light of the evidence mounting against it as either stuck in an outmoded paradigm, engaged in wishful thinking, or overly beholden to environmentalist interests.

In the 1990s it once again became scientifically respectable to defend diversity-stability hypotheses, but many ecologists remained wary of the influence of environmental advocacy on the interpretation and presentation of scientific results. As will be shown in greater detail later, these concerns came to a head in 1999 when critics complained that an Ecological Society of American *Bulletin* presented a biased and politically motivated account of the biodiversity-ecosystem functioning research results.

Diversity-stability relationships and the holism-reductionism debate in ecology

The study of diversity-stability relationships also takes place in a context framed by the historical schism in ecology between holistic and reductionistic research traditions and worldviews. A belief in a positive diversity-stability relationship is commonly associated with some kind of commitment to holism, while skepticism is more commonly associated with reductionism. Thus, in addition to biases arising from environmental policy considerations as outlined above, we must also consider biases arising from philosophical predispositions toward holism or reductionism in ecology.

These claims require some elaboration. In ecology, holistic and reductionistic theses come in several varieties, but they can generally be divided *ontological* or *epistemological*. Ontology pertains to the nature of reality, of what exists. Epistemology pertains to knowledge and the justification of beliefs about the world (in a scientific context, issues concerning scientific methodology fall into this category). For example, ecologists may differ on the ontological constitution of communities and ecosystems (e.g. whether they have "emergent causal properties" at the community and ecosystem level), and they may differ on the best way to represent and analyze ecological systems in ecological theories (e.g. whether community- and ecosystem-level phenomena can be exhaustively explained in terms of the behaviors of their component parts). The latter is an epistemological issue, the former an ontological issue.

There are several reasons why a belief in a positive diversity-stability relationship is commonly associated with holism:

(1) There is an historical association between diversity-stability theses and traditional notions of the "balance of nature", the view that ecological systems are naturally driven toward an equilibrium state in which community composition persists and population sizes are (roughly) stable. In its original formulation with the Greeks, the balance of nature was explained in terms of teleological principles governing nature as a whole. In the Medieval period the common explanation was divine providence. In the modern period the favored explanations have referred either to density-dependent regulation or the stabilizing effects of network redundancy (as articulated, for example, in the arguments of Odum, MacArthur, and Elton). Whether these modern explanations are properly described as "holistic" depends

largely on how one defines the term, but the point is that the diversity-stability hypothesis has an historical association with worldviews that are widely regarded as holistic.

(2) We noted that the diversity-stability hypothesis fell out of favor in the 1970s and 1980s in the wake of theoretical studies that seemed to undermine any positive relationship between diversity and stability. It is notable that this period also saw the rise to prominence of a new "non-equilibrium" paradigm in ecology that rejected the balance of nature hypothesis outright (Botkin, 1990). This paradigm reconceptualized the default state of nature as one of constant flux and change, and its proponents were often motivated to label the paradigm as reductionistic to contrast it with the holism associated with equilibrium views of nature (Simberloff, 1980). Proponents of the non-equilibrium paradigm were also inclined to associate the rejection of the diversity-stability hypothesis with the broader move toward reductionism during this time period.

These developments were, and continue to be, significant for research aimed at reviving the diversity-stability hypothesis. The fact is that within mainstream academic ecology – particularly plant ecology – there is a general bias toward reductionistic and away from holistic hypotheses and methods. The default view is to be skeptical of holistic hypotheses. Insofar as a positive diversity-stability relationship is associated with ecological holism one can expect it to face the same default skepticism.

As contemporary research on biodiversity-ecosystem functioning relationships continues to mature these default attitudes may slowly be changing, but among plant ecologists who continue to strongly identify with reductionism (e.g. neo-Gleasonian views on plant dynamics) one is likely to encounter resistance to any diversity-stability hypothesis that are perceived as appealing to holistic mechanisms or properties to account for experimental results.

BIODIVERSITY AND ECOSYSTEM FUNCTIONS: KEY CONCEPTS

One of the lessons learned from earlier studies of diversity-stability relationships is the importance of being clear about the definitions of key theoretical terms and their empirical measures. Biodiversity-ecosystem functioning research is particularly vulnerable to charges that their key concepts, "biodiversity" and "ecosystem function", either are too vague, multi-faceted or value-laden to properly serve the needs of empirical science. In this section we

discuss the various meanings with which these terms are used in the ecological literature, identify some of the conceptual challenges facing the use of these terms in a scientific context, and clarify their usage in the biodiversity-ecosystem functioning literature.

Biodiversity

<u>Biodiversity and Conservation</u>

The concepts of biological and ecological diversity are as old as natural history, but the term "biodiversity" only appeared in the scientific lexicon in the late 1980s, coinciding with the emergence of conservation biology as an applied science aimed at preserving and conserving biological diversity in the facing of a looming biodiversity "crisis" (Soule, 1985).

Attempts to define "biodiversity" as an object of conservation have always been complicated by the fact that, in this context, the *objects* that comprise biodiversity are associated with conservation *values*, i.e. those aspects of the natural environment that we value and wish to preserve for current and future generations (or for their own sake). In principle this may include any biological entity or biological process of interest, a move that runs the risk of making biodiversity co-extensive with all of biology and consequently rendering biodiversity conservation impractical, since everything biological would become a goal of conservation (Sarkar, 2005).

Definitions of biodiversity are also complicated by the fact that objects of biological and ecological interest don't fall under a single hierarchy of nature. One can distinguish at least two distinct hierarchies: (i) a *taxonomic* hierarchy that includes genes and alleles, genotypes, subspecies, species, genera, families, orders, classes, phyla, and kingdoms; and (ii) a *spatial/compositional* hierarchy that includes biological molecules, cell organelles, cells, individuals, populations, meta-populations, communities and ecosystems (communities plus their physical environments), and extending ultimately to the entire biosphere. Complications arise from the fact that biological entities of interest may not fall cleanly into any specific category in either hierarchy (consider fungi, symbionts or asexual species), and at every level of each hierarchy there is significant variation – for example, any two individuals of the same species will differ in genetic profile, and no two communities of the same type will be identical (Sarkar, 2005).

Standard definitions of biodiversity attempt to simplify the problem by focusing on the diversity of entities at three levels of organization – alleles or genes, species, and ecosystems. The presumption is that if you can preserve allelic diversity then you'll likely preserve most of the variation of interest below the level of the individual; if you preserve species diversity then you'll preserve all of the taxonomic entities above the species level; and if you preserve ecosystem diversity then you'll preserve most kinds of communities.

This traditional approach to defining biodiversity has been criticized for being overly focused on conserving biological *entities* – individuals, species, communities, etc. In addition to entities, conservation efforts are also (or should be) aimed at conservation of unique or valuable biological and ecological *phenomena* that don't fit into either the spatial or taxonomic hierarchies. A standard example is seasonal migration patterns, such as the remarkable migration of monarch butterflies in North America from the eastern and western regions of the US and Canada to Mexico and back. This migration pattern would disappear if overwintering sites are destroyed, though the species itself may persist. Conservation of unique biological phenomena isn't guaranteed by conservation of genetic, species, and ecosystem diversity.

Conservation science and the associated literature on biological diversity has also been influenced by the rise to prominence of holistic conservation concepts like "biological integrity", "ecosystem integrity" and "ecosystem health". Here the focus is less on preserving individual species and more on preserving or restoring the biotic and abiotic conditions that allow different community and ecosystem types to persist. On this more holistic view, the targets of biological conservation also include ecosystem properties like network organization, characteristic rates of cycling and throughput of energy and materials, and dynamical properties related to adaptability and resilience.

These and other considerations have lead many writers to suggest that the concept of biodiversity – in the context of conservation science and policy – is necessarily pluralistic and value-laden (Norton, 2001; Sarkar, 2005). There is no single correct measure of biodiversity to be discovered but many, each representing different ways of valuing biotic and abiotic resources.

Biodiversity and ecosystem function experiments

Many of the complicating factors noted above (relating to, for example, the association between biodiversity and conservation values) are fortunately not present in the context of the common forms of biodiversity-ecosystem functioning experiments. In this context we are concerned with determining empirical relationships between biodiversity and various measures of community or ecosystem stability and function. The experimental context requires that all biodiversity concepts be operationally measurable and controllable in such a way that empirically significant conclusions can be drawn. In practice this amounts to a severe restriction on the scope of possible biodiversity measures. Typical experiments focus on one taxonomic group (usually plants, but sometimes microorganisms) and then consider only the species level of biodiversity, leaving the genetic and ecosystem levels out of the discussion. At the species level, various measures of diversity may be used, such as the Shannon-Weiner index which takes into account two components, *richness* (the number of species in an area) and *evenness* (the relative abundance of different species in an area).

Another class of biodiversity-ecosystem functioning studies focuses on relationships between *functional diversity* and ecosystem function. Functional diversity includes diversity of functional traits and groups. Functional *traits* are the characteristics of an organism that are considered relevant to its response to the environment and/or its effects on ecosystem functioning (Diaz and Cabido, 2001). Examples include leaf size, seed size, dispersal mode and canopy structure. A functional *group* or *type* is a set of organisms sharing similar responses to the environment (e.g. temperature, water availability, nutrients) or similar effects on ecosystem functioning (e.g. productivity, nutrient cycling). Like species diversity, common measures of functional diversity include two components: i) *functional richness* (the number of different functional groups or the proportion of a multi-dimensional trait space covered by a particular suite of species) and ii) *functional composition* (presence or absence of certain functional groups or traits). Although functional diversity can apply to an indefinite number of traits, it is commonly measured by measuring the diversity of *functional groups*.

Though biodiversity-ecosystem functioning experiments involving functional diversity are becoming more common, it remains the case that for the majority of biodiversity-ecosystem functioning studies, *the proxy for biodiversity is nothing more than plant species*

richness – the number of plant species in a plot. There are several practical reasons for this simplification: species are easy to identify; plant communities are easy to assemble, manipulate and maintain in pots and fields; and many interactions among plants are well documented in ecology. Also, policy makers tend to prefer single numerical measures over complex multidimensional indices to make decisions about conservation (Purvis and Hector, 2000)

Not surprisingly, this simplification imposes serious limitations on the interpretation of biodiversity-ecosystem functioning studies. Claims about the significance of *biodiversity in general* for ecosystem functioning, or about the applicability of observed biodiversity-ecosystem functioning relationships for *ecological systems in general* (in both experimental and non-experimental contexts) will be extremely tentative at best. This is a potentially serious concern because, as noted in section 2.4, one of the motivations for the biodiversity-ecosystem functioning research program is the perception that this research has policy implications. Indeed, one of the criticisms was that the authors were too hasty in drawing *general conclusions for environmental policy* from the biodiversity-ecosystem functioning literature (Wardle et al., 2000).

Ecosystem function

For some ecologists the term "ecosystem function" is suspect because it carries with it associations of holism and teleology that are perceived to be outdated and unscientific. The term seems to presuppose the existence of ecosystems as integrated entities with emergent properties that can properly be said to fulfill "functions". However: (i) the general trajectory of plant ecology over the past thirty years has been away from strongly holistic conceptions of communities and ecosystems, and (ii) the concept of "function" in ecology is historically associated with Clementsian teleology and group-selection mechanisms of community and ecosystem development, both of which are now widely viewed as empirically falsified and/or inconsistent with neo-Darwinian evolutionary theory.

Defenders of the concept of "ecosystem function" should have something to say in response to objections such as these. In this section we take a closer look at these objections and clarify the meaning of the term "ecosystem function" as it is employed in the biodiversity-ecosystem functioning literature. We will see that, as with the case of

"biodiversity", in the context of biodiversity-ecosystem functioning experiments the operational meaning of the term "ecosystem function" is usually rather tightly circumscribed, and consequently is less problematic than it might otherwise be. Nevertheless, ecologists need to become more aware of the conceptual issues surrounding the use of "function language" in science if they wish to avoid confusion and misreading of their work.

Modern science and the challenge to natural functions

Tools and other artifacts have obvious functions (a carpenter's hammer has the function of hammering nails, a coffee maker has the function of making coffee, etc.), but the function of these artifacts is grounded in the intelligent design of human beings – these objects are built and used for a conscious purpose. But do the objects studied by the natural sciences have functions? Do water molecules, chemical reactions, cells, frogs or lakes have functions? If an object is not the product of conscious intelligent design, can it have a function?

Greek and Medieval natural philosophers believed the answer was "yes": in fact, all natural systems have functions, and these functions are essential to any explanation of what they are and why they behave the way they do. Within Aristotle's philosophy of nature, every object has a "final cause" or "telos", which is the goal or purpose of the object and every object strives to fulfill its natural goal or purpose. This is what is meant by saying that Aristotle has a "teleological" worldview.

Indeed, Aristotle believed that natural systems possess a set of functions that reflects a hierarchical and teleological conception of the cosmos as a whole. The cosmos is an organic whole composed of many parts nested in various hierarchies. The functions of the parts are partly defined in relation to the role they play within the greater wholes that contain them. Thus, one function of plants is to grow and develop as plants do, but for Aristotle another function of plants is to provide food for animals, and this function is part of the explanation for why plants exist with the properties that they do.

Greek and Medieval scholars working out of this teleological tradition agreed that dead, inert objects could not have natural functions of their own – any functions they have must be derived from some form of intelligent agency. For Plato and the Medieval theologians, this agency is derived from the creative work of an external designer (a "demi-urge" for Plato, a theistic God for theologians). For Aristotle this agency is not external, but internal, immanent

in the fundamental nature of objects. Thus, while not all objects are conscious in the way that higher animals and human beings are, all objects possess "mind-like" qualities in some sense. Within this context, traditional ecological notions like the "balance of nature" were articulated in explicitly teleological language, appealing either to the immanent teleology of Aristotle or the external teleology of divine creation.

However, the scientific revolution of the 16th and 17th centuries brought about a dramatic change in cosmological worldview. The "mechanical philosophy" developed by (among others) Bacon, Galileo, Kepler, Hobbes, Boyle, Gassendi, Descartes, and Newton was grounded in the notion that the physical universe was entirely made up of small solid corpuscles in motion, and that these corpuscles are inert, devoid of any of the "psychic characteristics" that were common to the earlier frameworks. Within this framework, natural phenomena are explained as the result of mechanical interactions of inert particles. The immanent teleological principles of Aristotle were "squeezed out", and the origin of natural functions was consolidated in the external agency of God.

The more serious challenge to the concept of natural functions arose as scientific explanation became increasingly "naturalized" and explicit references to God were discouraged. Without reference to God or other forms of intelligent agency, how are we to understand natural functions?

Natural functions, "function talk" and the philosophy of biology

The view that came to dominate the physical sciences was that appeal to natural functions could not be justified, and reference to them should be eliminated in scientific explanations. By the end of the 18th century the dominant research programs in physics and chemistry were mechanistic in orientation.

In the biological sciences the mechanical revolution had a less dramatic impact on the use of natural function concepts in scientific explanation. To most scientists there seemed no hope of explaining the striking adaptedness of organisms to their environments, or phenomena such as embryonic development, in purely mechanical terms. Darwinian evolutionary theory eventually offered a non-teleological explanation for biological adaptations, but in many areas of biology teleological explanations continued to flourish under the banners of vitalism, Lamarckism, and orthogenesis.

It was not until the neo-Darwinian synthesis of the 1930s and 1940s and the discovery of the molecular basis of heredity that overt teleological explanations were eliminated from most areas of biology and the prevailing view in the physical sciences was finally endorsed: teleological explanations are illegitimate outside the context of human intentional explanation.

But of course function talk *didn't* disappear in the biological sciences. Biologists and ecologists continue to use expressions like "the function of", "the role of", "for the sake of", "serves as" and "for the purpose of" in discussing biological and ecological entities, processes and mechanisms. Function talk also persists in the social sciences and in medicine. This linguistic fact poses a puzzle: on the one hand, modern scientists officially disavow teleological explanations in science; on the other hand, they routinely use the language of functions in scientific description and explanation. Is this usage justified? And if so, how is it justified? This question has spawned a large philosophical literature on the relationship between function talk and teleology.

Early work by philosophers was uniformly hostile to teleology and attempted to show how function talk can be reinterpreted in non-teleological terms without loss of meaning (Hempel, 1959; Nagel, 1961). This project had only limited success. The problem is that function talk – and especially reference to "natural functions" – seems to presuppose a degree of *normativity* that resists analysis in purely descriptive terms.

To give a standard example, we might say that the heart can perform a number of functions in virtue of its causal properties: it can produce rhythmic sounds, for instance; it can also be used to train medical students in physiology and dissection. But we also want to say that producing rhythmic sounds or assisting the training of medical students isn't the *proper* or *natural function* of the heart – the proper or natural function of the heart is to pump blood through the circulatory system of an organism. And when a heart fails to pump blood, then it's *malfunctioning*. The concepts of "natural function" and "malfunction" appear to be normative concepts in the sense that they refer not only to what hearts *in fact* do, but what they *should* do. This kind of normative function attribution is quite common in biology, but where and how does the normativity arise in the absence of immanent teleological properties (as in Aristotelian science) or intelligent design by an external agent like God?

More recent work on the philosophy of functions has attempted to *naturalize* the teleology that is evident in normative function ascriptions. The most discussed theory of normative functions is based on the observation that Darwin's theory of natural selection seems to justify a certain kind of teleology (Millikan, 1984). We say that certain traits were "selected for". For what? For the effects of that trait that contributed to its persistence within a population over evolutionary time frames. Hearts haven't persisted in populations because they make rhythmic sounds; they persisted because they perform a particular adaptive function – pumping blood – that contributed to the survival of organisms; they were selected *for* this causal effect. Thus, the selection history of a trait allows us to distinguish between causal effects of a trait that are merely accidental and causal effects that contributed to survival because they performed an adaptive function. This conception of natural functions justifies a certain kind of normative teleological language without recourse to intelligent agencies or immanent teleological principles in nature.

However, not all philosophers are happy with theories of natural functions based on evolutionary history. If an organism didn't have any evolutionary history – if, say, it was an entirely new species created in a laboratory – but it still had a heart, wouldn't we still want to say that the heart has a function, and that function is to pump blood? Considerations such as these have motivated philosophers to develop alternative accounts of functions that are not based on evolutionary history.

For current purposes there is no need to survey the (vast) philosophical literature on functions any further (for an extended survey see Wouters, 2005), suffice it to say that, while there is currently no consensus theory of functions among philosophers or biologists, there is widespread agreement that function talk is unlikely to be eliminated from biology, and that certain kinds of normative function attributions may be justified without presupposing Aristotelian or theological conceptions of nature.

Functions and ecology: the holism-reductionism split once again

Though biologists and ecologists have conducted their affairs largely in ignorance of the philosophical debate over functions, we should not conclude that philosophical attitudes toward functions and functional explanations have played no role in shaping the practices of

scientists. These philosophical attitudes are revealed in general attitudes toward scientific methodology and holistic versus reductionistic research programs.

With respect to methodology, it is a generally accepted principle of modern scientific reasoning that a proper scientific explanation is either causal-mechanical in nature or grounded in general laws that describe uniform regularities; overt appeals to teleological principles in explaining the properties of natural systems are either discouraged or dismissed. This is the legacy that modern science has inherited from the scientific revolution of the 17th century.

In addition, the history of 20th century ecology is marked by a schism between holistic and reductionistic research programs that reveal differing views on the proper role of functions and function language in ecology. Put succinctly, holists are more willing than reductionists to attribute functions to higher-order ecological entities and processes.

Some of the reasons for these predilections should be obvious. In the non-human world, function talk is most naturally applied to well-organized systems with component parts that play distinctive roles in maintaining the structure and behavior of the system as a whole. Organisms are the quintessential example of such integrated systems and consequently function talk is most naturally applied to organisms. There is a long-standing tradition of holistic theorizing in ecology that is grounded in analogies between ecological systems and organisms. The most obvious historical example is the Clementsian concept of the plant community as a kind of "superorganism" that has an ontogeny and phylogeny directly analogous to that of individual organisms (Clements, 1916). Organismal metaphors are also prominent in ecosystem ecology via the language of respiration, metabolism, growth, development and self-organization, and in the work of certain theorists who self-consciously defend non-trivial analogies between organismal and ecosystem development (e.g., Odum, 1969)There are also holistic traditions of population and community ecology that emphasize the roles of individual species in contributing to the stability of higher level ecological properties, such as resistance to invasion (Elton, 1958; Elton, 1966). It is within these holistic traditions of ecological theorizing where one is most likely to find the language of functions and functional roles applied to populations, communities and ecosystems.

By contrast, within more reductionistic approaches to ecology that are more strongly under the influence of either neo-Gleasonian individualist conceptions of plant communities and succession (Egler, 1954; Gleason, 1939), and/or the view that ecological principles must at least be consistent with, if not ultimately grounded in, neo-Darwinian evolutionary theory (Mayhew, 2006; Pianka, 1999), one is far less likely to find the language of functions applied to ecological entities above the levels of individuals and populations. And when it is used the tendency is to have the function language grounded in natural selection history.

There are at least two reasons for this. First, research within these traditions emphasizes the changing, stochastic, non-equilibrium aspects of ecological systems, and by and large rejects the holistic view of communities and ecosystems as coherent, organized entities with emergent causal properties. By rejecting the organismal metaphor they consequently reject function attributions that are predicated on strong analogies between ecological systems and organisms.

Second, attitudes toward function language in ecology have been influenced by the group selection debate that took place in the 1960s (Williams, 1966; Wynne-Edwards, 1962). The critique of group selection was based on the affirmation that within orthodox evolutionary theory, natural selection acts primarily at the level of individual organisms (or, indeed, the level of individual genes), and rarely if ever at the level of groups. This debate raised awareness among ecologists of the broader implications of the theoretical perspective represented in population genetics and the neo-Darwinian synthesis, and was partly responsible for the rise of evolutionary ecology in the late 1960s and early 1970s. Evolutionary ecologists tend to associate the language of functions with organism-environment relationships relevant to selection and adaptation (e.g. "functional traits"). But if natural selection only acts at the level of individuals within species populations, then the language of functions should only apply at this level. Consequently, evolutionary ecologists are inclined to be skeptical of function attributions at the community and ecosystem level.

To sum up, in ecology the language of functions is historically and conceptually tied to philosophical and theoretical debates between holists and reductionists that have played central roles in the intellectual history of the discipline. The biodiversity-ecosystem functioning literature is notable for its heavy use of function talk. It is an open question

whether and to what extent differing philosophical attitudes toward functions (and their affiliation with holistic research traditions) influence the work of researchers within this field, but it would be naïve to assume that they play no role at all. There is no doubt, however, that some ecologists (generally, those not directly involved in biodiversity-ecosystem research) view this research program with suspicion because of its affiliations with what they regard as a discredited ecological holism.

Functions in the biodiversity-ecosystem functioning literature

We have seen that function attributions come with a certain amount of philosophical baggage associated with commitments to holism and the normativity of so-called "natural" or "proper" functions. But not all function talk in biology or ecology carries this baggage. In many cases the term "ecological function" is used synonymously with "ecological process", and merely refers to an ecologically relevant causal process. The biodiversity-ecosystem functioning literature uses the term "function" in a wide range of senses, some of which are innocuous and with no implications for the philosophical issues described earlier. But this is not always the case. In some cases the language of functions is used in ways that invoke the normative sense of function and that presuppose a certain kind of holism with respect to ecosystems.

Kurt Jax (2005) offers a helpful review of function language in ecology and specifically in the context of biodiversity-ecosystem functioning research. Jax distinguishes four major uses of the term "function" in ecology:

(1) *to characterize processes and interactions between pairs of objects, and the causal relations that sustain them*. This sense of function refers to pair-wise interactions. Examples: a fox eats a mouse; a plant assimilates nutrients. In most cases the term "function" can be replaced by "process" or "interaction" without loss of meaning.

(2) *to characterize processes and interactions between a collection of objects, and the causal relations that sustain them*. At this level we are viewing the objects as constituting or as situated within a larger system, and asking how the objects (now conceived as "parts") contribute to or relate to the larger system (now conceived as a "whole"). Examples: biomass production and phosphorus cycling within a lake; community population dynamics. These kinds of investigations are the stock-in-trade of a great deal of ecological research.

(3) *to characterize the overall processes that sustain an ecological system as a whole, and the role of the component parts in these processes*. At this level the focus is on whole-system properties and processes. The parts of the system and their behaviors are reconceived as bearers of functions in relation to properties and processes of the whole. Examples: describing a plant species as a "primary producer" or a bacterium as a "decomposer"; a species conceived in terms of its Eltonian "functional role" niche.

(4) *to characterize those aspects of an ecological system that are useful or important to humans*. Examples: the concept of an "ecosystem service", such as providing oxygen or purifying water. Though this concept of function is most generally used in relation to human needs and interests, in principle it could be applied to other living beings.

Another important distinction that cross-cuts these categories is between functions conceived as "means" and as "ends". When conceiving of functions as "ends" we are simply focusing on the activity or performance of various objects within a temporal sequence or causal chain. When conceiving of functions as "means" we are asking about the role or contribution that an object makes for something else (e.g. "what is the function of biodiversity to ecosystem functioning?"; "what function does species X play in the service of ecosystem property Y?"). Studies that focus on functions as ends are generally unproblematic since they involve nothing more than empirical investigation of a process (like productivity, or drought resistance). Studies that focus on functions as means are more problematic because they require that we consider the "aims", "goals" or "purposes" served by the function, and this brings into play the issues of teleology and normativity discussed earlier. We argued earlier that certain kinds of normative function attributions can be justified in biology, but raised questions about their applicability to ecosystem processes (we return to this issue below).

The question to be asked is this: How is the language of functions used in the biodiversity-ecosystem functioning literature? And are these uses problematic or unproblematic?

Jax distinguishes three kinds of research questions in the biodiversity-ecosystem functioning literature that employ different meanings of "function" (Jax, 2005):

(1) How does biodiversity relate to *ecosystem processes* (= ecosystem function)?

(2) How does biodiversity relate to the *functioning of ecosystems*?

(3) How does biodiversity relate to *ecosystem services* (= ecosystem functions)?

The bulk of the experimental work on biodiversity-ecosystem functioning relations is focused on answering the first question, where the variables of interest (productivity, drought resistance, decomposition of litter, etc.) are treated as ends, not as means to some other end. This usage is largely unproblematic since it is does not invoke the normativity of functions conceived as means to some other end.

The second question employs a sense of "function" that can be problematic when the expression "functioning of ecosystems" (or "ecosystem functions") refers to the overall behavior or performance of an ecosystem, because this usage often presupposes a certain conception of ecosystems as entities in the world. Consider how the expression is used in the controversial ESA article on "Biodiversity and ecosystem functioning":

Ecosystem functioning reflects the collective life activities of plants, animals, and microbes and the effects these activities – feeding, growing, moving, excreting waste, etc. – have on the physical and chemical conditions of the environment. (Note that 'functioning' means 'showing activities' and does not imply that organisms perform purposeful roles in ecosystem-level processes.) A functioning ecosystem is one that exhibits biological and chemical activities characteristic of its type." (Naeem et al., 1999)

The authors try to head off worries about their use of function language but the last line betrays a normative interpretation of this language. A functioning ecosystem is one that "exhibits biological and chemical activities characteristic of its type". As Jax puts it,

The aim of investigating "functioning" ecosystems here is clearly not to observe any activities of organisms in a particular area, but specific activities that sustain some "typical" ecosystem. Here "functioning" clearly receives a normative dimension in the sense that it refers to some pre-defined reference states of an ecosystem (those that "exhibit biological and chemical characteristics of its type"). The "functioning" of the ecosystem thus is a desirable state, and the organisms in fact are investigated as if they perform purposeful roles in its perpetuation. This is a legitimate aim of applied ecological research, but it goes beyond a pure description of processes that occur in some aspect of nature. (Jax, 2005)

In short, this usage presumes that one can describe ecosystems as functioning or malfunctioning relative to some reference state that characterizes an idealized ecosystem "type". The problem here isn't so much the normativity of the function ascription as the conception of ecosystems and ecosystem individuation that is being presupposed. Very few ecologists believe that ecosystem "types" are part of the furniture of the world. By far the more common view (even among holists) is that the boundaries and variables that characterize an ecosystem *are chosen by observers*, they're not given in nature as such. Consequently, making statements about the functioning of ecosystems demands that observers delimit the ecosystem in question and specify the relevant reference states. The problem, as Jax sees it, is that this is almost never done in a careful, explicit and motivated fashion. As a result, the concept of a "functioning ecosystem" is never operationally defined. This kind of usage lends support to critics who charge that expressions like "ecosystem function" are nothing more than trendy buzzwords that don't belong in the scientific lexicon of ecology.

Jax (2005) identifies a number of other examples in the biodiversity-ecosystem functioning literature where distinctions between ecosystem processes and ecosystem functions, and between normative and descriptive senses of function, are blurred, resulting in semantic confusions that hinder rather than help the empirical investigation of biodiversity-ecosystem functioning relationships. We agree that this research can benefit from a theoretical framework that encourages greater precision in the use of key concepts and that is more mindful of the historical and philosophical issues associated with the use of these concepts.

THE BIODIVERSITY-ECOSYSTEM FUNCTIONING DEBATE

We now turn to the historical account of key events of the biodiversity-ecosystem functioning debate, dividing the continuum into four sections: the beginning of the research program (early 1990s), the critical response (late 1990s), the heat of the debate (2000), and the conciliation process (2000-01). The history of the biodiversity-ecosystem functioning debate has been marked by considerable interplay among theoretical developments, empirical results, institutions, policy concerns, the media, and the personalities of the scientists

involved (Kinzig et al., 2001; Mooney, 2002; Mooney et al., 1996b; Naeem, 2002; Naeem et al., 2002).

The Program begins (early 1990s)

As concerns about biodiversity loss and the impact of humans on ecosystems grew (Vitousek et al., 1997), national and international organizations started to define the problem and set conservation and research priorities for biodiversity. Examples of international organizations include the UNESCO, SCOPE, and ICSU (see Box 1). The relevant point here is that the biodiversity-ecosystem functioning research program did not start motivated just by the scientific curiosity of understanding another interesting relationship in nature. It was an organized effort of the international scientific community to provide evidence on the utilitarian value of biodiversity for human society in order to convince policy makers to take serious action towards conservation of biodiversity.

In 1991, SCOPE organized a conference in Germany (Bayreuth) to summarize the status of the knowledge on the relationship between biodiversity and the functioning of ecosystems (Mooney, 2002). A new SCOPE research program (biodiversity-ecosystem functioning) was thus started with the explicit goal of answering two questions: 1) Does biodiversity count in the system processes? and 2) How is system stability affected by species diversity? (Schulze and Mooney, 1993). A SCOPE report review was published later (Mooney et al., 1996a). Also in 1991 the first phase of the DIVERSITAS program started, and in 1992 the Global Change in Terrestrial Ecosystems program of the IGBP was launched (see Box 1). As a consequence of this investment in new experimental and observational research, an increasing scientific production followed, as expressed by number of papers published (Fig. 2.1).
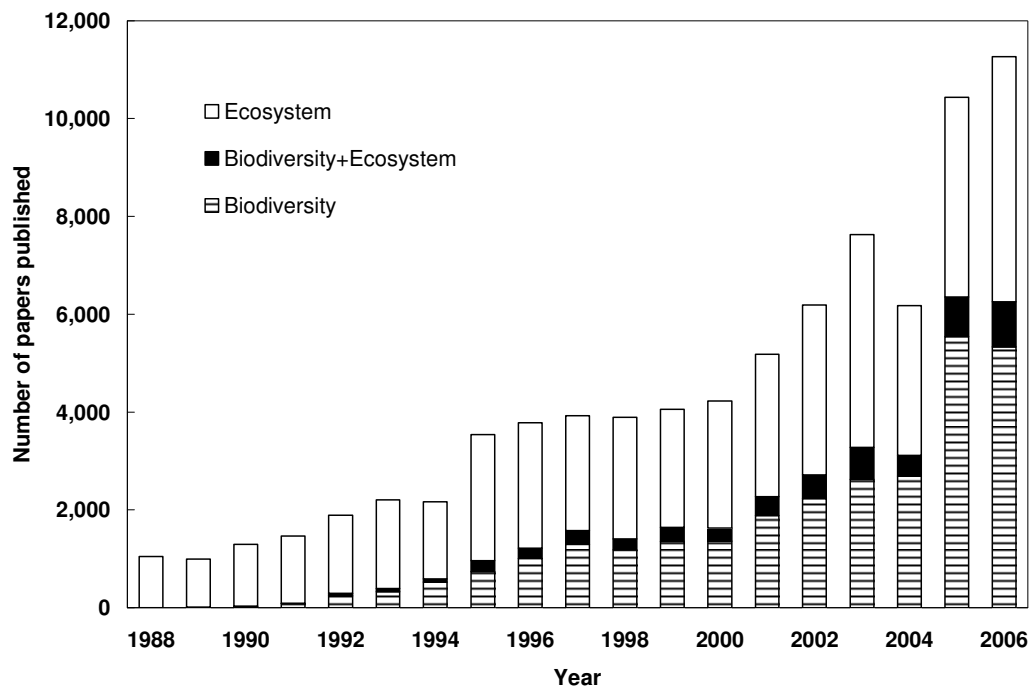
Figure 2.1.Number of publications per year including the terms "ecosystem", "biodiversity", or both in their titles or abstracts. Elaborated from BIOSIS Preview database, web search September 2007.

BOX 1: Institutions shaping the research agenda

International Council for Science (ICSU) – NGO founded in 1931, comprised by both 112 national scientific bodies and 29 international scientific unions, promotes scientific activity applied for the benefit of humanity. ICSU's broad scientific expertise addresses major issues by creating Interdisciplinary Bodies and Joint Initiatives with other organizations. Major programmes are IGBP, DIVERSITAS, IHDP, and WCRP. These four comprise the Earth System Science Partnership, to study the Earth System, its changes and implications.

United Nations Educational, Scientific and Cultural Organization (UNESCO) – founded on 1945 with the goal to build peace by education, science, culture, and sustainable development. The Man and the Biosphere Programme (MAB), started in 1970, aims to reduce biodiversity loss and maintains a network of Biosphere Reserves. UNESCO co-sponsors DIVERSITAS with ICSU.

Scientific Committee on Problems of the Environment (SCOPE) – international scientific organization, comprised by 38 national science academies and 22 international scientific unions, since

1969, sponsored by ISCU. SCOPE develops scientific reviews of environmental issues on three cluster areas: Managing Societal and Natural Resources, Ecosystem Processes and Biodiversity, and Health and Environment. The biodiversity-ecosystem functioning program was part of the second cluster.

International Geosphere Biosphere Programme (IGBP) – one of ICSU's interdisciplinary boards to study global change starting in 1987. On of its projects, Global Change in Terrestrial Ecosystems (GCTE) 1992–03, addressed how global change would affect terrestrial ecosystems and feedbacks to the climate system. One focus of GCTE was the link between ecosystem functioning, biodiversity, stability, resilience, and buffering capacity to natural and human perturbations. A new program, the Global Land Project (GLP) was launched in 2005 co-sponsored by IHDP and IGBP with the goals of measuring, modeling and understanding the coupled human-environmental system.

DIVERSITAS - joint initiative by SCOPE, UNESCO, ICSU, IUBS, and IUMS, starting in 1991. It provides an international multi-disciplinary framework to promote integrative biodiversity science, by synthesis of scientific knowledge, promoting new interdisciplinary research, and communicating policy implications. In 2003 DIVERSITAS-II defined three core areas: bioDISCOVERY, ecoSERVICES, and bioSUSTAINABILITY. The three foci of the ecoSERVICES project are biodiversity-ecosystem functioning research (spatial and temporal scales, microbial diversity, and "second generation" research), linking ecosystem functioning to ecosystem services, and human responses to those.

National Science Foundation (NSF) - a USA federal agency created in 1950 to promote the progress of science; to advance the national health, prosperity, and welfare; and to secure the national defense. With an annual budget of about $5.92 billion, it funds 20 % of all federally supported basic research conducted by America's colleges and universities. The Directorate of Biological Sciences, Division of Environmental Biology, funded much of the biodiversity-ecosystem functioning research.

European Science Foundation (ESF) - association of 75 member organizations (European national research councils) devoted to scientific research in 30 European countries. Established in 1974, it has coordinated a wide range of pan-European scientific initiatives. LINKECOL, a program to promote a synthesis between population, community, and ecosystem ecology, funded much of the biodiversity-ecosystem functioning research between 1999 and 2004.

Three main experiments characterize the initial phase of the research program: the ECOTRON (UK), Cedar Creek (USA), and BIODEPTH (Europe). In the ECOTRON, Naeem et al. (1994) assembled communities of plants, microorganisms, and animals (representing trophic levels of decomposers, producers, and consumers) with three different biodiversity levels (9, 15, and 31 species), in replicated controlled growth chambers, and observed an increase of plant productivity and community respiration in the more species rich communities. They explained this positive association between biodiversity and ecosystem functioning by the mechanism of niche complementarity: diverse communities of plants have a canopy structure that intercepts more light; therefore, there is more energy for ecosystem processes.

The second set of experiments was conducted at Cedar Creek, Minnesota, USA, where Tilman and colleagues established several experiments in grasslands communities. In the first experiment, they used different nitrogen fertilizer rates to alter the species composition and diversity of native grasslands, and observed an increase in stability with species richness (and fertilizer), which they measured as resistance and recovery after a major drought (Tilman and Downing, 1994). In the second experiment, they assembled communities of native grassland species with different species richness levels (1 to 24 species) drawing species at random from a list, and measured an increase in productivity and nutrient use with greater diversity (Tilman et al., 1996). A similar mechanistic model was used to explain these results: diverse communities make more complete use of the resource space, increasing the resources available for ecosystem processes. This experiment also provided evidence to support the diversity-invasibility hypothesis: species rich communities were less invaded than low diversity ones (Knops et al., 1999).

The third major experiment was the European BIODEPTH (Biodiversity and Ecological Processes in Terrestrial Herbaceous Ecosystems). Hector et al (1999) manipulated replicated artificially assembled grassland communities with varying species richness (1 to 32) at eight different sites (Silwood and Sheffielf in UK, Sweden, Portugal, Ireland, Greece, Germany, and Switzerland) and observed a reduction in total plant productivity with decreasing diversity levels. They explained the results by niche complementarity and positive species interactions, as well as the sampling effect (see below). These experiments and others

provided evidence for a general and positive relationship between species richness and productivity. All these experiments were featured in prestigious scientific magazines (like Science and Nature), as well as the media to support the urgent need for biodiversity preservation. The biodiversity-ecosystem functioning research program was succeeding.

Some experiments looking at other ecosystem processes such as soil organic matter decomposition fail to provide evidence for a positive relationship of diversity and ecosystem functioning (e.g., Griffiths et al., 2000). Other studies highlighted the greater contribution of functional composition rather than species diversity to ecosystem processes (Hooper, 1997; Tilman et al., 1997b). Because species diversity and functional composition may not necessarily be correlated, the interpretation of the functional composition effects also became an issue of debate.

Critical response (late 1990s)

Two main sorts of scientific criticisms challenged the results of the previous experiments: 1) observational studies contradicted the experimental results (e.g. Wardle et al., 1997) and 2) the design of the experiments made the interpretation of results difficult or invalid (Huston, 1997; Huston et al., 2000). First, most of the high productivity ecosystems in the world have low species richness, and this contradicted the results of the experiments (Huston and McBride, 2002). If diversity was positively related with productivity, this association should be evident in natural ecosystems. One of the central concepts of community ecology was the hump-backed model of diversity-productivity (Grime, 1973) which predicted that species numbers would be maximized in environments with intermediate productivity. Indeed, at low levels of environmental productivity (e.g. poor soils), species diversity in natural ecosystems is low because few species can survive. Diversity increases as more resources become available to species to exploit, reaching a maximum at intermediate levels of productivity. Then diversity declines at higher levels of productivity because dominant species out-compete others (competitive exclusion). A similar patter is observed with disturbance (Connell, 1979). From this perspective, critics defended that environmental conditions are the driver of diversity, and not the other way around. Only when the environment is controlled the relatively small effects of species composition on productivity can be found (Huston and McBride, 2002).

A similar issue occurred in the diversity-invasibility dimension of the debate: at geographic scales larger than field level (e.g., landscape, biomes) areas of high native species diversity were more invaded than areas of low species diversity (Stohlgren et al., 1999), which contradicted the results of small scale experiments. Areas of high diversity are often correlated with higher environmental heterogeneity, higher species turnover, nutrient pulses, and more opportunities for invasive species to become established (Stohlgren et al., 2003).

Second, experiments with randomly assembled plant communities have several "hidden treatments" confounded with the diversity effect. The most important of these is the sampling effect, also known as selection probability effect (Huston, 1997; Tilman et al., 1997a): the probability to include the most productive species increases at higher diversity levels, thereby the effect of one key species is confounded with the effect of diversity (Huston and McBride, 2002). To the critics, the sampling effect was not a biological valid mechanism to explain an increase in productivity with species richness, but an artifact of the way the experiments were conducted. Other design problems of the first experiments included quasi replication (low diversity replicates are less represented, and there is more chance that the most productive individual species are not included) and variance reduction effects (high diversity replicates are more similar than low diversity replicates, confounding experimental error with the diversity effect). All these design problems made critics state that all conclusions about the relationship diversity-ecosystem function based on previous experiments was invalid (Huston et al., 2000). In reply, Tilman et al. proposed that the sampling effect was indeed the simplest valid mechanism to explain the relationship. Given that the nature of the species extinction process it is poorly understood, assuming that the species loss was random it was a reasonable thing to do (Tilman et al., 1997a). The interpretation of the role of the sampling effect in biodiversity experiments remained a contentious issue. The debate "deepened" (Grime, 1997).

"War among ecologists"

The acrimony exploded in 1999, when a panel of scientists reported in "Issues in Ecology", an Ecological Society of America (ESA) publication aimed to the general public and policy makers, that there was scientific evidence that loss of biodiversity impacted ecosystem functioning by reducing plant productivity, decreasing ecosystem resistance to

environmental perturbations, and increasing the variability of soil nitrogen levels, water use, and pest cycles (Naeem et al., 1999). A group of critics of the biodiversity-ecosystem functioning experiments wrote a letter to the ESA Bulleting heavily criticizing the Issues in Ecology report, claiming the authors stated opinion as facts, did not represent one of the two schools of thought in the debate, and did un-ethically selective citation of literature (Wardle et al., 2000). This immediately reached the media, with articles like this one in Science: "*An acrimonious dispute has broken out over whether the data on biodiversity are robust enough to inform public policy. A long-simmering debate among ecologists over the importance of biodiversity to the health of ecosystems has erupted into a full-blown war. Opposing camps are dueling over the quality of key experiments, and some are flinging barbs at meetings and in journals*" (Kaiser, 2000). Debate is usually welcomed within the academic community but when the goal is to inform policy-makers, debate among scientists is viewed as uncertainty and lack of evidence. No clear message, no actions taken in pro of biodiversity conservation. The biodiversity-ecosystem functioning was turning into a failure.

Several sociopolitical factors fueled this process. As stated earlier, the biodiversity-ecosystem functioning research program was intended to inform public policy for biodiversity conservation. This had a first implication relating to the psychological dimension of hypothesis testing (Loehle, 1987): scientists have a tendency to seek confirming evidence (confirmation bias) and usually they have a persistent belief in a theory in spite of contrary evidence (theory tenacity). These two features can impair scientific progress especially in research concerning long time scales and complex systems. To a certain extent this may have influenced both sides of the debate. A second implication relates to funding, given that biodiversity experiments received considerable grant money. For instance, Tilman's Cedar Creek experiment between 1994 and 2007 was awarded US$ 10 million in NSF grants (NSF awards online database http://www.nsf.gov/awardsearch). Naeem's ECOTRON cost the UK Natural Environment Research Council about £ 1 million to build (Kareiva, 1994). The BIODEPTH project cost the European Commission 2 million euros between 1996 and 1999 (Imperial College, http://www.ic.ac.uk/P1200.htm). Competition from other groups for funding may have intensified the debate in an effort to garner some of the funds. A third implication of the direct policy connection is the exposure of primary research projects and

their methodology to the media. Probably other heated debates in scientific methodology do not reach the public arena as much, because the policy implications may not be as relevant.

Conciliation and synthesis

A conference was held in Paris in December 2000 as an attempt to bring everybody to the table, and reach a consensus on the issues regarding biodiversity-ecosystem functioning. This "Synthesis Conference" was an effort to reconcile the different viewpoints, and also to reconcile ecologists and the general public. A synthesis framework came about in part as a consequence of the same policy implications which caused the acrimony. After the heated discussion, scientists lost their public credibility, and that was uncomfortable. After the conference it was celebrated that "the conference was a delight" (Naeem et al., 2002). "Perhaps it was the rich desserts and the French wine, but there were few signs of acrimony at the conference" (Hughes and Petchey, 2001). There was a clear effort to reach the public again showing the scientific consensus among civilized ecologists.

In the conference results from the main experiments were discussed, and new statistical analyses integrating data from various experiments were conducted. The concepts and terms had been interpreted in different ways, and at this conference they were better defined, thereby reducing confusion. Clarification of the potential mechanisms operating in the experiments and observational studies was a major advance. The conference pointed to new experiments to test the issues which remained uncertain.

The consensus framework was structured by pointing out the issues that were clear, and for each of those which questions remained to be answered, so that the framework served as a guide for future research endeavors. First, it is clear that a large number of species is required to maintain ecosystem functioning, but whether this is because more rich communities have some key species that affect ecosystem function or complementary among various species has a great effects on ecosystem function is still unknown. This provided a focus for further studies: separating and measuring the effects of these two non-exclusive mechanisms: the sampling effect and complementarity among species. Whether or not species extinctions are random is an important future area of inquiry to settle the issue of the relevance of the sampling effect (Loreau et al., 2001). Furthermore, the selection effect was also defined as a potential mechanism (see below). Second, greater number of species may be

needed to maintain stability in ecosystems (insurance hypothesis), according to theoretical models and some empirical work. Further experiments should test this hypothesis specifically controlling diversity and the environmental variation.

A third area of consensus was the reconciliation of the observational versus experimental studies. Observational studies of natural ecosystems show the humped back curve of diversity (y axis) as a function of productivity (x axis) because they intend to explain the causes of changes in diversity by examining underlying environmental gradients (Fig. 2.2a). Therefore, the x axis (productivity) is a composite variable consisting of various environmental aspects such as soil fertility and disturbance regime. In contrast, experimental studies which hold environmental factors constant show the positive relationship productivity (y axis) as a function of diversity (x axis) (Fig. 2.2.b). Rather than being contradictory, they are showing different mechanisms in different conditions. Because of this, the feedbacks between diversity, ecosystem functioning, and environmental factors should be explored in further research. This is also important for the diversity-invasibility debate: although at small scales species diversity may reduce resources available for invaders, at large scales environmental variables (and anthropogenic impacts) may be more important than species diversity to control exotic invasions. Finally, it was acknowledged that most of the experimental evidence came from grasslands ecosystems, where only plant diversity was manipulated. Therefore, before making generalizations to other ecosystems (e.g. aquatic) and other trophic levels (e.g., consumers, decomposers) further research was needed in that area (Loreau et al., 2001).

Finally it was agreed that functional traits of species and its interactions are the ones who affect ecosystem functioning. Much more research was needed on the relationship between species diversity and functional diversity, and in defining functional groups or types relevant for ecosystem functioning (Loreau et al., 2001).
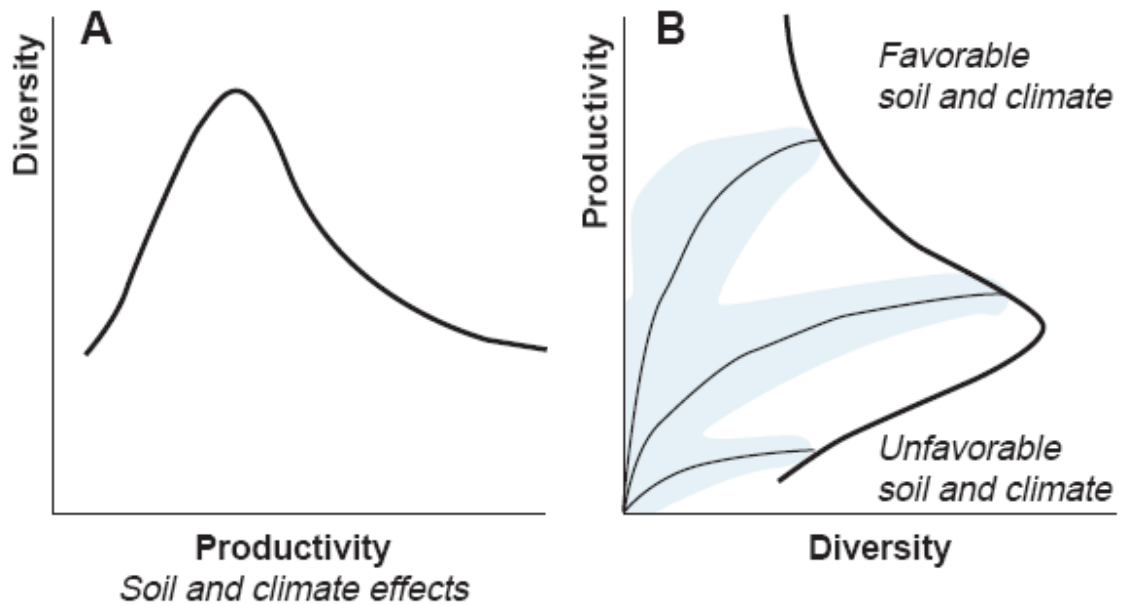
Figure 2.2. a. Diversity as a function of productivity, driven by environmental conditions across sites. b. Productivity as a function of diversity under constant environmental conditions. Reproduced from Loreau, Naeem et al. 2001

RECENT WORK IN BIODIVERSITY-ECOSYSTEM FUNCTIONING

Refining the mechanisms

After the synthesis framework, further refining of the mechanisms was elaborated, and mathematical equations derived to calculate the magnitude of each mechanism. One way of differentiating mechanisms explaining the biodiversity-ecosystem functioning relationship is by considering the "biological" effects, i.e., complementarity and selection (Loreau and Hector 2001). Another way of differentiating mechanisms is by considering community assembly effects, i.e., whether sampling effect is present (Loreau, Naeem et al. 2001). Complementarity involves niche partitioning and/or facilitation. Species with complementary traits can use different resources or niches, providing the community as a whole access to more resources and making it more productive than its constituent species individually (niche partitioning). Positive interactions among species can also increase the performance of the community (facilitation). It is a non-competitive species interaction (any interaction that is not competition). Selection processes such as interspecific competitive interactions cause one

species to dominate the community (higher relative abundance). It can be positive or negative depending whether the dominant species is positively or negatively associated with ecosystem functioning (e.g., monoculture yields are high or low). The term does not imply any connection with natural selection (Stachowicz et al., 2007).

Sampling effect (also called sampling model, sampling hypothesis, selection-probability effect) occurs in randomly assembled communities because high diversity communities are more likely to contain a species (or a set of species) that contributes significantly to observed levels of ecosystem functioning. For instance, the probability of including a highly productive species in the community increases as the number of species increases. Note that sampling effect can operate both for selection and complementarity mechanisms, although most often is identified with selection. In a high diverse community, the probability of having two complementary species (e.g. legumes and grasses) also increases with diversity. Early definitions of the sampling effect sometimes combined/confounded it with the selection effect.

The selection effect can be partitioned also in two effects: dominance and trait-dependent complementarity (Fox, 2005). When all species have the same productivity in polyculture as in monoculture but species with higher monoculture yields are more competitive and dominate the mixture, the dominance effect equals the selection effect. However, when species that are more productive in monoculture overyield in polyculture but do not displace other species, some of the selection effect involves trait-dependent complementarity, i.e., the portion of the complementarity effect that is correlated (covaries) with the trait of interest. Fox (2005) relabeled the complementarity term of Loreau and Hector (2001) as trait-independent complementarity, i.e., the portion of the complementarity effect that is not correlated with the trait of interest, but is instead shared between all species. Another different partitioning of mechanisms was also formalized later (Fox, 2006) , although it has not had considerable attention in empirical work.

Several new experiments and re-analyses of old experiments have focused on measuring the magnitude of complementarity versus selection effect. As a general trend, complementarity increases over time, while selection is more variable (Cardinale et al., 2007; Fargione et al., 2007; Loreau and Hector, 2001).

Second generation biodiversity experiments

As a consequence of the synthesis several second generation biodiversity experiments were started to address the issues raised in the previous years of the debate. One example is the Jena Project in Germany (Roscher et al., 2007; Temperton et al., 2007), another one is the forest biodiversity mega-project in Sabah, Malaysia (Scherer-Lorenzen et al., 2005). These experiments were many and diverse, and usually have some of the following characteristics: 1) the treatments included as much monocultures as possible, in order to make comparisons of overyielding, complementarity, and selection, 2) they had a balanced design to allow contrasts for plots with and without certain species or groups of species, 3) they were designed with the objective of testing specific mechanisms directly beyond the general overyielding in a specific function, 4) they extended for longer time periods, and larger spatial scales, 5) experimental design was thoroughly evaluated including replications, and local environmental control, 6) they consider more trophic levels (producers, consumers, predators).

Balancing the synthesis

As a follow up of the Synthesis Conference, a committee of scientists from the Ecological Society of America (ESA) published a review in Ecological Monographs titled: "Effects of biodiversity on ecosystem functioning: A consensus of current knowledge" (Hooper et al., 2005). Like every other paper in the literature this report started describing the threats that biodiversity loss and environmental degradation pose to society, and finished recommending to policy makers to set biodiversity as a priority for action. The tone of this report was moderate and balanced though, discussing uncertainties and contradictions present in the literature avoiding generalizations, and describing the many factors other than diversity influencing ecosystem functions. The main points stressed throughout the report were: 1) functional composition is more important than species richness in affecting ecosystem functioning, 2) abiotic controls (climate, resources, disturbance) interact with biodiversity to influence ecosystem properties, and the feedbacks between biotic and abiotic controls are central to understanding ecosystem functioning, and 3) diversity effects and the underlying mechanisms can differ among ecosystem properties and ecosystem types. Diversity may have

no effect on some ecosystem processes (e.g., when multiple species carry out similar functional roles or abiotic conditions primarily control the process) but as larger spatial and temporal scales are considered, greater diversity is needed to maximize functioning. With less certainty: complementarity of resource use by certain combinations of species can increase productivity, species richness decreases exotic species invasion under similar environmental conditions, usually not across environments, and species diversity can stabilize ecosystem process in response to disturbances and variation in abiotic conditions. Finally, the uncertainties that need further research include: the relationships between taxonomic diversity, functional diversity, and community structure, multiple trophic levels response to varying composition and diversity of consumer organisms, the need of long-term experiments to assess temporal stability, and perturbations to assess response to and recovery from disturbances.

Quantitative synthesis

One of the most recent advances where the meta-analyses of the more than 150 biodiversity experiments conducted in terrestrial and marine ecosystems (Balvanera et al., 2006; Cardinale et al., 2006; Cardinale et al., 2007; Stachowicz et al., 2007). These studies using some standardized measure of response of ecosystem functions to changes in diversity, found that on average the effect of biodiversity on ecosystem processes was positive, although there was variation between studies. Biodiversity effects were weaker in field versus microcosms experiments (e.g., pots, bottles), stronger at the community level (e.g., polyculture biomass) than ecosystem level (e.g., soil nutrients) and negative at population level (e.g., species biomass). The effects on stability measures were stronger than the ones on performance measures in the review of marine ecosystems, but as strong in the first review which included mainly grasslands ecosystems. Although in most cases diverse communities performed better than the average of monocultures (i.e., overyielding was the norm), in very few cases diverse communities were better than the best monoculture (i.e., transgressive overyielding was infrequent). On average there was no transgressive overyielding across trophic levels and ecosystems, although 12 % of plant experiments and 25 % of marine experiments reported transgressive overyielding. A critical finding was that overyielding and the probability of transgressive overyielding increased in experiments that ran for longer

timeframes because complementarity effects among species increased with time. Since most experiments have been short term, and transgressive overyielding in plant communities may take 5 years to be observed, experiments may have underestimated it.

Other issues

Experiments have looked at dimensions of diversity other than species richness, like evenness, and diversity indices (e.g., Simpson's) and found that richness alone does not capture the variation in diversity (Wilsey et al., 2005). When evenness and richness were manipulated in plant experiments, evenness did not change the relationship richness–productivity (Wilsey and Polley, 2004), but high evenness was positively associated with controlling invasions (Losure et al., 2007). A new methodological approach to disentangle richness and evenness effects on productivity has shown that evenness and species interactions consistently affect productivity across multiple sites (Kirwan et al., 2007).

There have also been advances in the measurement of functional diversity. Rather than defining functional groups a priori, multivariate approaches that summarize species traits data are being used, and then comparing them using cluster techniques, distances measure between species in trait space, dendrograms, and species abundances. These techniques promise a better understanding of the relationship between species diversity, functional diversity, and ecosystem functioning (Petchey and Gaston, 2006). A recent experiment documented the role of plant genotypic diversity in plant productivity and abundance of arthropods (Crutsinger et al., 2006) expanding the boundaries of biodiversity –ecosystem functioning studies to the often overlooked genetic dimension.

A concept that emerged in recent years was multifunctionality: ecosystems perform several processes simultaneously and are managed for various ecosystem services. Different species often influence different processes, so focusing on one single process like plant productivity provides an incomplete picture. When multiple functions are considered together, higher levels of diversity are needed to maximize ecosystem performance. Several studies confirm this mechanism of multivariate complementarity (Hector et al., 2007; Stachowicz et al., 2007).

DISCUSSION: INTERPRETATIONS OF THE BIODIVERSITY-ECOSYSTEM FUNCTIONING DEBATE

The biodiversity-ecosystem functioning debate is an extremely interesting case study for various disciplines. In this section we provide a brief account of some interpretations of the debate from the perspectives of environmental policy and philosophy of ecology. Finally, we suggest an original interpretation of the debate from the perspective of agriculture and agroecology.

Success or failure?

Srivastava and Vellend (2005) questioned small spatial scales of experiments, and the single focus on one variable, and trophic system, and concluded that biodiversity-ecosystem functioning was irrelevant for conservation ecology. In a similar way, a "Review for policy makers" of the debate (Thompson and Starzomski, 2007) concluded that results were inconsistent regarding the role of biodiversity in productivity and stability, and the relationships changed with scale, while had failed to address critical issues like the loss of rare species or the identification of keystone species. Furthermore, they state that the debate may affect the positive value society places on biodiversity, and using this research to justify biodiversity protection is very difficult. Addressing these criticisms various reviews assigned to each ecosystem function or process an overall ecosystem service and emphasized that there was clear evidence that biodiversity had positive effects on most of these services. Indeed, the new research agenda from DIVERSITAS, for instance, focuses on how biodiversity, ecosystem function, and ecosystem services are related. Future work on this area may provide direct linkages between ecological research and environmental policy that were absent in the earlier stages of the debate.

The great irony of the process is that it started with the goal to provide evidence to policy makers for the conservation of biodiversity, but maybe rushed to generalizations, and after a heated debate policy makers may have became more skeptical about the utilitarian value of biodiversity (Thompson and Starzomski, 2007). It should be clear, though, that the dependence of ecosystem services on biodiversity was never a debated issue. The contented issues were the mechanisms, and what was the role of species, functional groups, and traits

on ecosystem functions. The program indeed provided scientific evidence of how different ecosystem functions depend on biodiversity. And all quantitative and qualitative reviews agree with in the main conclusions: there is a positive role of biodiversity on ecosystem functioning and therefore ecosystem services with utilitarian value. Furthermore, regardless of the utilitarian value, there are other ethical, cultural, and aesthetic reasons for slowing the rate biodiversity loss due to human activities (Hughes and Petchey, 2001).

A new paradigm for ecology?

The biodiversity-ecosystem functioning debate is an interesting case study in the history of science, and has been interpreted as a process of scientific revolution *sensu* Kuhn (1970), where the previous paradigm of community ecology was challenged by new evidence and a alternative hypotheses were articulated into a new paradigm (Naeem, 2002). Naeem also suggested here a dialectic evolution of ideas, where the central thesis of community ecology (i.e., biodiversity is a consequence of evolutionary adaptation of individuals and populations to variable environmental conditions) was contradicted by the antithesis that biodiversity determines ecosystem functioning. This dialectic thesis-antithesis evolution will eventually lead to a new synthesis between ecosystem and community ecology. Indeed, some models have started to be created looking at the feedback between resource supply, species richness, resource use, and biomass production (Gross and Cardinale, 2007). These two branches of ecology had advanced separately and without interacting much, and probably the most important success of the program was bringing them together.

Ecology, agriculture, and Darwin's legacy

In The Origin of Species Charles Darwin (1859) wrote: "it has been experimentally proved that if a plot of ground be sown with one species of grass, and a similar plot be sown with distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised." For this statement, Darwin was considered the father of the biodiversity-ecosystem functioning debate (Hector and Hooper, 2002). Interestingly enough, Darwin pointed to a "sown" plot rather than native grasslands. Furthermore, in the next line Darwin continues: "The same has been found to hold good when first one variety and then several mixed varieties of wheat have been sown on equal spaces of ground." Darwin was

referring to an agriculture situation, rather than a natural ecological situation, more precisely, to an intercropping experiment. As he did throughout the book starting with "variation under domestication" and then moving to "variation under nature", Darwin draws many examples from familiar agriculture situations.

Perhaps one of the most interesting aspects of the biodiversity-ecosystem functioning debate was the interplay between Ecology and Agriculture. Although both fields have considerable overlapping, for instance, in ecosystem restoration, crop ecology, and agroecology, the research traditions, mindsets, and focus of interest (one could even say paradigms) are very different. A contrast of both disciplines is out of the scope of this chapter, and can be found in the vast agroecology literature (Altieri, 1987; Gliessman, 1998; Jackson, 1985; Vandermeer, 1989) but the main differences could be drawn from a simplified sketch. In Andy Hector's words ecologists are "people who can work with partial differential equations who can also climb up a 70-metre rainforest tree to collect pollen" (2007, Nature 448:7150, p. xi). An agronomist in contrast has been defined as "confronter of world hunger" and "keeper of the land" in a major recruiting campaign at a leading agriculture university (see www.imanagronomist.net). Although both fields are concerned with protecting the environment, the methodological approaches are different. Agriculture systems are normative systems: they have goals, and they must perform certain functions (Vandermeer et al., 2002). Furthermore, ecologists are interested in descriptive and explanatory models of natural variation, whereas agronomists are interested in management decisions to maximize functions.

Biodiversity-ecosystem functioning research had the potential to inform Agriculture in various ways. Sustainable agriculture systems must be productive and stable, control invasions of pests and diseases, and recycle nutrients efficiently among other ecosystem functions. Modern agriculture systems usually have very low planned and associated biodiversity, being the annual grain monocultures an extreme situation. It is not a novel idea that if diversity had benefits in terms of ecosystem functions, agriculture should build on that. In fact, several publications out of biodiversity-ecosystem functioning research suggested recommendations to agriculture systems, particularly for European grasslands (Minns et al., 2001), forage production and grazing systems (Sanderson et al., 2004; Tracy and Sanderson,

2004a; Tracy and Sanderson, 2004b; Tracy and Faulkner, 2006), and bio-fuel oriented systems (Tilman et al., 2006a).

On the other hand, it can also be said that the agriculture perspective played a central role in the biodiversity-ecosystem functioning program. One could even go deeper, and interpret the whole debate as a dialogue between these two contrasting perspectives. Ecologists initially neglected the literature on intercropping and crop mixtures (Wardle et al., 2000). Intercropping literature showed that diverse mixtures of few species usually are more productive than the average of the species grown in monoculture, but not greater than the most productive species in monoculture (non transgressive overyielding), with the exception of legume–grass mixtures (Trenbath, 1974). The interest of agriculture researchers is to achieve transgressive overyielding and therefore ecological research celebrating the role of diversity in non transgressive overyielding in randomly assembled communities was called into question (Garnier et al., 1997). The first reaction from ecologists was to reveal their assumptions: agriculture systems fall in the low end of the diversity range, and agroecosystems usually operate at higher nutrient concentrations (e.g., soil nitrogen) than natural systems, therefore agroecology literature was considered irrelevant (Naeem, 2000).

Furthermore, the hottest area of debate, i.e., the interpretation of the sampling effect as an artifact of the experiment (Huston, 1997) or as an assembly mechanism (Tilman et al., 1997a), was actually a debate between the agricultural and ecological perspectives. Farmers do not plant a random assortment of crops in their fields, so experiments where the sampling effect is operating have little use if any for farmers. In contrast, at least in theory extinctions in natural ecosystems could be considered random, and therefore the biodiversity experiments are informative.

While much of the heat of the debate may have come form the contrasting paradigms of agriculture and ecology, the dialogue between the two contributed to solving many issues in the debate. Indeed, the use of intercropping indices like Relative Yield Totals to understand overyielding and the focus on proper statistical design of experiments (true replication of treatments and local control) can be seen as two central contributions from Agriculture to the debate.

Although the hypothesis that the agriculture perspective was central in articulating the debate cannot be readily confirmed from the institutional affiliation of most authors involved in the discussions, some insights are suggestive. Michael A. Huston, the leading voice of the criticisms of the interpretations of the biodiversity experiments, grew up in Iowa and was very aware of agriculture (Krause, 1996). John Vandermeer, a co-author in the critical response to the BIODEPTH first results, is the author of most of intercropping theory. Both authors contributed in the synthesis conference and the publications that followed.

The dialogue between agriculture and ecology during the debate certainly went both ways, and that was what made it a fertile debate. Introducing the concepts of transgressive and non transgressive overyielding for instance, was important, but as much important was to point out that complementarity among species may exist and exert a strong effect in absence of transgressive overyielding (Loreau, 1998). Both fields expanded the understanding of reality in this process. Hopefully the legacy of Darwin will continue to provide insight in the much needed dialogue between Ecology and Agriculture. "As has always been my practice, let us seek light on this head from our domestic productions. We shall here find something analogous".

CONCLUSION

Several lessons may be learned from the history of the biodiversity-ecosystem functioning debate about how Science works and the interplay between Science and Policy. A central lesson is that considering any research project as a linear and simple process of hypothesis testing based on logic and empirical evidence is a naive and incomplete picture of Science. Any research project is immersed in several concentric contextual spheres: a disciplinary context, a scientific paradigm, an institutional framework, and a socio-political context. All of these influence the evolution of scientific inquiry, and are relevant to understand the scientific discourse.

Scientific debates may become heated and passionate. Consensus and scientific progress can occur by focusing on clarifying definitions, making methodological and conceptual assumptions explicit, and embracing a perspective that help transcending the disciplinary boundaries and blindness. In the case of the biodiversity-ecosystem functioning debate, the dialogues between the disciplines of ecology and agriculture, and between community and

ecosystem ecology have been and will continue to be essential for advancing towards a strong scientific basis for policy decisions in biodiversity conservation and sustainability.

CHAPTER III. CROP SPECIES DIVERSITY AFFECTS PRODUCTIVITY AND WEED SUPPRESSION IN PERENNIAL HERBACEOUS POLYCULTURES UNDER TWO MANAGEMENT STRATEGIES

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ABSTRACT

Species diversity can increase natural grasslands productivity but the effect of diversity in agricultural systems is not well understood. Our objective was to measure the effects of species composition, species richness, and harvest management on crop and weed biomass in perennial herbaceous polycultures. In 2003, 49 combinations of seven species (legumes, C_3-, and C_4-grasses) including all monocultures and selected 2 to 6 species polycultures were sown in small plots at two Iowa, USA locations in a replicated field design. Plots were split in half and managed with either one or three harvests in each of 2004 and 2005. Biomass increased log-linearly with species richness in all location-management environments and the response was not different between managements. Polycultures outyielded monocultures on average by 73 %. The most productive species in monoculture for each management best explained the variation in biomass productivity. The biomass of plots containing this species did not increase with richness in most environments but biomass of plots without this species increased log-linearly in all cases. Weed biomass decreased exponentially with richness in all environments. On average, increasing species richness in perennial herbaceous polycultures increased productivity and weed suppression, but well-adapted species produced well regardless of richness.

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INTRODUCTION

Diverse multispecies agroecosystems have been proposed as a viable alternative to sustain agriculture productivity in the near future (Kirschenmann, 2007). Perennial herbaceous polycultures are mixtures of perennial crops grown for biomass, forage, or food production. Such mixtures can produce agronomic and environmental benefits derived from perennial cover and species diversity (Jackson, 2002). Relative to annual crop species, perennial crops can produce more ground cover, thereby reducing soil erosion (Pimentel et al., 1987); minimize nutrient leaching (Dinnes et al., 2002); sequester more carbon in soils (Freibauer et al., 2004); and provide continuous habitat for wildlife (Entz et al., 2002). Mixtures of species in intercrops or polycultures have the potential to improve the performance of a cropping system in terms of yield, nutrient cycling efficiency, weed suppression, and other pests control (Holland and Brummer, 1999; Liebman, 1995; Vandermeer et al., 2002). Perennial herbaceous polycultures are commonly used in forage production, especially as legume-grass mixtures (Barnes and Collins, 2003). Mixing legumes with cool-or warm-season grasses can improve forage yield, nutritive value, stand longevity, and seasonal distribution of forage compared to grass monocultures, including those fertilized with nitrogen (George et al., 1995; Sleugh et al., 2000). Perennial grain production and bioenergy are two additional uses of perennial herbaceous polycultures that have been proposed. Perennial grain crops for human food or animal feed are being developed in the USA (Cox et al., 2002; DeHaan et al., 2005) and elsewhere (Sacks et al., 2003; Weik et al., 2002a). Finally, with the increased interest in bioenergy, perennial polycultures offer a low-input, less polluting, and more efficient alternative to annual monocultures (Tilman et al., 2006a).

The contribution of plant species diversity to productivity and other ecosystem functions is a controversial issue in ecology (Loreau et al., 2001). Species diversity refers to the number of species present in an area (i.e. richness) and their relative abundance (i.e. evenness), and most studies use species richness as a proxy for diversity. The current consensus among ecologists is that ecosystem functions are influenced by individual species' traits, complementarity among them, and environmental factors (Hooper et al., 2005). Although increasing diversity can have a range of effects on ecological processes, depending

on species composition and environmental context, diversity can increase productivity because of: a) the major effect of one or few very productive species (Huston et al., 2000); b) positive interactions among species due to complementarity or facilitation (Tilman et al., 2006b); and c) a combination of both (Loreau and Hector, 2001). In most experiments with randomly assembled plant communities from natural grasslands, plots with greater species diversity tend to out-yield plots with low diversity (Hector et al., 1999; Tilman et al., 2006b). However, diversity may not change ecosystem functions that are controlled primarily by abiotic factors or by the dominance of a single species (Hooper et al., 2005). When environmental factors are held constant, increasing species richness generally decreases community susceptibility to invasion by weeds or other pests, because fewer resources are available to invaders and because species that are strongly competitive or that offer biotic control of a prospective invader are more likely to be included (Knops et al., 1999). Diversity may also increase ecosystem stability by reducing variability in response to environmental fluctuations and increasing resistance and resilience to perturbations (Loreau et al., 2002).

In agriculture, research on forage crop mixtures and on intercrops has focused on the role of diversity in productivity and other agronomic variables. The effect of diversity on biomass productivity depends on the particular system, species, and processes considered (Sanderson et al., 2004; Trenbath, 1974). Mixtures of forages have received considerable attention because domesticated pastures and hay fields often are seeded with multiple species and natural grazing lands contain a diversity of species. A review of the literature on forage mixture experiments shows that productivity can be maximized at either low or high diversity, but complex mixtures (i.e. mixtures with more than 2 species) can maximize more ecosystem functions at the same time, e.g., temporal distribution of production, persistence, resistance to invasion, tolerance to fluctuating environmental conditions, and positive impacts on water quality (Sanderson et al., 2004). Experiments using management strategies such as cattle grazing instead of clipping indicate that complex mixtures comprising grasses, legumes, and composites are more productive in dry years, and have less weed invasion than simple mixtures (Sanderson et al., 2005).

Most ecological research modeling the relationship between diversity and ecosystem function cannot be extrapolated directly to agriculture. First, ecologists typically use a

relatively large number of native species in randomly assembled communities, without including "true replications" (sensu Huston and McBride, 2002) of the same species combinations in their experimental design. Second, the research is often conducted in low fertility soils and with a single management scheme, i.e., one-time biomass harvest (see for example Tilman et al., 1996). Finally, the experiments usually include just a few dominant species, which comprise most species in agriculture and which can have major effects on ecosystem functions (Hooper, 1997). In contrast, most agricultural research considers only a subset of mixtures of well-adapted species (Soder et al., 2007), and consequently does not provide a range of species richness to fit a model of productivity-richness.

Our objective was to measure the effect of species composition, species richness, and harvest management on aboveground crop and weed biomass in perennial herbaceous polycultures in fertile agricultural soils in central Iowa, USA. We tested the hypotheses that: a) crop biomass productivity increases with increasing species richness; b) weed biomass is reduced with increasing species richness; c) the presence or absence of certain species changes the slope of the regression of biomass production on species richness; and d) harvest management changes the slope of the regression of biomass production on species richness. Our intent was to bridge the gap between agronomic and ecological experiments by conducting the study under agricultural conditions (i.e., well adapted species grown on fertile soils) using true replication and a set of mixtures large enough to model the relationship between diversity and ecosystem function.

MATERIALS AND METHODS

Experimental design

Eight perennial species from four functional groups were included in the experiment (Table 3.1): legumes (alfalfa, [*Medicago sativa* L.], white clover [*Trifolium repens* L.], Illinois bundleflower [*Desmanthus illinoensis* (Michx.) MacM. ex B.L. Robins. & Fern.]), cool-season grasses (orchardgrass [*Dactylis glomerata* L.] and intermediate wheatgrass [*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey]), warm-season grasses (switchgrass [*Panicum virgatum* L.] and eastern gamagrass [*Tripsacum dactyloides* (L.) L.]), and a composite (Maximilian sunflower [*Helianthus maximiliani* Schrad.]). These species were chosen because they are widely sown forage and biomass species or, in some cases, are potential perennial grain crops (Cox et al., 2006). Within functional groups, the species possess different traits that give rise to divergent phenotypes (e.g., depth of rooting or spreading vs. bunch-type growth).

We assembled 52 plant community entries (i.e., treatments), including all monocultures (8 entries) and certain polycultures of two (19 entries), three (13 entries), four (7 entries), six (3 entries), and eight species (1 entry); an unseeded plot was also included for weed biomass comparisons. Maximilian sunflower was poorly adapted and did not survive well, so the three entries with this species were dropped from all analyses (one monoculture and two polycultures with four and eight species). Table 3.2 shows the 49 entries considered in the analyses. For all levels of species richness some entries included each individual species and other entries did not. We included at least one legume species in all plots except for non-legume monocultures and two-species combinations of grasses. The same individual grasses and grass mixtures were included with each of the three legumes. Each entry was replicated three times in a 12 by 13 lattice design at two locations in Iowa, USA: the ISU Agronomy and Agricultural Engineering Research Farm, east of Boone, Boone Co., IA, with a Nicollet loam soil (fine-loamy, mixed, superactive, mesic Aquic Hapludolls) and the ISU Hinds Research Farm, north of Ames, Story Co., IA, with a Spillville loam soil (fine-loamy, mixed, superactive, mesic Cumulic Hapludolls). The Boone site had a long-term history of forage breeding nurseries (primarily alfalfa, birdsfoot trefoil, white clover, and orchardgrass) in a

seven year rotation with corn, soybean, and oat, while the Ames site was previously in row crops (corn, soybean, and oat experiments).

The entire plot area was tilled before planting in spring 2003. Seed density was based on the recommended seeding rates for monoculture stands (Barnhart, 1999; Piper and Pimm, 2002) corrected for germination percentage (Table 3.1). Seed density for species in mixtures was reduced proportionally to the number of species in the mix (e.g., a two-species mix included half of the seeds of each monoculture). The experiment was planted on 18 May 2003 in Ames and 21 May 2003 in Boone. Seeds were drilled into 4-m by 3-m plots consisting of 20 rows spaced 0.15-m apart. Plots were separated by 1.5-m borders planted with tall fescue (*Festuca arundinacea* L.) managed as turfgrass. No fertilizer or lime was applied. Soil samples were taken on 1 July (Boone) and 2 July (Ames) 2003. Six soil cores 0.15 m deep per plot were sampled from 5 plots in each replication and location, and analyzed in the ISU Agronomy Soil Testing Lab. Analysis for Boone was 42 ± 5 mg.kg^{-1} P, 143 ± 14 mg.kg^{-1} K, 11.3 ± 1.9 mg.kg^{-1} N-NO$_3$, and 4.1 ± 0.4 mg.kg^{-1} N-NH$_4$, and for Ames 82 ± 5 mg.kg^{-1} P, 157 ± 14 mg.kg^{-1} K, 14.7 ± 1.9 mg.kg^{-1} N-NO$_3$, and 6.2 ± 0.4 mg.kg^{-1} N-NH$_4$.

Plots were mowed on 18 June and 12 Sept. 2003 in Boone, and on 20 June and 13 Sept. 2003 in Ames, to a 0.15-m height to control weeds; biomass was not measured or removed. In October 2003, we measured plant establishment by counting the number of plants of each species present along a 1-m transect per plot. Eastern gamagrass was reseeded by hand in April 2004, because no plants were found in 2003.

In 2004, each plot was split in half to form two 2-m x 3-m sub-plots that were allocated to either a three harvest management, simulating a hay system with removal of all biomass, or to a one harvest management, simulating a perennial grain system with only seed biomass of selected species being removed. The same allocations were used in 2005 as well. Plots were machine clipped with a flail-type harvester (Carter Mfg., Brookston, IN) equipped with an electronic weigh system. A single 1-m wide by 3-m long strip was harvested for biomass through the center of each small plot. The adjacent 50-cm strips on either side of the measured area were cut immediately after data collection so that all forage was clipped to ground level. In the three harvest management the clipped material was removed from the

plot area while in the one harvest management it was not. These two contrasting managements allow us to compare a forage system where all biomass is removed (three harvests) with a perennial grain crop system, where most nutrients remain on the plots (one harvest).

Plots in the hay management were harvested on 26 May, 13 July, and 13 Sept. 2004 and 25 May, 8 July, and 22 Aug. 2005 in Boone, and on 28 May, 15 July, and 16 Sept. 2004 and 3 June, 27 July, and 15 Sept. 2005 in Ames. In the grain management, the reproductive structures of the four species with the highest seed yield and most easily harvested seeds (Illinois bundleflower, orchardgrass, intermediate wheatgrass, and switchgrass) were hand harvested from the entire plot area as each species matured, dried, weighed, and added to the total plot biomass. Although some seed was produced by alfalfa, pollinators were infrequent in the plots and the seed yield was minimal. Biomass on these plots was harvested once at the end of the growing season, on 8 Nov. 2004 and 4 Oct. 2005 in Boone, and 9 Nov. 2004 and 27 Oct. 2005 in Ames.

Before each harvest, biomass was sampled by clipping two 0.09-m^2 quadrats per plot. Samples were weighed fresh, species were identified and sorted in the laboratory, dried, and dry mass was recorded. The dry matter percentage of the samples and the fresh weight of the machine harvested strips were used to calculate total biomass dry weight per square meter. Relative proportion of each species was also calculated and used to differentiate biomass productivity of the seeded species versus weeds. Due to field labor constraints, samples were not collected immediately before the third harvest in the three-harvest management in 2004 at Ames although machine harvest was conducted. Therefore, because data on the relative proportion of each species and of weeds are missing for this harvest the data were dropped from the analysis and the total yield for the hay management in Ames, 2004 comprised only the first two harvests.

The dominant species in each plot was defined as the seeded species with maximum biomass production in the plot. The Berger-Parker dominance index, which represents the proportion of whole plot biomass produced by the dominant species, was calculated for each plot (Wilsey and Polley, 2004).Values of the dominance index close to one indicate communities that are dominated by one single species.

In this paper, "biomass of seeded species" refers to aboveground plant biomass of the species deliberately seeded into the plot; "biomass of cultivated weeds" refers to seeded species that occurred in plots where they were not intended, either because they were in the soil seed-bank, or seeds were carried from adjacent plots by the wind, or in few cases the planter; "biomass of wild weeds" refers to species outside the seeded list. We define "biomass of cultivated species" as the sum of the biomass of seeded species plus the biomass of cultivated weeds; "weed biomass" is the sum of biomass of cultivated and wild weeds; and "total biomass" of a plot comprises biomass of seeded species plus weed biomass. Although crop species diversity comprises species richness and evenness, in this experiment we manipulated only crop species richness as a proxy for crop diversity.

Data analysis

To determine differences among entries and relevant interactions, an overall analysis of variance for biomass was performed including location, management, year, and species combinations as fixed effects and replication and block within replications as random effects. If interaction effects were significant, further analyses by location, management, or year were conducted. The yield of monoculture plots was separated using Fisher's protected least significant difference (LSD) with $\alpha=0.05$.

A series of nine linear models of biomass of seeded species as the dependent variable and seeded species richness as the independent variable and transformations of each variable using natural logarithm and inverse functions were compared using R^2 and Akaike's Information Criterion (AIC) statistics (data not shown). Biomass of seeded species as a function of natural logarithm of seeded species richness was the best model using this criterion and was used in all further analyses. The linear effect of seeded species richness on seeded biomass, cultivated biomass, weed biomass, and total biomass was tested with contrasts.

To determine the relative importance of the presence or absence of a single species and the importance of seeded species richness on the biomass of seeded species, we used a model selection procedure as described by Deutschman (2001). Several mixed models were constructed using biomass of seeded species as the dependent variable, with entries nested

within the following explanatory variables, which were considered to be fixed effects: (1) the presence or absence of each species individually, (2) the natural logarithm of seeded species richness, (3) both the natural logarithm of seeded species richness and the presence or absence of the single species that individually best explained the variation in biomass, and (4) both variables included above together with their interaction. Models were compared using AIC, where models with smaller AIC values indicated a better fit. The single species that best explained the variation in biomass within each environment was denoted the "driver species" for that environment. We used contrasts to test the linear effects of logarithm of seeded species richness on biomass of seeded species in plots with and without the driver species. If the linear contrasts were significant, we calculated the regression coefficients, standard error, and their 95% confidence intervals on the original data (not means). Two slopes were considered different from each other if their 95% confidence intervals did not overlap. To test for functional group composition effects, contrasts in each environment were performed among plots with different functional group composition.

For the weed biomass data, a similar set of analyses was conducted to that described for biomass of seeded species. The best model for total weed biomass as a function of seeded species richness across all environments was an exponential function (i.e., natural logarithm of weed biomass as a linear function of seeded species richness). The same model selection procedure, based on the AIC values, was conducted to determine the relative importance of the presence or absence of single species and of seeded species richness on total weed biomass. Linear effects of seeded richness were then tested with contrasts on entries with the most weed suppressive species and on those without the most weed suppressive species.

All analyses of variance and contrasts were performed using PROC MIXED, and regression coefficients were calculated using PROC REG, in the SAS statistical software package (SAS-Institute-Inc., 2003).

RESULTS

Because the entry x year x location and entry x year x management interactions were generally absent, and the trends of biomass productivity as a function of richness were similar across the two years in which biomass was measured (data not shown), all subsequent analyses were averaged across years (2004 and 2005). In contrast, the presence of an entry x

location x management strategy interaction suggested we analyze each location by management combination separately. For simplicity, we refer to location-management combinations as "environments" and these are Boone-one harvest (B1), Boone-three harvests (B3), Ames-one harvest (A1), and Ames-three harvests (A3).

The observed number of seeded species increased linearly as actual seeded richness increased (R^2=0.69 overall, 0.76 for B1, 0.73 for B3, 0.68 for A1, and 0.59 for A3, P<0.0001 in all cases). Therefore, seeded species richness was a good estimator of observed seeded species richness. The species which were most often missing were eastern gammagrass and switchgrass, particularly at higher seeded richness levels. Because the analyses with seeded and observed richness produced very similar results, we report the results using seeded richness to be able to make planned comparisons based on the original experimental design. Evenness was not controlled experimentally and all mixture plots showed a high level of dominance (Table 3.3). The species that dominated most plots based on the Berger-Parker dominance index were alfalfa for B3, orchardgrass for A1, and both alfalfa and orchardgrass for B1 and A3 (Table 3.3).

Biomass of seeded species

Entries (i.e., treatments) differed for biomass of seeded species in all environments (i.e., we rejected the ANOVA null hypothesis that all entries are the same, data not shown). Among monocultures, the most productive species under three harvests was alfalfa, while for the one harvest management, intermediate wheatgrass was the most productive (Table 3.4). The differences in biomass among species grown in monocultures also varied greatly with environments, with alfalfa yielding 7.3 times the average of the other monocultures in B3, while the best species outyielded the average of the other monocultures by 2.4 times for A3, 3.4 times for B1, and 3.5 times for A1 (Table 3.4). The average yield of polycultures was 73% greater than the average yield of the monocultures across all environments (61% for B1, 102% for B3, 49% for A1, and 79% for A3; P <0.0001 in all cases).

Seeded biomass, cultivated biomass, and total biomass increased log-linearly with seeded richness in all environments (Fig.1). There was no evidence of differences in the slopes of the regressions of biomass of seeded species on seeded species richness across management

strategies (Fig.1). For B1, 95% confidence intervals for slopes were 222 ± 74 g.m^{-2}: for B3, 339 ± 98 g.m^{-2}: for A1, 164 ± 68 g.m^{-2}: and for A3, 227 ± 52 g.m^{-2}.

Effect of driver species on biomass of seeded species

In each environment the species that yielded the most in monoculture (Table 3.4) was also the species whose presence or absence best explained the variability in biomass of seeded species based on the AIC values obtained through our model selection process (Table 3.5). For this reason we refer to these species as the "driver species" in each environment. For the three harvest environments, alfalfa was both the driver species and the species that dominated most plots (Table 3.3). However, for the one harvest environments, intermediate wheatgrass was the driver species, having lower AIC values than both alfalfa and orchardgrass, which dominated most plots (Table 3.3). Models of biomass as a function solely of the driver species in each environment had lower AIC values than models including only seeded species richness (Table 3.5) suggesting that the driver species had a greater effect on productivity than did richness *per se*. Nonetheless, of the ten models compared using AIC (Table 3.5), the one that included seeded species richness, the presence or absence of the driver species, and their interaction produced the best fit for three out of four environments. For the fourth environment, A3, the best model included both variables but not their interaction.

On average plots including the driver species in a particular environment produced 2.4 times as much biomass as the plots without a driver species (B1=1.7 times, B3=3.7 times, A1=2.2 times, A3=2.0 times; P <0.0001 in all cases). In plots without the driver species, the biomass of seeded species increased log-linearly with increasing seeded species richness (Fig. 3.2) and the slopes of the regressions were not different across management strategies (slopes were 198 ± 97 g.m^{-2} for B1, 188 ± 53 g.m^{-2} for B3, 99 ± 72 g.m^{-2} for A1, and 165 ± 59 g.m^{-2} for A3). In contrast, plots containing driver species produced the same or less biomass as species richness increased. The one exception to this trend was A3, where all plots consistently increased biomass with richness. In this environment the slopes of regressions of biomass of seeded species as a function of seeded species richness were not different, because the interaction of intermediate wheatgrass by richness was absent in the

model (Table 3.5) and the 95% confidence intervals for the slopes overlapped (slope for A3 plots with alfalfa was 105 ± 69 g.m^{-2}).

Weed biomass

The most frequent wild weeds were *Taraxacum officinale* G.H. Weber ex Wiggers, *Conyza canadensis* (L.) Cronq.*, Chenopodium album* (L.), and *Setaria* spp. Alfalfa and orchardgrass were the most frequent cultivated weeds. Species in monoculture varied in their ability to suppress weeds, with alfalfa the most suppressive in Boone and orchardgrass in Ames (Table 3.4). White clover and intermediate wheatgrass were also weed suppressive.

Cultivated weed biomass, wild weed biomass, and total weed biomass decreased exponentially with seeded richness in all environments (Figs.1 and 3). Models of ln transformed weed biomass as a function of seeded species richness had higher AIC values than models including only the most weed suppressive species in each environment (Table 3.5). Therefore, the impact of particular species on weed suppression was greater than richness *per se*. As with biomass, of the ten models compared using AIC (Table 3.5), the best was a factorial model of seeded species richness and the most weed suppressive species. For B1, the best model also included the interaction between species richness and the presence or absence of the most weed suppressive species, but for the other three environments, the best model did not include the interaction.

On average, plots not including the most weed suppressive species in the environment had 6.4 times more weed biomass than the plots with the most weed suppressive species (6.3 times for B1, 3.8 times for B3, 10.7 times for A1, and 4.8 times for A3; $P < 0.0001$ in all cases). In three out of four environments, total weed biomass decreased with seeded species richness in all plots regardless of the presence or absence of the most weed suppressive species (Fig. 3.3). In A1, where orchardgrass exerted very high weed suppression, there were no significant trends. As expected, because the interaction of species by richness was not present for most environments (Table 3.5) slopes for regressions of weed biomass as a function of seeded species richness in plots with and without the most weed suppressive species (Fig. 3.3) were not different. The only exception was B1, where the reduction in

weed biomass in plots without alfalfa was greater than the reduction in plots with alfalfa, and where the interaction of alfalfa by richness was also present in the model (Table 3.5).

A strong negative exponential relationship between total weed biomass and biomass of seeded species was observed in each environment. All linear regressions of logarithm of total weed biomass as a function of biomass of seeded species were significant at $P<0.0001$. Equations for total weed biomass (y, in g m^{-2}) as a function of biomass of seeded species (x, in g m^{-2}) were: $y=70.8*0.997^x$ (Adj. $R^2 =0.17$) for B1, $y=213.0*0.997^x$ (Adj.$R^2 =0.34$) for B3, $y=174.4*0.995^x$ (Adj.$R^2 =0.30$) for A1, and $y=304.7*0.995^x$ (Adj.$R^2 =0.31$) for A3.

Functional composition effects on biomass of seeded species and weeds

Plots including both C_3 grasses and legumes outyielded plots with only legumes or only C_3 grasses in almost all environments (Table 3.6). The two exceptions were in B3, where legume-only plots outyielded legume – C_3 grass mixtures, and in A1, where C_3 grasses were no different from legume – C_3 grass mixtures. As a group, legumes outyielded C_3 grasses in the three harvestmanagement at Boone, and C_3 grasses outyielded legumes in the one harvest management in both locations. The contribution of C_4 grasses to biomass production was marginal overall during the period of measurements of this study as expected for newly establishing warm-season grasses. Adding a C_4 grass to a plot with legumes and C_3 grasses did not change the productivity in any environment.

Plots including both C_3 grasses and legumes had less weed biomass than plots with only legumes or only C_3 grasses in almost all environments (Table 3.6). The three exceptions were in B3, where legume-only plots and legume – C_3 grass mixtures had no differences in weed biomass, and in the one harvest managements, where C_3 grasses-only were no different from legume – C_3 mixtures. Legume-only plots had lower weed biomass than plots with only C_3 grasses in B3; they were not different in B1 and A3; plots with only C_3 grasses had lower weed biomass than legumes-only plots in A1. Adding a C_4 grass to a plot with legumes and C_3 grasses did not reduce weed biomass in any environment except A3.

DISCUSSION

Our first hypothesis that crop biomass productivity increased with increasing species richness was supported by the evidence. Therefore, in our agriculture systems with fertile soils and highly productive forage species, polycultures on average yielded more than monocultures, and more diverse polycultures yielded more than less diverse ones. We measured this trend at richness levels with six or fewer species, which may be relatively low for natural systems, but which are relevant for agricultural systems, Our results are consistent with previously published research from natural grasslands and forage mixtures (Hector et al., 1999; Loreau et al., 2001; Sanderson et al., 2004; Tilman et al., 2006a).

However, a deeper analysis of the data revealed that the highest yields were from plots including a single driver species, and that plots at any species richness (even monocultures) that included this species had nearly equivalent yields and were the highest of those observed for a given environment. This is also consistent with a recent meta-analysis of ecological research: yields of diverse polycultures do not differ from the best yielding monoculture (Cardinale et al., 2006).

The diversity-productivity relationship can be explained by complementarity among species or by selection effects (Loreau and Hector, 2001). Different species with complementary traits (e.g., rooting depth) can use different resources or niches, providing the community as a whole access to more resources and making it more productive than its constituent species individually. Positive interactions among species can also increase the performance of the community, a process called facilitation. Selection effects are apparent when highly productive species dominate a mixture due to processes such as inter-specific competition (Loreau and Hector, 2001). Selection effects can result from sampling species for inclusion in randomly assembled communities (Huston and McBride, 2002), because the probability of including a highly productive species in the mixture increases as the number of species in the mixture increases.

In our experiment, species combinations were not assembled at random, but rather designed so that each level of species richness had plots with and without each species. This design does not avoid the sampling effect, because the proportion of plots with each single species has to increase with increasing species richness. However, we were able to separate

the individual species effects from richness effects. We showed that individual species had major effects on productivity: the presence or absence of alfalfa in the three harvest management and intermediate wheatgrass in one harvest management better explained biomass productivity than did species richness. This suggests that the relationship between biomass productivity and species richness may change depending on the presence or absence of certain "driver" species. These driver species are well adapted to the agronomic environment (soils, climate, and management) and are highly productive. The driver species can dominate the plant community when it has a higher competitive ability than other species (e.g., alfalfa in B3) but in other situations, other species that are less productive but more competitive can dominate instead (e.g., orchardgrass in A1). The inclusion of a driver species in the polyculture is the main factor that explained the increase in average productivity of the more species-rich communities. Polycultures where this driver species was present did not show an increase in biomass productivity with species richness. However, biomass productivity increased with species richness in the absence of the driver species. Seeding a monoculture or a binary mixture of the best adapted, highest yielding species is easier to manage and may be a better option than seeding a complex polyculture in some circumstances (see for instance Tracy and Sanderson, 2004a). Nevertheless, polyculture yields were typically as high as the best monoculture, and in some environments were even higher (e.g., A3). Because increasing species richness may offer other benefits than simply biomass productivity, as we discuss below, mixture planting may be a better option.

The results of this study also support our second hypothesis that weed biomass is reduced with increasing species richness. These findings are consistent with the hypothesis that resident diversity increases the competitive environment and makes invasions by other species more difficult (Elton, 1958). Our results are limited to the context of the species, soil types, and high weed pressure of the agricultural conditions studied. Nevertheless, these results add to the experimental evidence supporting the contention that plant species richness increases resistance of ecosystems to weeds and other pests (Dukes, 2002; Knops et al., 1999; Tracy and Sanderson, 2004b). Highly weed-suppressive species had strong effects on weed invasion; some monocultures (alfalfa in Boone, orchardgrass in Ames) were as

effective at suppressing weeds as polycultures. However, the same species may not maximize both biomass productivity and weed suppression together simultaneously. In our experiment, alfalfa monoculture in B3 maximized both productivity and weed suppression, but in the other three environments, different species maximized each function (combinations of intermediate wheatgrass, alfalfa, and orchardgrass). This suggests that as more agronomic and ecological functions are considered, species-rich polycultures may simultaneously optimize more functions, and may be more beneficial than simple monocultures (Sanderson et al., 2004).

In this paper we reported results from the second and third year after establishment of perennial plant communities. Although for these two years the trends of productivity vs. richness were the same, we expect that succession in further years may change species richness and evenness of the community, and possibly identity of driver species and the slope of the regression productivity vs. richness. The potential of polycultures in maintaining stable communities over time under agricultural conditions is a relevant issue to be explored in further years of this experiment.

Our final hypothesis that harvest management changes the relationship between productivity and richness can be rejected because the overall trends were similar for both management strategies (i.e., they had equal slopes [Fig. 3.1 and 3.2]). This means that species-rich plots had higher yields and lower weed invasion under both one- and three-harvest managements, and that the increase in yield with richness was similar for both managements. These findings suggest that species rich polycultures should be considered even in intensively harvested agroecosystems, such as herbaceous perennial mixtures harvested as biofuel feedstocks (Tilman et al., 2006a). However, the identity of the driver species changed for each management regime, suggesting that harvest management needs to be considered when choosing the species to include in a polyculture. Furthermore, in farming systems where management practices may change due to unplanned conditions such as weather or market fluctuations, polycultures may offer the advantage of more flexibility in management options, whereas monocultures are more rigid in their requirements.

Differences in biomass productivity among plots with different functional group composition can be explained by differences in species composition. For instance, in

environments where alfalfa was the driver species, plots with legumes outyielded plots with C_3 grasses, but where intermediate wheatgrass was the driver, plots with C_3 grasses outyielded legume plots. Plots with a combination of legumes and C_3 grasses in most cases were the highest yielding plots, as is well known in forage production. The marginal contribution of the C_4 grasses is explained because C_4 grasses tend to take longer to establish, and this is particularly the case in our experiment with Eastern gamagrass, which did not establish at all in the first year. We expect that the contribution of C_4 grasses will increase in future years of the experiment.

In a sustainable agriculture context, crop communities need to simultaneously optimize various ecosystem functions, including but not limited to productivity. Although dominance effects explained the majority of the relationship between diversity and productivity in our study, the productivity of perennial monoculture and polyculture plots over longer time frames is needed to determine the ultimate role of complementarity effects in explaining the relationship between diversity and stability over time. Because single species may have great effects on the relationship between diversity and ecosystem function, experiments where species effects cannot be discriminated from richness effects should be considered with caution. Controlling experimentally both richness and species composition increases the number of plots exponentially, necessitating the judicious choice of species adapted to the environments considered.

This experiment yielded two main conclusions. First, increasing species richness in perennial herbaceous polycultures has measurable benefits in terms of productivity and weed suppression. This finding, well acknowledged by ecologists, should be applied to the design of agriculture systems. Second, well adapted species have major effects on the relationship between diversity and ecosystem function. This finding, more widely understood by the agricultural community, should inform more ecological theory. More research bridging these two scientific traditions is needed to advance towards a more sustainable agriculture.

Table 3.1.Species included in the experiment, their functional group classification, the cultivar planted, and seeding rate of pure live seeds (PLS) of monocultures.

Functional Group	Species name and cultivar	Seeding rate (PLS) $g \cdot m^{-2}$	$Seeds \cdot m^{-2}$
Legume	Alfalfa –54H91	1.7	838
Legume	White clover – Alice	0.5	795
Legume	Illinois bundleflower – UMN (PNL 730 and 723)[1]	1.2	199
C_3 grass	Orchardgrass – Duke	1.1	1625
C_3 grass	Intermediate wheatgrass – Oahe	1.4	239
C_4 grass	Switchgrass – Cave in Rock	1.1	621
C_4 grass	Eastern gamagrass – PMK-24	1.1	15

[1] Illinois bundleflower seed was increased from two Iowa collections (PNL 545 at Dubuque, IA, and PNL 539 at Spirit Lake, IA) at the University of Minnesota.

Table 3.2. Entries included in the experiment, arranged by species richness and functional group richness, and total number of entries by species richness. Entries in each cell are separated by commas. An unseeded plot was also included for weed biomass comparisons.

		Species richness				
		1	2	3	4	6
Number of functional groups	1	AA[z], WC, IB, OG, IW, SW, EG	AA-WC, AA-IB, WC-IB, OG-IW, SW-EG	AA-WC-IB		
	2		AA-OG, AA-IW, AA-SW, AA-EG, WC-OG, WC-IW, WC-SW, WC-EG, IB-OG, IB-IW, IB-SW, IB-EG, OG-SW, IW-EG	AA-OG-IW, AA-SW-EG, WC-OG-IW, WC-SW-EG, IB-OG-IW, IB-SW-EG	AA-WC-OG-IW, AA-WC-SW-EG, AA-IB-OG-IW, AA-IB-SW-EG, WC-IB-OG-IW, WC-IB-SW-EG	
	3			AA-OG-SW, AA-IW-EG, WC-OG-SW, WC-IW-EG, IB-OG-SW, IB-IW-EG		AA-WC-OG-IW-SW-EG, AA-IB-OG-IW-SW-EG, WC-IB-OG-IW-SW-EG
Total		7	19	13	6	3

[z] Abbreviations of species: AA = alfalfa, WC = white clover, IB = Illinois bundleflower, OG = orchardgrass, IW = intermediate wheatgrass, SW = switchgrass, EG = eastern gamagrass.

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Table 3.3. Dominance in polyculture plots. Observed dominance index (maximum proportion of biomass of a single species per plot) and its standard error (SE) for each level of seeded species richness, by environment. Percent of total number of polyculture plots dominated by each species and percent of polyculture plots seeded with each species dominated by that species, by environment. Each species was seeded in the same number of polyculture plots (42.5% of total) in the experiment.

Seeded species Richness	B1		B3		A1		A3	
	Dom	SE	Dom	SE	Dom	SE	Dom	SE
2	0.85	0.01	0.86	0.01	0.91	0.02	0.87	0.01
3	0.75	0.02	0.78	0.02	0.86	0.02	0.77	0.02
4	0.72	0.03	0.81	0.02	0.78	0.02	0.71	0.03
6	0.55	0.04	0.70	0.04	0.73	0.03	0.59	0.04

Dominant species	% total plots	% plots with sp.	% total plots	% plots with sp.	% total plots	% plots with sp.	% total plots	% plots with sp.
Alfalfa	28	67	41	99	19	46	33	80
White clover	14	33	25	60	9	21	18	43
Illinois bundleflower	5	13	7	17	2	5	3	8
Orchardgrass	27	65	15	35	40	96	31	75
Intermediate wheatgrass	20	48	8	20	18	44	8	20
Switchgrass	6	14	3	8	11	27	5	13
Eastern gamagrass	1	2	1	3	1	2	1	3

Table 3.4. Monocultures biomass. Means and least significant differences for biomass of seeded species (SS), cultivated (CW), wild (WW), and total weeds (TW)of monoculture plots in two Iowa locations under two harvest managements averaged over two years.

Species	B1				B3				A1				A3			
	SS	CW	WW	TW	SS	CW	WW	TW	SS	CW	WW	TW	SS	CW	WW	TW
								Biomass (g m^{-2})								
Alfalfa	688	26	15	41	1209	9	51	60	437	36	53	89	507	28	68	97
White clover	96	45	7	52	371	23	7	30	147	1	64	65	306	71	52	111
Illinois bundleflower	326	343	26	370	141	300	140	439	98	249	181	430	50	234	159	394
Orchardgrass	198	30	3	33	142	153	17	169	447	14	3	17	382	44	10	54
Intermediate wheatgrass	958	128	2	129	247	271	46	317	896	37	0	37	356	295	52	347
Switchgrass	312	121	30	151	71	228	85	314	352	70	122	193	146	223	61	284
Eastern gamagrass	53	130	144	274	17	230	85	315	51	136	239	375	17	198	188	386
Unseeded plot	0	179	130	309	0	197	109	305	0	50	338	389	0	32	252	284
LSD	*282*	*119*	*35*	*121*	*186*	*119*	*86*	*127*	*138*	*98*	*53*	*103*	*185*	*104*	*47*	*113*

Table 3.5. Model selection results. Akaike's Information Criterion (AIC) values of several models for biomass of seeded species and logarithm of total weed biomass in two Iowa locations under two harvest managements averaged over two years. Values for the driver species model and the best model for each environment are italicized.

	Seeded biomass				Ln (total weed biomass)			
	B1[1]	B3	A1	A3	B1	B3	A1	A3
Null model	4070.3	4105.7	3990.8	3888.0	1222.6	1164.7	1308.0	1201.5
Seeded species richness	4016.9	4094.6	3959.8	3856.2	1196.3	1134.5	1297.2	1176.6
Alfalfa	3992.0	*3838.5*	3960.6	*3801.3*	*1152.1*	*1097.1*	1303.0	1191.7
White clover	4031.2	4112.6	3969.2	3886.8	1219.3	1145.6	1308.8	1193.3
Illinois bundleflower	4032.4	4109.4	3968.5	3886.0	1220.6	1149.9	1302.1	1205.7
Orchardgrass	4027.9	4112.7	3962.1	3865.5	1201.3	1143.6	*1243.5*	*1100.0*
Intermediate wheatgrass	*3979.7*	4112.8	*3855.1*	3882.9	1221.6	1155.6	1264.7	1197.7
Switchgrass	4030.1	4113.1	3965.9	3894.7	1221.6	1160.4	1308.9	1209.1
Eastern gamagrass	4031.6	4113.2	3970.1	3891.6	1222.6	1160.7	1302.9	1200.4
Richness + driver species (no interaction)	3979.8	3832.5	3856.4	*3776.7*	1142.5	*1085.5*	*1246.9*	*1092.9*
Richness + driver species + interaction	*3977.2*	*3821.2*	*3851.6*	3782.5	*1140.3*	1090.3	1250.8	1096.5

[1] B1= Boone-one harvest, B3 = Boone-three harvests, A1 = Ames-one harvest, A3 = Ames-three harvests

Table 3.6. Contrasts for functional groups. Estimated values (Est), standard error (SE), and significance value (P) for contrasts for biomass of seeded species (Seeded) and total weeds biomass (Weeds) among plots with different functional groups composition in two Iowa locations under two harvest managements averaged over two years.

	Contrast	B1			B3			A1			A3		
		Est	SE	P	Est	SE	P	Est	SE	P	Est	SE	P
							$g.m^{-2}$						
Seeded	Leg-C_3-C_4 vs. Leg-C_3	1	34	NS[1]	46	25	NS	32	25	NS	0	22	NS
	Leg-C_3-C_4 vs. Leg-C_4	254	34	<.0001	73	25	0.0052	393	25	<.0001	179	22	<.0001
	Leg-C_3 vs. Legume	235	36	<.0001	-114	27	<.0001	357	27	<.0001	155	24	<.0001
	Leg-C_3 vs. C_3 grass	116	49	0.0215	464	37	<.0001	38	37	NS	182	32	<.0001
	Legume vs. C_3 grass	-119	53	0.0263	579	40	<.0001	-319	39	<.0001	27	35	NS
Weeds	Leg-C_3-C_4 vs. Leg-C_3	-14	15	NS	-33	15	0.0243	8	18	NS	-6	14	NS
	Leg-C_3-C_4 vs. Leg-C_4	-49	15	0.0016	-60	15	<.0001	-167	18	<.0001	-112	14	<.0001
	Leg-C_3 vs. Legume	-40	16	0.0158	-15	16	NS	-160	19	<.0001	-87	15	<.0001
	Leg-C_3 vs. C_3 grass	-37	22	NS	-138	21	<.0001	-5	26	NS	-101	21	<.0001
	Legume vs. C_3 grass	3	23	NS	-123	23	<.0001	154	28	<.0001	-15	22	NS

[1] NS = Not significant at 0.05
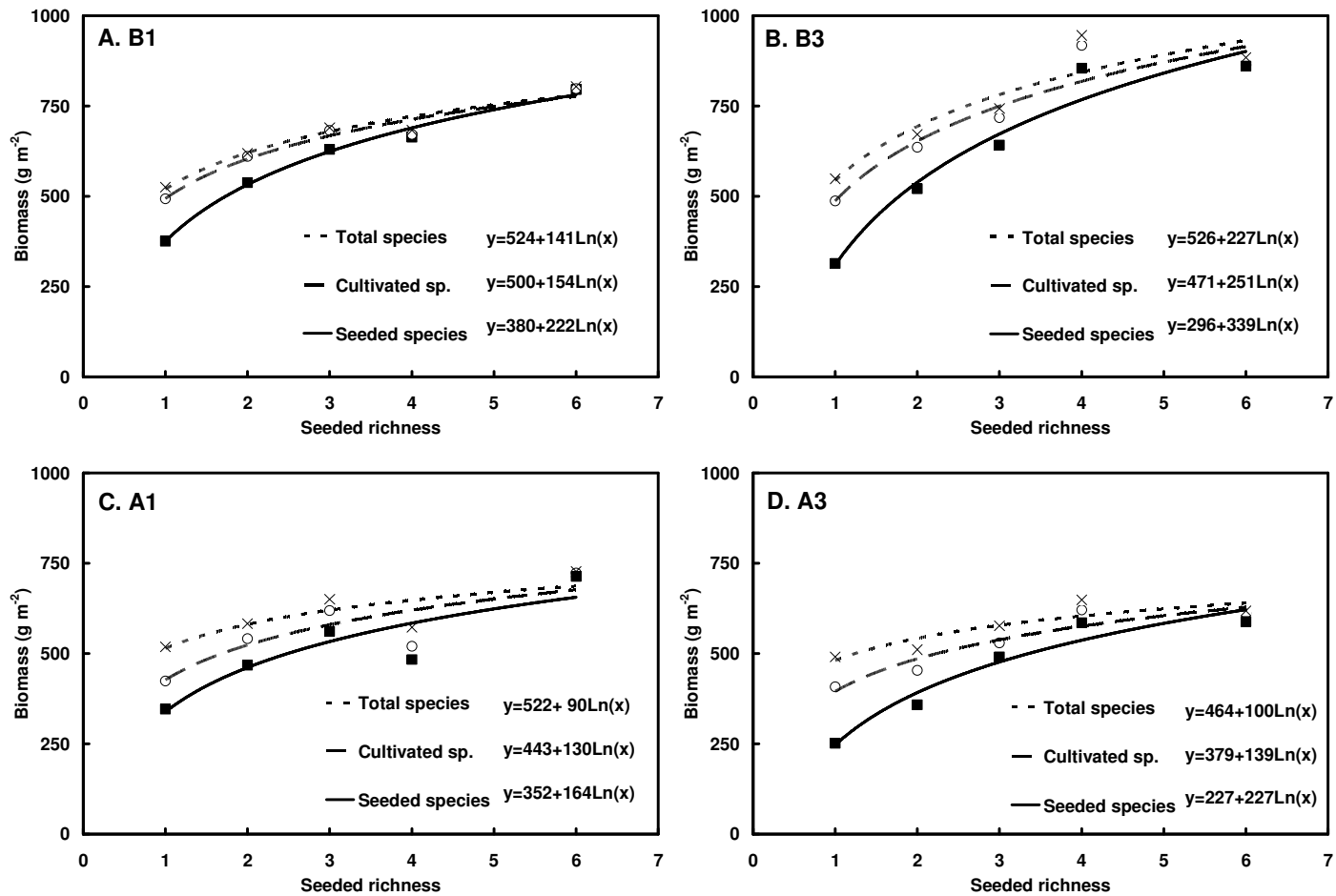
Figure 3.1. Mean biomass of seeded species, cultivated species biomass (seeded species plus cultivated weeds), and total biomass (cultivated species plus wild weeds) by seeded species richness and log-linear regression lines as a function of seeded species richness in two Iowa locations under two harvest managements averaged over two years: A. Boone-one harvest; B. Boone-three harvests; C. Ames-one harvest; and D. Ames-three harvests. All linear regressions are significant at P<0.0001. Regression coefficients are given for each line.
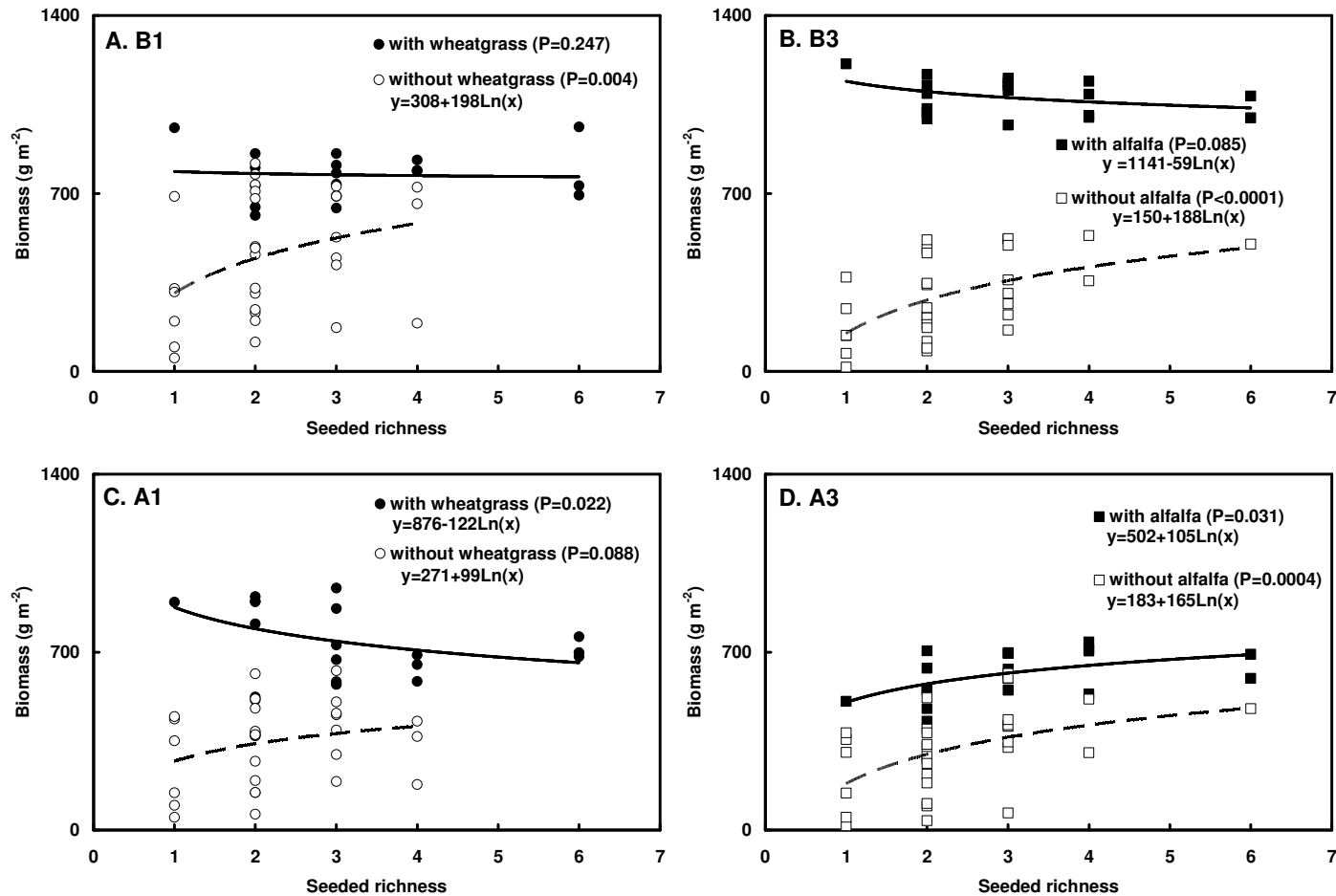
Figure 3.2. Biomass of seeded species means by entries and log-linear trends for plots including the driver species (closed symbols) and not including the driver species (open symbols) as a function of seeded species richness in each environment: A. Boone-one harvest; B. Boone-three harvests; C. Ames-one harvest; and D. Ames-three harvests. P values for the contrasts of the log-linear trends on the means are shown. Equations for regressions with slopes different from zero (P<0.10) are shown.

A. B1

Weeds biomass (g m^{-2})

□ without alfalfa (P=0.0020)
Y=149*0.55^x

■ with alfalfa (P=0.0061)
Y=5*0.84^x

Seeded richness

B. B3

Weeds biomass (g m^{-2})

□ without alfalfa (P=0.0031)
Y=222*0.71^x

■ with alfalfa (P=0.0107)
Y=46*0.70^x

Seeded richness

C. A1

Weeds biomass (g m^{-2})

○ without orchardgrass (P=0.1268)

● with orchardgrass (P=0.2955)

Seeded richness

D. A3

Weeds biomass (g m^{-2})

○ without orchardgrass (P=0.0069)
Y=244*0.70^x

● with orchardgrass (P=0.0401)
Y=19*0.76^x

Seeded richness

Figure 3.3. Total weed biomass means by entries and exponential trends for plots including the most weed suppressive species (closed symbols) and excluding such species (open symbols) as a function of seeded species richness in two Iowa locations under two harvest managements averaged over two years: A. Boone-one harvest; B. Boone-three harvests; C. Ames-one harvest; and D. Ames-three harvests. P values for the linear contrasts on log transformed weed biomass are shown. Equations for significant regressions (P<0.05) are shown. There was no evidence of differences in the two slopes in each graph for environments B, C, and D, at P=0.05.

Picture 1. Polyculture plots in Boone, Iowa, June 2006.

CHAPTER IV. DIVERSITY AFFECTS PRODUCTIVITY OVER TIME THROUGH COMPLEMENTARITY AND STABILITY IN PERENNIAL POLYCULTURES

A paper to be submitted to Crop Science

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ABSTRACT

The mechanisms responsible for increases in productivity with increased species diversity are subjects of debate, as is the consistency of diversity effects across time and environments. The effects of species richness, species composition, and time on biomass production was measured for perennial herbaceous polycultures under two management systems in a replicated experiment over four years at two locations in Iowa, USA. Biomass increased with richness in all environments but one, and year did not change the biomass-richness relationship. Individual species differentially affected the biomass-richness relationship between years under the single harvest management regime, but not under the multiple harvest management regime. The observed polyculture overyielding was due to complementarity among species in the community rather than selection effects of individual species at all richness levels across environments. Legume-grass facilitation may explain this complementarity effect. Polycultures with high richness had lower variability in yield (i.e., greater yield stability) than the highest yielding monocultures measured as deviations of the regression between entry means and the overall environment-year means. Diverse perennial polycultures may be a stable and sustainable alternative for low input production situations.

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INTRODUCTION

Most current agriculture systems are structured with the goal of maximizing productivity in the short term, sometimes at the expense of stability over time (Brummer, 1998). Diversification of farming and cropping systems with multiple species can enhance simultaneously productivity and stability. For instance, polyculture systems may reduce the dependence on external inputs, economic risk, and food insecurity, while protecting natural resources (Liebman, 1995). Perennial herbaceous polycultures for grain, forage, or biomass production offer an alternative to increase diversity in agricultural landscapes, especially in highly erodible lands suitable for low input systems (Cox et al., 2006; Jackson, 2002; Schulte et al., 2006).

Plant species and functional diversity can increase productivity compared to monocultures, a phenomenon termed overyielding, but the mechanisms responsible for these effects are debated (Fargione et al., 2007; Hector et al., 2007; Loreau et al., 2001). Species rich communities have a greater diversity of traits (e.g., various rooting depths) and may use resources more completely than monocultures. Positive interactions among species can enhance productivity in diverse communities (e.g., legumes can improve nitrogen availability to other species). These mechanisms, collectively referred as complementarity, provided the initial hypothesis for the relationship between diversity and productivity (Loreau and Hector, 2001; Tilman et al., 1996). Experimentally assembled diverse communities also have greater chance to include highly productive dominant species that increase community productivity (Huston, 1997), an example of the selection effect (Loreau and Hector, 2001). Because complementarity and selection have different practical implications for the management of agroecosystems and both may operate at the same time, it is relevant to distinguish between these effects in biodiversity experiments.

A second issue of debate is whether overyielding effects observed in diversity experiments are consistent across time and environments. Long term studies in grasslands have shown a consistent and increasingly positive diversity effect on productivity and stability (Tilman et al., 2006b), and experiments conducted at multiple locations throughout Europe have shown in general a consistent increase in productivity with diversity across locations (Hector et al., 1999). However, experiments may operate at spatial and temporal

scales smaller than relevant to capture community dynamics (Hooper et al., 2005; Srivastava and Vellend, 2005).

Stability of a system has many dimensions that are not necessary correlated: variability of production over time, the ability to maintain productivity in face of external disruptions (resistance), the speed of recovery after a perturbation (resilience), and the amount of perturbation tolerated before reducing productivity substantially (robustness) (Loomis and Connor, 1992; Loreau et al., 2002; McCann, 2000). Stability of production may be observed at the community level while drastic changes at the population level occur over time (Lehman and Tilman, 2000). Because of this hierarchical aspect of stability, research should focus on precise definitions that could provide practical information for management decisions. The plant breeding concept of yield stability of crop varieties (Finlay and Wilkinson, 1963) is proposed here as a potential contribution to the study of stability in biodiversity experiments.

Previous research with herbaceous perennial polyculture communities in central Iowa, USA, showed an increase in mean biomass production with seeded species richness, but with a strong effect of individual species on that relationship (Picasso et al., 2008). In this paper, we examine the richness—productivity relationship over a longer time frame (three years) to test three hypotheses: (1) that the observed relationship between richness and biomass productivity was due to complementarity among species and not to a selection effect; (2) that the richness—productivity relationship remained the same across two harvest management regimes at each of two locations across three years; and (3) that diverse polycultures were more stable across environments than monocultures.

MATERIALS AND METHODS

Experimental design

Fifty-two plant community entries (i.e., treatments) were assembled using eight perennial species from four taxonomic groups: legumes (alfalfa, [*Medicago sativa* L.], white clover [*Trifolium repens* L.], Illinois bundleflower [*Desmanthus illinoensis* (Michx.) MacM. ex B.L. Robins. & Fern.]); C3 grasses (orchardgrass [*Dactylis glomerata* L.] and intermediate

wheatgrass [*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey]); C4 grasses (switchgrass [*Panicum virgatum* L.] and eastern gamagrass [*Tripsacum dactyloides* (L.) L.]); and a composite (Maximilian sunflower [*Helianthus maximiliani* Schrad.]). All monocultures (8 entries) were included, as well as selected polycultures of two (19 entries), three (13 entries), four (7 entries), six (3 entries), and eight species (1 entry); an unseeded plot was also included for weed biomass comparisons. The suite of treatments was not random but rather was intended to balance species composition; for all levels of species richness some entries included each individual species and other entries did not, so we could analyze the effect of individual species. Because legumes have shown to have a major impact on biodiversity experiments (Hector et al., 2007; Spehn et al., 2002), we included at least one legume in all entries except for monocultures and two-species combinations of grasses, and the same grass species and mixtures were included with each of the three legumes. Monoculture seed identity and seed density were: alfalfa (cv. 54H51) 838 PLS m^{-2}, white clover (cv. Alice) 795 PLS m^{-2}, bundleflower (Univ. of Minnesota accessions) 199 PLS m^{-2}, orchardgrass (cv. Duke) 1625 PLS m^{-2}, intermediate wheatgrass (cv. Oahe) 239 PLS m^{-2}. switchgrass (cv. Cave-in-Rock), 621 PLS m^{-2}, eastern gamagrass (cv. PMK-24) 15 PLS m^{-2}, and Maximilian sunflower (local prairie seed) 332 PLS m^{-2} based on standard agronomic recommendations for Iowa (Barnhart, 1999; Piper and Pimm, 2002). A replacement design was used (Jolliffe, 2000), such that seed density for species in polycultures was reduced proportionally to the number of species (e.g., a two-species mix included half of the seeds of each monoculture). Thus, the expected proportion of each species in the polyculture was 0.50, 0.33, 0.25, 0.17, and 0.13 for two, three, four, six, and eight species respectively, and expected evenness was 1 for all polycultures.

Each entry was replicated three times in a 12 by 13 alpha lattice design at two locations in Iowa, USA: the Iowa State University Agronomy and Agricultural Engineering Research Farm, east of Boone, Boone Co., IA, with a Nicollet loam soil (fine-loamy, mixed, superactive, mesic Aquic Hapludolls) and the ISU Hinds Research Farm, north of Ames, Story Co., IA, with a Spillville loam soil (fine-loamy, mixed, superactive, mesic Cumulic Hapludolls). In spring 2003 tillage was conducted before drilling the mix of seeds into 4-m by 3-m plots consisting of 20 rows spaced 0.15-m apart. Plots were mowed in June and Sept.

2003 to a 0.15-m height to control weeds. In October 2003 the number of plants of each species present along a 1-m transect per plot was counted. Eastern gamagrass was reseeded by hand in April 2004, because no plants were found in 2003. More details on the sites can be found elsewhere (Picasso et al., 2008).

In 2004, each plot was split in half to form two 2-m x 3-m sub-plots that were allocated to either a multiple harvest system with removal of all biomass, or to a single harvest management simulating a perennial grain system with only seed biomass of selected species being removed. The same allocations were used in 2005 and 2006 as well. Plots were machine clipped with a flail-type harvester (Carter Mfg., Brookston, IN) equipped with an electronic weigh system. A single 1-m wide by 3-m long strip was harvested for biomass through the center of each small plot. The adjacent 50-cm strips on either side of the measured area were cut immediately after data collection so that all biomass was clipped to ground level. Dry matter percent of samples taken from each plot immediately before each harvest were used to calculate dry biomass weight per plot (hereafter referred as total biomass).

In the multiple harvest system, plots were harvested three times per year in 2004 and 2005, in late May, mid July, and mid Sept.; and twice in 2006, in late June and mid Aug. In Ames in 2004 the third harvest was incomplete, and so this harvest data was dropped from the analyses. In the single harvest management, plots were harvested in late Oct. to early Nov. each of the three years. Reproductive structures of four species (bundleflower, orchardgrass, wheatgrass, and switchgrass) were hand harvested from the entire plot area as each species matured, weighed, and added to the total plot biomass in 2004 and 2005, but no seed harvest was conducted in 2006.

Two different methods were used to estimate relative abundance of each species (both seeded and weeds). In 2004 and 2005, individual species biomass was measured by clipping two 0.09-m^2 quadrats per plot, sorting species in the laboratory, and weighing them. In 2005 and 2006, individual species ground cover percentage was recorded from visual observations on each plot by the same observer. Linear regressions for the relative abundance of each species based on biomass and ground cover for 2005 revealed a strong association between the two variables for most seeded species (all P values <0.0001 and average R^2 = 0.78),

although linear coefficients were not equal to one for several species. Therefore relative abundance in 2006 was estimated using relative cover data for 2006 and regression coefficients from 2005. We estimated the biomass using the regression coefficients, rather than using the cover estimates, because the linear coefficients differ among species because of density differences, i.e., the biomass per percent of cover varies among species.

Data analyses

Because previous analyses (Picasso et al., 2008) demonstrated the existence of location and management system x entry interactions, all analyses were conducted by location and management, hereafter referred as environments: Boone-one harvest (B1), Boone-three harvests (B3), Ames-one harvest (A1), and Ames-three harvests (A3). For each environment a heterogeneous regression lines mixed model was fit including observed richness of seeded species (natural log transformed, continuous variable), year (repeated measures on each plot), richness x year interaction, replications, and blocks within replication. All factors were considered fixed except for replication and block(rep) which were considered random. An autoregressive covariance structure for the residuals was used. In order to fit the correct model, we first tested the hypothesis that the effect of richness was zero for all years by fitting a model with only year and year x richness effects, which we rejected if the year x richness effect was significant. If the first hypothesis was rejected, we tested a second hypothesis of no year x richness interaction by fitting a full model with year, richness, and year x richness, and rejecting if year x richness was significant (Littell et al., 1996). Least square means for each entry were calculated, and means were separated using Fisher's protected LSD. Because the presence of individual species was shown to affect the relationship between biomass and richness (Picasso et al., 2008), the effect of the single species with higher monoculture yields (i.e., alfalfa in the multiple harvest management and intermediate wheatgrass in the single harvest system) at each location was tested. First, the three way interaction of richness x year x species was tested, and if found significant the richness x species interaction was tested for each year independently, using the same iterative procedure as described before.

In order to identify the ecological mechanisms behind the relationships between total biomass and richness, we partitioned the net richness effect into complementarity and selection effects using the method of Loreau and Hector (2001) as follows:

$$\Delta Y = Y_O - Y_E = N\overline{\Delta RY}\,\overline{M} + N\operatorname{cov}(\Delta RY, M)$$

where the net richness effect ΔY is the difference between the observed yield of the polyculture (Y_O) and the expected yield (Y_E) based on the sum of the component species' monoculture yields weighted by their proportion in the mixture. A positive net richness effect means that the polyculture yields were greater than the average of the monocultures, a condition we define as "polyculture overyielding."

The complementary effect is denoted by $N\overline{\Delta RY}\,\overline{M}$, where N is the number of species in the mixture, $\overline{M}$ is the mean monoculture yield of the component species, and $\overline{\Delta RY}$ is the mean relative yield deviation across the i species in the polyculture. The relative yield deviation of a given species, ΔRY_i, is the difference of that species' observed relative yield (RY_i)—its polyculture yield divided by its monoculture yield—and its expected relative yield (ERY_i) based on the proportion seeded in the polyculture. A positive value of ΔRY_i means that the species in polyculture yielded greater than expected, a condition we define as "species overyielding." The selection effect is defined as $N\operatorname{cov}(\Delta RY, M)$, i.e., the covariance between relative yield deviations and monoculture yields.

Complementarity occurs when the species in the polyculture, on average, yield more (or less) than expected based on their monoculture yield and their proportion in the mixture. The selection effect is present if the relative yield deviation is related to monoculture performance (i.e., as monoculture yield increases, relative yield deviations in polycultures also increase). The net richness effect, complementarity, and selection effect can each be positive or negative independently, so this method provides a practical framework to understand the mechanisms involved in the productivity- richness relationships.

A mixed model similar to the one used for biomass was fit for each of the three effects (i.e., net richness effect, complementarity, and selection effects) and least square means by richness were calculated across years by environment, and compared using Fisher's protected LSD. In our calculations we used the monoculture yields averaged over the three replications

in the experiment, so the mean monoculture yield by environment and year was the basis for comparisons to polyculture yield and relative yield as is recommended for intercropping experiments by Federer (1993). Monoculture yield of eastern gamagrass was zero in 2004 in Boone, so we excluded it from the analyses for that environment and year to avoid the problem of relative yields approaching infinity when monoculture values are too small (Fargione et al., 2007).

Stability of the entries across environment-years was analyzed using the same approach used for crop varieties in plant breeding programs (Bernardo, 2002; Eberhart and Russell, 1966; Finlay and Wilkinson, 1963). Each of the 12 combinations of location, management system, and year was defined as a unique environment-year combination. The overall mean biomass across all entries was used as a measure of the productivity potential of each environment-year. Entry means by environment-year were regressed against the environment-year means. Also, a second group of regressions were calculated by richness level, to test the effect of richness in stability. The linear regression coefficients (b_1) and root mean squared errors of the regression (RMSE) were used to evaluate the stability of each entry or richness group. The linear coefficient measures the amount of yield change along the environmental gradient and RMSE is associated with the variability of yields and the fit to the linear regression model (Becker, 1981). Three agricultural definitions of stability where considered (Bernardo, 2002): Type I stability occurs when $b_1 = 0$, thus the entry yields the same in all environment-years; Type II stability occurs when $b_1 = 1$, thus the entry performs parallel to the mean for the environment-years; Type III stability considers the RMSE, where lower RMSE values mean higher stability. Finally, a plot of b_1 against the means by entry across environment-years was used to analyze the adaptation of the entries across environment-years (Finlay and Wilkinson, 1963).

All analyses of variance and contrasts were performed using PROC MIXED, and regression coefficients were calculated using PROC REG, in the SAS statistical software package (SAS-Institute-Inc., 2003). Statistical significance is assessed at the 5% level unless otherwise indicated.

RESULTS

Monoculture plots differed for biomass yield among species within environments for all years (Table 4.1). Alfalfa in the multiple harvests management and intermediate wheatgrass in the single harvest management were the highest yielding species in monoculture in most years. In the single harvest system there was no evidence of differences in alfalfa and switchgrass monoculture yields to intermediate wheatgrass some years. White clover, eastern gamagrass, Maximilian sunflower, and orchardgrass usually had the lowest yields across environments and years.

Richness x year interaction

There was a strong association between the observed richness of seeded species (hereafter, S) and the original richness of seeded species at the time of sowing (S_0) for each combination of environment and year (P<0.0001). However, linear coefficients and the R^2 values for the fitted regressions decreased after the first year under the three harvest management system in both locations, indicating that the association became weaker as some species were apparently lost from the plots across richness levels. The upper bounds on the 95% confidence intervals for the linear regression coefficients were lower than 1 for all environments in all years, so S was consistently lower than S_0. In order to reflect accurately the observed richness of seeded species in the plots, S was used for analyses of richness by year interaction.

We found an overall effect of species richness on biomass in A3 (P=0.047), B1 (P=0.0004), and B3 (P=0.055), but not in A1 (P=0.37). The three-harvests environments had no richness x year interaction (P=0.42 for A3 and P=0.91 for B3), therefore, a model without interaction was fit, where biomass was a log linear function of richness (b_1=91.7, P=0.012 for A3 and b_1=138.4, P=0.0065 for B3). A richness x year interaction was found only in B1 (P=0.052), although the slopes for all years were positive (b_1=106.4, P=0.041 for 2004, b_1=241.4, P<0.0001 for 2005, and b_1=163.1, P=0.011 for 2006). There was not a consistent trend of either strengthening or weakening of the relationship with time. For all environments biomass differed among years (P<0.0001).

Alfalfa in the multiple-harvests regime and intermediate wheatgrass in the single-harvest regime were two individual species that were shown previously to affect the biomass-richness relationship (Picasso et al., 2008). The three way interaction of richness x year x species (intermediate wheatgrass for single-harvest and alfalfa for multiple-harvests) was found for the single-harvest management (P<0.0001 for A1 and P=0.002 for B1), but not for the multiple-harvests (P=0.05 for A3 and P=0.08 for B3). Biomass of plots with alfalfa was consistently higher than that in plots without alfalfa across richness levels (i.e., no interaction richness by alfalfa was found). The interaction richness x species was tested for each year separately in the single harvest system, and it was found for B1 in 2004 and A1 in 2005. However, in these two situations biomass of plots with intermediate wheatgrass was usually higher than that in plots without intermediate wheatgrass across richness levels (i.e., there was no crossover, only magnitude differences).

Overyielding and mechanisms

A positive net richness effect was observed across all environments for all richness levels (Fig. 4.1). Therefore, polyculture yields were greater than the average of the component species in monoculture; in other words, the polycultures exhibited overyielding. In Boone, overyielding was similar across richness levels, but in Ames, the overyielding was larger for polycultures with more than three species. A positive complementarity effect was also observed across all environments, and the effect was larger at higher richness levels (Fig. 4.1). This indicated that on average the species in polycultures had relative yields greater than expected based on their seeded proportion (i.e., species overyielding was observed). No selection effect was present at any richness level in A1, A3, and B3. However, in B1, a negative selection effect was observed, in which polycultures with higher richness values had a larger negative selection effect.

The relative yield deviation ($\Delta RY_{i,}$) of orchardgrass ranged from 0.4 to 1.8 and was the largest of all species in polycultures across all richness levels in all environments, indicating orchardgrass overyielding was highest. Relative yield deviation for alfalfa ranged between 0 and 0.3 across richness levels in all environments. The relative yield deviations for all other species were usually zero across richness levels in all environments.

Stability analysis

Monocultures and polycultures displayed a wide range of linear coefficients and RMSE (Table 4.2). Entries with linear coefficients equal to zero had the lowest mean yields across environment-years. Alfalfa had the highest coefficient (b_1=2.4 ± 1.3), which was significantly greater than one (P<0.1), indicating that this species in monoculture has yields above average in high productivity environment-years, and below average in low productivity situations. White clover, Illinois bundleflower, intermediate wheatgrass, and Maximilian sunflower had coefficients equal to one, indicating that these species had yields parallel to the environment-year mean, and therefore are stable according to the Type II stability definition. Orchardgrass, switchgrass, and eastern gamagrass had coefficients lower than one and not different from zero (P<0.1), indicating that they have constant yields across environment-years. The two monocultures with highest yields across environment-years (alfalfa and intermediate wheatgrass) had the two highest RMSE values for monocultures, and therefore, the lowest Type III stability. All polycultures with more than four seeded species had higher Type III stability than the two highest monocultures.

When the regressions were calculated across entries by richness level, all linear coefficients of polycultures were equal to one (Fig 2a), indicating Type II stability. Monocultures had average linear coefficient lower than one. Also, polycultures with increasing seeded richness had increasingly lower RMSE values as a trend, and therefore, higher Type III stability.

All entries with alfalfa had both higher linear coefficients and higher yield across environment-years than entries without alfalfa (Fig 2b). Within the entries with alfalfa, those with wheatgrass had lower linear coefficients than those without wheatgrass. Within the entries without alfalfa, those with wheatgrass had higher overall means than those without wheatgrass.

DISCUSSION

Effect of richness over time

The lack of richness x year interaction across environments in our experiment with high yielding species in agricultural conditions provides further evidence that richness effects are not transient, as many ecological studies have shown (Hector et al., 2007; Hooper and Dukes, 2004; Tilman et al., 2006b; van Ruijven and Berendse, 2005). The diverse polycultures had similar yields as the highest yielding species in monoculture, which were the same for the three years. The production difference between the highest yielding species in monoculture and the other species decreased over time, and changes in the ranking of species for monoculture yields are likely in future years (e.g., switchgrass in the single harvest system continuously increased its yields and reached the yields of wheatgrass by 2006, while wheatgrass continuously decreased yields over time). In perennial plant communities, long term changes are central to deciding which species or combination of species to plant. Although in the short term the best adapted monocultures are no different than the polycultures, in the long term polycultures may be advantageous and transgressive overyielding may be observed more often.

Complementarity and selection effects

Across all environments and richness levels, the net richness effect was positive; that is, polyculture overyielding was observed. Complementarity effects were positive and the selection effects either negative or zero. Complementarity arises when the average relative yield deviation is greater than zero. In the absence of a selection effect, the polyculture will exhibit overyielding if complementarity is present. However, complementarity may be counteracted by a negative selection effect, resulting in a polyculture that does not exhibit overyielding. In our experiment the two species, orchardgrass and alfalfa, showed overyielding—i.e., they consistently had ΔRY greater than zero, whereas most other species had ΔRY consistently less than zero. This suggests that orchardgrass and alfalfa were largely responsible for the positive complementarity effect. The largest complementarity effect was the result of orchardgrass overyielding in polycultures with legumes. Although we did not

measure plant nitrogen, orchardgrass leaves in polycultures were visually greener than leaves in monocultures. This suggests that nitrogen facilitation may have explained the complementarity effect, consistent with other experiments that measured nitrogen pools (see e.g., Fargione et al., 2007).

Positive selection effects are observed when species with highest yields in monoculture overyield in polycultures and low yielding monocultures perform poorly in polycultures. In contrast, negative selection effects exist when species with lowest yields in monoculture overyield in polycultures and species with high monoculture performance underyield. In our experiment, alfalfa in general was highly productive in monoculture and overyielded in mixtures, intermediate wheatgrass was highly productive in A1 but did not overyield in mixtures, and orchardgrass yielded poorly in monocultures but highly overyielded in mixtures in all environments. As a result, in most environments no selection effects were observed because the positive effect of alfalfa was cancelled out by negative effect of orchardgrass. In A1, a negative selection effect was observed due to orchardgrass overyielding and intermediate wheatgrass, with a high monoculture performance not overyielding in mixture.

Our results are consistent with the BIODEPTH experiment at multiple sites throughout Europe (Hector et al., 1999) where across sites polycultures overyielded and complementarity effects were positive, but selection effects were variable. Also, long term experiments on Minnesotan grasslands showed that the complementarity effect increased consistently over time, whereas the selection effect was positive during the first two years and negative later (Fargione et al., 2007). This shift occurred because monoculture yields changed with time as initially low yielding species became the highest yielding ones in later years (Fargione et al., 2007). A negative selection effect has been observed in communities with varying evenness and richness (2003) and in polycultures containing a grass (*Arrhenatherum elatius* [L.] P.Beauv. ex J. Presl et C. Presl) with high monoculture performance which reduced all other species in mixtures (Roscher et al., 2007). Species that increase overyielding by increasing the relative yields of other species, due to improving nitrogen availability for instance, can produce a positive selection effect, as observed for *Trifolium pratense* L., T. repens L. (Roscher et al., 2007). Finally a recent meta-analyses of

plant experiments found that complementarity increased with time in experiments, while selection effects remained constant (Cardinale et al., 2007). Overyielding and the probability of transgressive overyielding (i.e., when the polyculture yield is greater than the highest yielding monoculture) increased in experiments that ran for longer timeframes because complementarity effects among species increased with time (Cardinale et al., 2007). Since most experiments are short term and transgressive overyielding in plant communities may take five years to be observed, the potential for transgressive overyielding has likely been underestimated.

Stability, productivity, and adaptation

From an agricultural perspective stability must be evaluated together with productivity. Three ways to define agricultural stability were considered: Type I stability refers to constant yields across environments; Type II stability occurs when the entry performs parallel to the mean of all other entries for the environments; and Type III stability refers to the variability in yields measured as deviations to the regression line of entry means versus environmental mean (Bernardo, 2002).

The ideal perennial polyculture would have at the Type I stability and maximum yields. However, Type I stability in our experiment was usually expressed by entries with low yields (Table 4.2), as is also the case in plant breeding (Bernardo, 2002). The two exceptions to this general rule were the intermediate wheatgrass monoculture and the intermediate wheatgrass-white clover mixture, which had yields above the average and expressed Type I stability (Table 4.2). These entries may be worth considering for low productivity environments.

Polycultures of all richness levels had Type II stability because polycultures had linear coefficients equal to one and more Type III stability than the average of monocultures because of lower RMSE. Furthermore, polycultures with increasing richness had increasing Type III stability as a trend (Fig 2a). Compared to the two top yielding monocultures (alfalfa and intermediate wheatgrass), the more species rich polycultures (i.e., those comprising 4, 6, or 8 species) had lower variability in yields (Type III stability) and they were more productive in environment-years when the top monocultures did not perform well (Fig 2a).

Entries with linear regression coefficients greater than one are considered to be adapted to high productivity environments, whereas entries with linear coefficients lower than one are considered adapted to low productivity environments (Fig. 4.2a) (Finlay and Wilkinson, 1963). A specific polyculture is ecologically adapted to a certain environment if it shows higher productivity in that environment relative to the other environments. Polycultures with alfalfa, for instance, located in the top right corner of Fig. 4.2b, can respond to high productivity environments better than other polycultures. The inclusion of wheatgrass in polycultures either increased yield (in absence of alfalfa) or increased stability (in presence of alfalfa). Species-rich polycultures that included alfalfa and intermediate wheatgrass provided the best alternative for optimizing yields and stability across environment-years (Figs. 2a, b). In fact, in high productivity environment-years, polycultures yielded as much as alfalfa, and in low productivity environment-years polycultures yielded as much as intermediate wheatgrass.

These analyses revealed that biomass productivity should not be the only variable considered when comparing polycultures to monocultures, or polycultures across different richness levels. Stability, productivity, and ecological adaptability to specific environments are important criteria to consider, especially in those perennial polyculture systems designed for marginal lands. The combined use of regression and stability diagrams as described here may enhance the interpretation of results of other biodiversity – productivity experiments across environments and years.

Table 4.1. Mean biomass (g m⁻²) and least significant difference (LSD) of monoculture plots for two locations in Iowa, under two managements, for three yr.

| | One cut | | | | | | Three cuts | | | | | |
| | Boone | | | Ames | | | Boone | | | Ames | | |
Species	2004	2005	2006	2004	2005	2006	2004	2005	2006	2004	2005	2006
Alfalfa	453	914	343	475	396	72	1321	1085	1113	442	556	516
White clover	86	92	122	254	56	129	311	416	152	274	347	189
Illinois bundleflower	157	565	127	104	114	42	127	149	55	74	25	16
Orchardgrass	141	240	188	553	309	317	146	106	204	536	234	255
Int. wheatgrass	1165	626	456	971	752	494	267	203	339	467	244	194
Switchgrass	250	426	464	254	459	485	64	107	116	242	75	71
Eastern gamagrass	3	108	263	24	70	337	0	31	122	15	27	68
Max. sunflower	175	137	13	299	105	21	273	57	10	356	76	58
LSD		199			149			159			119	

Table 4.2. Stability analyses results. Seeded species composition, seeded richness (S0), mean biomass across environment-years (g m-2), linear regression coefficient (b1) and root mean square error (RMSE) of the regression of entry means over environment-year means, and three types of stability criteria (Type I, II, and III) for each entry over 12 environment-year combinations.

Species composition	S_0	Mean	b_1	RMSE	Stability type		
					Type I[†]	Type II[†]	Type III[§]
		g m^{-2}					
Alfalfa (ALF)		783	2.45	212		>1	Low
White clover (WCL)		268	0.46	139	0	1	Med
Illinois Bundleflower (IBF)		583	1.01	130		1	Med
Orchardgrass (OGR)		347	0.09	138	0	<1	Med
Intermediate wheatgrass (IWG)	1	732	0.42	236	0	1	Low
Switchgrass (SWG)		494	-0.18	95	0	<1	High
Eastern gamagrass (EGG)		436	0.13	135	0	<1	Med
Maximilian sunflower (MSF)		379	0.04	226	0	1	Low
ALF-WCL		726	2.12	139		>1	Med
ALF-IBF		828	2.30	193		>1	Low
WCL-IBF		335	0.50	102	0	1	High
OGR-IWG		489	0.50	136	0	1	Med
SWG-EGG		519	-0.13	95	0	<1	High
ALF-OGR		801	1.49	187		1	Low
ALF-IWG		865	1.54	151		1	Med
ALF-SWG		792	2.03	131		>1	Med
ALF-EGG		793	2.18	143		>1	Med
WCL-OGR	2	476	0.33	91	0	<1	High
WCL-IWG		681	0.76	238	0	1	Low
WCL-SWG		401	1.07	117		1	High
WCL-EGG		385	0.48	138	0	1	Med
IBF-OGR		477	0.70	98		1	High
IBF-IWG		664	1.15	190		1	Low
IBF-SWG		544	0.55	160	0	1	Low
IBF-EGG		475	1.05	87		1	High
IWG-EGG		564	0.23	210	0	1	Low
OGR-SWG		340	-0.04	89	0	<1	High
ALF-WCL-IBF		807	2.21	156		>1	Low
ALF-OGR-IWG	3	797	1.38	121		1	High
ALF-SWG-EGG		795	2.16	116		>1	High
WCL-OGR-IWG		593	0.46	104	0	1	High

Table 4.2. continued

					Type I[†]	Type II[‡]	Type III[§]
WCL-SWG-EGG		400	0.19	158	0	1	Low
IBF-OGR-IWG		566	0.96	121		1	High
IBF-SWG-EGG		500	0.47	168	0	1	Low
ALF-OGR-SWG		816	1.68	151		1	Med
ALF-IWG-EGG		900	1.62	147		1	Med
WCL-OGR-SWG		546	0.17	116	0	<1	High
WCL-IWG-EGG		658	0.60	214	0	1	Low
IBF-OGR-SWG		463	0.91	141		1	Med
IBF-IWG-EGG		633	0.80	244	0	1	Low
ALF-WCL-OGR-IWG		820	1.74	120		>1	High
ALF-WCL-SWG-EGG		750	1.89	188		1	Low
ALF-IBF-OGR-IWG	4	835	1.54	154		1	Med
ALF-IBF-SWG-EGG		786	2.04	165		>1	Low
WCL-IBF-OGR-IWG		645	0.86	150	0	1	Med
WCL-IBF-SWG-EGG		411	0.54	131	0	1	Med
IBF-IWG-EGG-MSF		580	0.73	94		1	High
ALF-WCL-IWG-OGR-EGG-SWG		825	1.60	100		>1	High
ALF-IBF-IWG-OGR-EGG-SWG	6	800	1.25	167		1	Low
IBF-WCL-IWG-OGR-EGG-SWG		600	0.52	114	0	1	High
ALF-WCL-IBF-OGR-IWG-EGG-SWG-MSF	8	794	1.46	139		1	Med

[†] Entries with Type I = 0 have b_1 no different than 0 at P<0.1.

[‡] Entries with Type II <1, =1, or >1 have b_1 <1, =1, or >1 respectively at P<0.1.

[§] Entries with Type III = Low, Med, or High have RMSE values in the top third, medium third, or bottom third of the RMSE ranking respectively
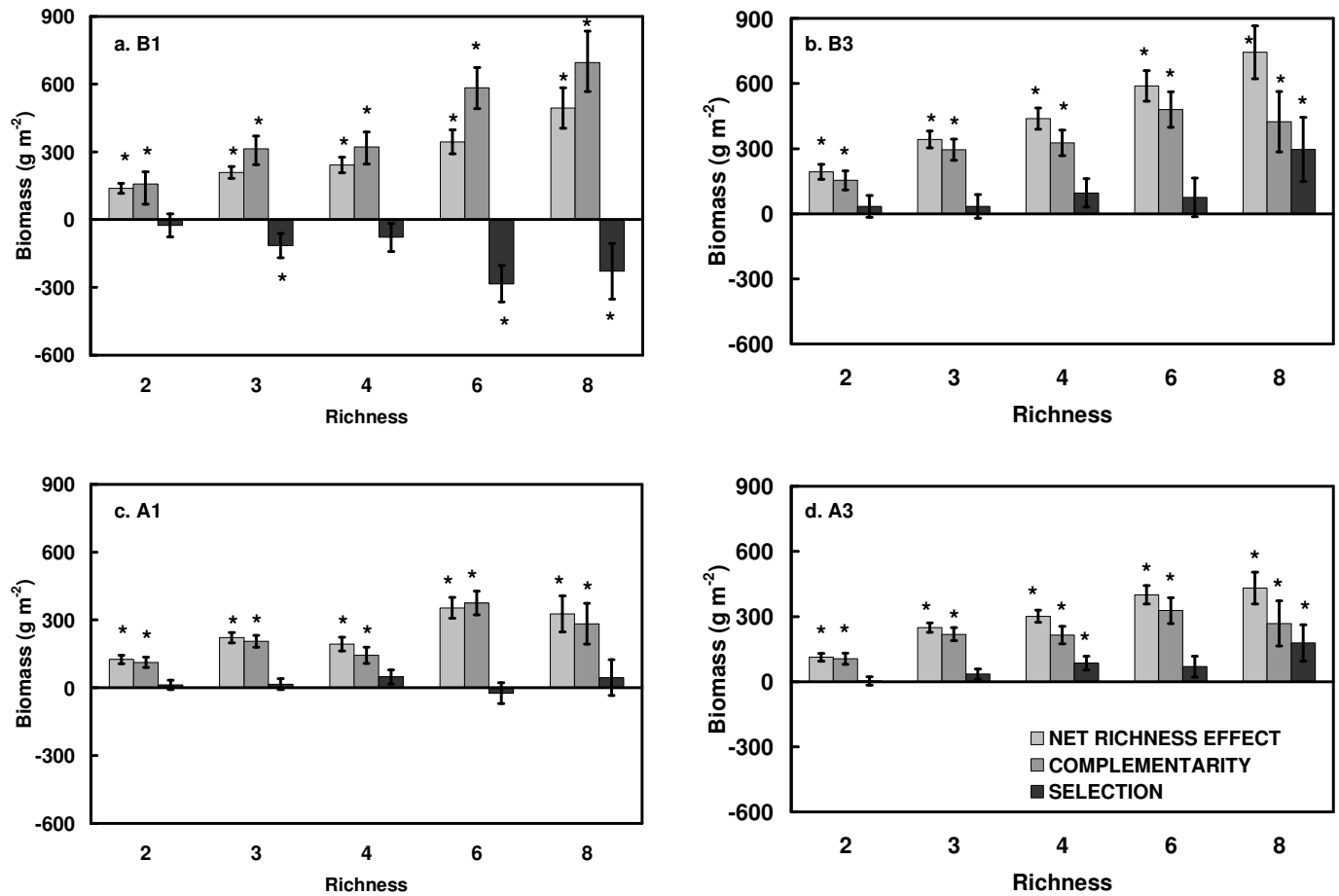
Figure 4.1. Means and standard errors for net richness effect, complementarity, and selection effects by seeded richness for each environment averaged over 3 yr. Means denoted with "*" are different from zero at 5 % probability level. Environments: B1 = Boone-one harvest, B2 = Boone-three harvests, A1 = Ames-one harvest, A3 = Ames-three harvests.
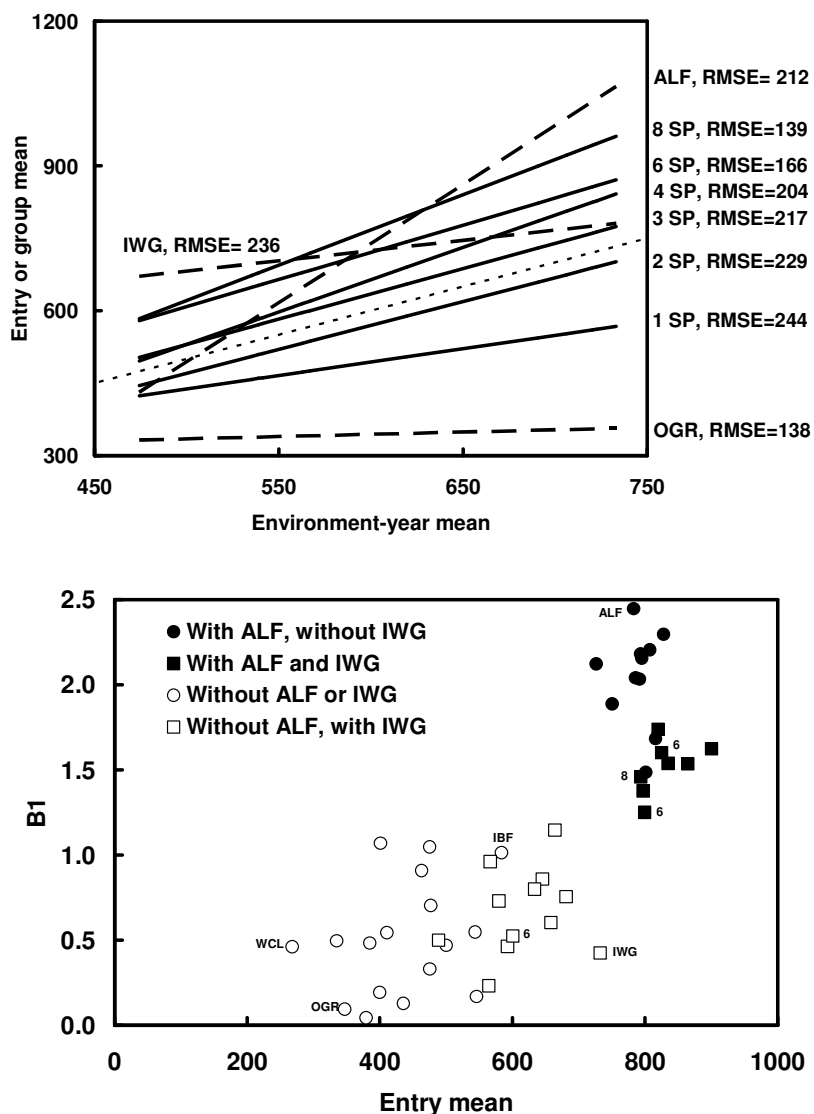
Figure 4.2. Stability plots. a) Linear regressions of the entry means by environment-year against the overall environment-year means for three monocultures (alfalfa, intermediate wheatgrass, and orchardgrass, dashed lines) and regressions by richness group (monocultures, and polycultures of 2 to 8 species, solid lines) with root means square errors of the regressions (RMSE). b Linear coefficient (b1) from the regressions by entry in a) against the entry means across all environment-years. Close symbols are entries with alfalfa, open symbols are entries without alfalfa; squares are entries with wheatgrass, and circles are entries without wheatgrass. Codes: ALF=alfalfa, WCL=white clover, IBF=Illinois bundleflower, OGR= orchardgrass, IWG= intermediate wheatgrass, 6= 6 species polyculture, 8= 8 species polyculture.

Picture 2. Illinois bundleflower leaves and pods.

Picture 3. Intermediate wheatgrass plants.

CHAPTER V. SEED YIELD, FORAGE PRODUCTION, AND COMPETITIVE ABILITY OF PERENNIAL CROPS IN POLYCULTURES

A paper to be submitted to Crop Science

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ABSTRACT

Perennial polycultures have ecological advantages over annual monocultures, but they must also produce high grain or forage yields and suppress weeds effectively to be grown profitably. In a replicated study at two sites in Iowa over three years, we measured seed and forage yield, and weed suppression of two perennial grains (Illinois bundleflower [*Desmanthus illinoensis* (Michx.) MacM. ex B.L. Robins. & Fern.] and intermediate wheatgrass [*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey]) in monoculture and polycultures. Wheatgrass produced its largest seed yield in the second year after seeding (65.8 ± 6.5 g m^{-2}), whereas bundleflower seed did so in the third year (55.0 ± 8.1 g m^{-2}). The mixture comprising both perennial grains produced as much seed as the best yielding monoculture each year. Polycultures of bundleflower with C4 grasses and of wheatgrass with legumes produced as much seed as the monocultures. Most polycultures produced more total forage than did monocultures of bundleflower or wheatgrass. Wheatgrass demonstrated high competitive ability by producing seed yields equal to or greater than expected based on its proportion in the polyculture in all cases. Polycultures containing bundleflower or wheatgrass with highly competitive companions exerted greater weed suppression than wheatgrass or bundleflower monocultures but in most cases they had reduced seed yields. Future research should focus on breeding and management of crop mixtures to minimize competition among crops while maximizing weed suppression.

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INTRODUCTION

Annual grain monoculture systems in the North Central USA are highly productive, but they contribute to serious ecological problems, including soil erosion (Pimentel et al., 1987), nutrient leaching (Dinnes et al., 2002), and hypoxia in the Gulf of Mexico (Rabalais et al., 2002). The native prairies replaced by modern agriculture were diverse mixtures of predominantly perennial species and they lacked these environmental problems, though they produced no harvestable grain (Jackson, 2002). Perennial grain polycultures, i.e., mixtures of herbaceous plants harvested for seed, have been proposed as food production systems with the ecological advantages of perennial cover and diversity (Glover, 2005). Development of perennial grain polycultures with adequate yield will require breeding of perennial grain crops (Cox et al., 2006; DeHaan et al., 2005; Sacks et al., 2003) and agroecological studies to develop best management practices (Cox et al., 2005; Crews, 2005). Perennial grain polycultures have potential application in current low input systems on marginal lands (Ploschuck et al., 2005; Scheinost et al., 2001; Weik et al., 2002a) and as double purpose crops for forage (or biomass) or grain.

Illinois bundleflower (hereafter, referred to as bundleflower) and intermediate wheatgrass (hereafter, wheatgrass) are two promising perennial grain species currently being bred for forage and grain production (Cox et al., 2002; DeHaan et al., 2005; Fischbach et al., 2005b). Bundleflower is a North American native perennial herbaceous warm-season (C4) legume, found in the USA from Minnesota to Florida. Its forage biomass yield in weed-free monocultures ranges from 4.9 Mg ha^{-1} in Iowa (DeHaan et al., 2003) to 23.8 Mg ha^{-1} in Florida (Adjei and Pitman, 1993). Its seed yield in monoculture ranges from 1.7 Mg ha^{-1} in Iowa (DeHaan et al., 2003) to 3.4 Mg ha^{-1} in Florida (Adjei and Pitman, 1993), with a seed protein content of 380 g kg^{-1} (Kulakow, 1999). Bundleflower has shown compatibility for forage production with various C4 grasses (Piper, 1998; Springer et al., 2001).

Wheatgrass is a cool season grass native to central Europe, the Balkans, and Asia Minor, with wide adaptation and high forage productivity in the USA (Sleugh et al., 2000). It is being bred to increase seed production and also being crossed with annual wheat (*Triticum aestivum* L.) to obtain perennial wheat hybrids (Cox et al., 2002; Jones, 1999). Seed yields of up to 1.0 Mg ha^{-1} have been reported in Canada (Kruger, 1997). Forage yields of 4.0 and 2.6

Mg ha^{-1} were reported for the second and third year after seeding in Iowa in fertilized monoculture plots (Sleugh et al., 2000). In Kansas, forage yield up to 12.1 Mg ha^{-1} was also reported (Harmoney, 2005)

Perennial polyculture systems need to include species that have the ability to yield well in competition with other plants and that can suppress weeds given that tillage and broad spectrum herbicides are not management options (Weik et al., 2002b). Plant spatial diversity at the field scale (e.g., mixtures of genotypes with resistance to different disease races or mixtures of species with contrasting resource use patterns) has been shown to suppress weeds, pests, and diseases in agroecosystems (Cox et al., 2005; Knops et al., 1999; Liebman, 1995; Loreau et al., 2001; Wolfe and Barrett, 1980; Zhu et al., 2000). Functional differences among species, usually summarized in terms of taxonomic functional groups (e.g., legumes, C3 grasses, C4 grasses) can explain the positive effects of diversity on productivity and suppression of invaders (Diaz and Cabido, 2001; Hooper and Dukes, 2004; Reich et al., 2004)). Species in polycultures may interact in multiple ways (e.g., competition or facilitation) resulting in positive or negative net outcomes, depending on the environment and the species competitive abilities relative to each other and to weeds. Therefore the species to include in the polyculture must be carefully chosen for each environment and their competitive ability in mixtures evaluated. Optimal polycultures for each environment will be those assemblies of species which maximize yield and suppression of weeds and pests. Some agronomic benefits, such as weed suppression or nitrogen fixation, may need to be contributed by species other than the perennial grains themselves.

The objective of this study was to determine seed yield, forage production, and competitive ability of two perennial dual purpose crops (Illinois bundleflower and intermediate wheatgrass) in monoculture and polycultures in order to detect optimal species combinations for polyculture systems. We hypothesized that (1) the binary mixture of bundleflower and wheatgrass would outperform the constituent monocultures in terms of seed, forage, and protein yields and competitive ability with weeds; (2) companion species from different functional groups would enhance production of the mixture compared to companion species from the same functional group; (3) bundleflower and wheatgrass would exhibit good competitive ability in polycultures with other perennial companions by

producing as much or more seed and forage than expected based on their proportion in the mixture; and (4) perennial polycultures including highly competitive companion species increase weed suppression without reducing yield compared to monocultures.

MATERIALS AND METHODS

Experimental design

We seeded the two perennial grains (Illinois bundleflower and intermediate wheatgrass) in monoculture and polycultures of two and three species. Five other companion perennial species represented three taxonomic functional groups: legumes (alfalfa, [*Medicago sativa* L.], white clover [*Trifolium repens* L.]), C3 grasses (orchardgrass [*Dactylis glomerata* L.]), and C4 grasses (switchgrass [*Panicum virgatum* L.] and eastern gamagrass [*Tripsacum dactyloides* (L.) L.]). These companion species also represented a range of competitive abilities with alfalfa and orchardgrass being highly competitive perennial forages, switchgrass and eastern gamagrass slow establishing species, and white clover a low-growing nitrogen source. These species were also considered proxies for species that may be developed for future grain polycultures and thus could serve to provide an estimate of the competitive ability of bundleflower and wheatgrass. A total of 21 species combinations (hereafter, referred to as entries) were analyzed for this experiment.

Bundleflower seeds were obtained from the University of Minnesota and derive from two collections in Iowa (PNL 545 at Dubuque, IA, and PNL 539 at Spirit Lake, IA). Wheatgrass seeds were from the commercial forage cultivar Oahe. Companion species seeds were commercial forage cultivars (alfalfa cv. 54H51, white clover cv. Alice, orchardgrass cv. Duke, switchgrass cv. Cave-in-Rock, and eastern gamagrass cv. PMK-24). Seed density for monocultures of bundleflower was 199 PLS m-2, and intermediate wheatgrass 239 PLS m-2. Monoculture seed density for alfalfa was 838 PLS m^{-2}, white clover 795 PLS m^{-2}, orchardgrass 1625 PLS m^{-2}, switchgrass 621 PLS m^{-2}, and eastern gamagrass 15 PLS m^{-2} based on standard agronomic recommendations for Iowa (Barnhart, 1999). Seed density for each species in polyculture was reduced proportionately to the number of species (e.g., the density of each species was half the monoculture rate for binary mixtures). Substitutive (i.e.,

replacement) designs like this one change simultaneously species richness and species density, so these two effects are impossible to separate in the interpretation of results (Connolly et al., 2001b). However, mixtures assembled in a substitutive design are more typical of agronomic situations than additive ones since the interest is identifying the highest yielding combination of species regardless of the causal mechanistic effects.

Each entry was replicated three times in an alpha-lattice design (Patterson and Williams, 1976) at two locations in Iowa, USA: the Iowa State University Agronomy and Agricultural Engineering Research Farm, east of Boone, Boone Co., IA, with a Nicollet loam soil (fine-loamy, mixed, superactive, mesic Aquic Hapludolls) and the ISU Hinds Research Farm, north of Ames, Story Co., IA, with a Spillville loam soil (fine-loamy, mixed, superactive, mesic Cumulic Hapludolls). Soil analyses for these sites were reported elsewhere (see Picasso et al., 2008). The entire plot area was tilled before planting in spring 2003. The experiment was planted on 18 May 2003 in Ames and 21 May 2003 in Boone. Seeds were drilled into 4-m by 3-m plots with row spacing of 0.15-m. No fertilizer was applied. Plots were mowed on 18 June and 12 Sept. 2003 in Boone, and on 20 June and 13 Sept. 2003 in Ames, to a 0.15-m height to control weeds; biomass was not measured or removed. Eastern gamagrass failed to establish in 2003 so it was reseeded by hand in April 2004. In the second year of the experiment (2004), each plot was split into two 2-m x 3-m sub-plots: in one sub-plot forage biomass was harvested three times (May, July, September each year) and removed during the season, while in the other sub-plot seeds were harvested by hand and removed, but total biomass was mowed in October and not removed. The same management was used in the third year (2005). These two contrasting managements represent the two extremes on a continuum of uses for double purpose crops in perennial polycultures, from forage harvest only to seed harvest only.

For the forage management system, aboveground plant biomass was harvested on 26 May, 13 July, and 13 Sept. 2004 and 25 May, 8 July, and 22 Aug. 2005 in Boone, and on 28 May, 15 July, and 16 Sept. 2004 and 3 June, 27 July, and 15 Sept. 2005 in Ames. A single 1-m wide by 3-m long strip was harvested for biomass through the center of each small sub-plot with a flail-type harvester (Carter Mfg., Brookston, IN). Before the harvest, biomass was sampled by clipping two 0.09-m^2 quadrats per plot, species were sorted in the laboratory,

dried, and weighed. For each plot weed biomass was defined as the sum of biomass of species not seeded in the experiment (e.g. *Conyza canadensis* [L.] Cronq.) as well as the species seeded in the experiment but not seeded in that particular plot (e.g. alfalfa in the bundleflower monoculture).

For the seed management system, the reproductive structures of bundleflower and intermediate wheatgrass were hand harvested from the entire sub-plot area as each species matured. Intermediate wheatgrass seeds were hand harvested on 19 July 2004 and 1 Aug 2005 in Boone and on 24 July 2004 and 3 Aug 2005 in Ames. Bundleflower seeds were hand harvested on 8 Sept 2004 and between 22 Aug and 1 Sept 2005 in Boone, and on 10 Sept 2004 and 13-21 Sept 2005 in Ames. The harvested material was dried in forced-air drier at room temperature (12-18 ºC) for 15 days and weighed dry. Seeds were then threshed using a small plot thresher (Wintersteiger Inc, Salt Lake City, UT) and further cleaned with a Clipper office tester and cleaner (Seedburo Equipment Co., Chicago, IL) and weighed. Because the Ames site was adjacent to a woodland, deer grazing severely reduced the bundleflower seed yield at this location both years, so only the Boone location was used for the bundleflower seed analyses. Similar feeding effects were not noted for intermediate wheatgrass. Bundleflower stem density was measured in October 2005 with two 0.5 m^2 quadrats per plot in Boone (stem density was not measured for bundleflower in Ames and was not measured for wheatgrass at either site).

In order to determine crude protein concentration of seeds and forage, samples from monoculture plots were ground to pass a 1-mm mesh screen (Cyclone Mill, UDY Mfg., Fort Collins, CO) and analyzed for nitrogen concentration using micro-Kjeldahl procedure (Bremner and Breitenbeck, 1983) in the Plant and Soil Analysis Laboratory, Iowa State University. Crude protein concentration was calculated as nitrogen concentration x 6.25. Total protein yields were calculated multiplying crude protein concentration by seed or forage yield for each species. We assumed that protein concentration was characteristic of each species regardless it was grown in monoculture or in mixture, which may underestimate the protein concentration of the grass in the mixture (Jorgensen et al., 1999).

Climatic conditions, in particular rainfall, influence seed production. In our study rainfall between April and September was 657, 576, and 706 mm in 2003, 2004, and 2005

respectively, with a 50 year average of 621 mm. Therefore, establishment year was average, 2004 was a dry year (but May was exceptionally wet), and 2005 was a wet year (especially August and September).

Statistical analyses

The analysis of variance for seed yield, forage yield, and weed biomass was conducted using a mixed linear model that included locations, replications within location, incomplete blocks within replication, entry (main plot), and year (split-plot). All factors were considered fixed effects except replications within locations and blocks within replications. When significant interactions were found, data were analyzed by location and/or year as appropriate. Least square means were computed across locations and/or year in the absence of interactions or if the interactions were due to magnitude, rather than cross-over, effects. Contrasts were used to compare monoculture means between years, entry means against each monoculture, and means of polycultures with similar functional composition against monocultures. A simple linear regression between seed yield and stems per m^2 for bundleflower was calculated using mean values for each entry.

In order to evaluate the relative performance of the binary mixture of bundleflower and wheatgrass, contrasts for the means of the mixture against each monoculture and against the average of the monocultures were calculated for seed yield, forage yield, protein content in forage and seed, and weed biomass for each system. Transgressive overyielding (Trenbath, 1974) can occur when the contrast for the mixture against the highest yielding monoculture is greater than zero; non transgressive overyielding occurs when the contrast against the average of monocultures is greater than zero.

In order to evaluate the competitive ability of each perennial grain species against the companion species in the polyculture, the proportion of expected yield of the target species in each polyculture (PEY_{Xp}) was calculated as: $PEY_{Xp} = Y_{Xp} / (Y_{Xm} * p_X)$, where Y_{Xp} is the yield of species X in polyculture, Y_{Xm} is the yield of species X in monoculture (averaged over replications), and p_X is the proportion seeded of species X in the polyculture, i.e., $p_X = 1$ / number of species seeded in our case (adapted from Loreau, 1998). PEY_{Xp} is a useful index to analyze the performance of a species in a polyculture in which only one target species was harvested, as it was in our case for seed. In order to test whether the yield of a given species

in polyculture was different from that expected based on its proportion in the mixture, natural logarithm transformed PEY_{Xp} values were compared with t-tests to the null hypothesis of zero to avoid the statistical problems of bias of ratios. If $\ln(PEY_{Xp}) > 0$ then $PEY_{Xp} > 1$, meaning that species X yielded more than expected and inter-specific competition would be less significant than intra-specific competition in the monoculture. If each species in a polyculture has a PEY_{Xp} value greater than one, complementarity of resource use exists between the species in the polyculture and non-transgressive overyielding is observed. However, this is not a sufficient condition for transgressive overyielding because the yield gain of the low yielding species compared to expected may be smaller than the yield loss of the high yielding one compared to the monoculture yield, particularly when they have very different monoculture yields (Loreau, 1998). Furthermore, overyielding can occur even if one species has PEY_{Xp} smaller than one, and the other species have PEY_{Xp} larger than one, because yield gain of one species may be larger than yield loss of the other(s). This lack of ability to show overyielding has also been pointed out for common aggregate indices of intercropping research, such as Land Equivalent Ratio (Vandermeer, 1989) or Relative Yield Total (de Wit and van den Bergh, 1965) by Connolly et al. (2001a). The unique value of PEY_{Xp} is that it provides insight into the ecological mechanisms behind the polyculture performance.

All analyses of variance and contrasts were performed using PROC MIXED, t-tests were calculated with PROC TTEST, and regression coefficients were calculated using PROC REG, in the SAS statistical software package (SAS Institute Inc., 2003). Unless otherwise indicated, statistical significance was assessed at the 5% probability level.

RESULTS AND DISCUSSION

Monocultures

In monoculture, bundleflower seed yield increased four-fold from 14 ± 3 g m^{-2} in the second year after seeding to 55 ± 8 g m^{-2} in the third year in Boone. Wheatgrass produced its largest seed yield in the second year after seeding of 66 ± 7 g m^{-2}, which then dropped by half to 27 ± 2 g m^{-2} in the third year averaged over the two locations (Fig. 5.1a). Wheatgrass

produced three times more forage than did bundleflower in monoculture averaged over locations and years (Fig 1b).

Bundleflower stem density in monoculture plots averaged 43 ± 5 stems m^{-2} and was highly correlated with seed yield in October 2005 (r = 0.94, P<0.0001, N=12). Monoculture stem density was higher than for the mixtures with white clover, alfalfa, and wheatgrass at 9, 15, and 23 ± 5 stems m^{-2}, respectively but no different from the mixtures with switchgrass, eastern gamagrass, and orchardgrass at 35, 27, and 25 ± 5 stems m^{-2}, respectively.

Crude protein concentration in seed was 411 ± 8 g kg^{-1} for bundleflower and 150 ± 3 g kg^{-1} for wheatgrass. In the forage, crude protein concentration was 165 ± 5 g kg^{-1} for bundleflower and 112 ± 5 g kg^{-1} for wheatgrass, averaged over all three forage harvests, years, and locations. Protein yield of the mixture was no different than the monoculture with the highest protein yield (Figure 1c).

Weed invasion was highest in the bundleflower monoculture under the seed management during the second year after seeding (Fig 1d). Wheatgrass under the seed management was more competitive with weeds than bundleflower in the second year, but no different in the third year. Under the forage management, wheatgrass was more competitive than bundleflower on average over two years and locations (Fig 1d).

Bundleflower – wheatgrass binary mixture

The total seed yield of the bundleflower – wheatgrass binary mixture was no different than the highest yielding monoculture for each year (Fig. 5.1a). Also, the mixture was no different than the average of the monocultures both years. The mixture was less variable than each monoculture between years and provided a sort of insurance: while each monoculture yielded well in one year and poorly in the other, the mixture always yielded as high as the best monoculture each year. Total forage yield of the mixture was intermediate to the two monocultures. Protein concentration in the mixture of seeds and of the combined forage was also intermediate between both monocultures (Fig. 5.1c). Weed invasion of the mixture was no different from that of the most competitive monoculture (wheatgrass, Fig. 5.1d), but lower than the least competitive monoculture (bundleflower).

Considering all variables together, for the seed harvest system, the bundleflower–wheatgrass mixture produced as much or more seed than either monoculture, and had similar

weed suppression, while producing more protein than the grass monoculture. For the forage system, the mixture produced less forage, and suppressed the same amount of weeds, but with higher protein content than the grass monoculture. While we rejected our hypothesis that the mixture would outperform the monocultures in each individual variable, the advantage of the mixture was evident in terms of reducing yearly variability and maximizing all variables simultaneously, for the two years studied. Future measurements would be needed to test this trend in the long term.

Polyculture performance

Yield of each individual species in polycultures is expected to decrease as the number of species increases because species seeding density was reduced proportional to the number of species. Therefore individual species performance in polyculture must be evaluated by the PEY, which allows detecting complementarity among species. The functional group of the companion species in the polyculture had major effects on bundleflower seed yield and PEY. On average, polycultures including bundleflower with other legumes or C3 grasses had lower seed yields than the bundleflower monoculture, as expected. However, polycultures including bundleflower with C4 grasses were no different than the bundleflower monoculture (Fig. 5.2a) and switchgrass did not reduce seed yield in bundleflower mixtures (Table 5.1a). The PEY for bundleflower seed yield in polycultures with legumes or C3 grasses was lower than one, thus the competitive ability of bundleflower is low relative to the companion legumes and C3 grasses evaluated. In contrast, polycultures with C4 and both C3 and C4 grasses together had PEY no different from one (Fig 2a, Table 5.1a). Although some plots of bundleflower with switchgrass had very high seed yields, variability was also high and thus the observed PEY of 2.5 was no different than one (Table 5.1a). The higher competitive ability of bundleflower with C4 grasses may be more apparent than real, because C4 grasses were not fully established the first year. Data from future years are needed to confirm whether complementarity exists between bundleflower and C4 grasses.

The functional group of the companion species in the polyculture also had important effects on wheatgrass seed yield and PEY. Polycultures including legumes were no different than monoculture, whereas polycultures including other grasses had lower seed yields than the monoculture (Fig. 5.2b). Orchardgrass reduced seed yield and PEY in all mixtures with

wheatgrass (Table 5.2a), indicating that this C3 grass was more competitive than wheatgrass. Polycultures of wheatgrass with the legumes white clover or bundleflower had PEY greater than one (Table 5.2a), revealing complementarity among these species, likely due to the effect of nitrogen facilitation from the legumes to wheatgrass.

All polycultures including bundleflower had higher total forage yields compared to the monoculture, with the exception of the mixtures with C4 grasses, which were no different than the monoculture (Fig 3a). Bundleflower forage yield was lower than monoculture when mixed with other legumes, but no different in other polycultures (Fig 3a, Table 5.1b). The PEY for bundleflower forage was lower than one for mixtures with legumes and no different than one in all other polycultures (Table 5.1b). Thus, alfalfa and white clover outcompeted bundleflower (i.e., inter-specific competition was greater than bundleflower intra-specific competition).

All polycultures including wheatgrass had higher total forage yields compared to the monoculture (Fig 3b). Wheatgrass forage yield was lower than monoculture when mixed with orchardgrass but no different in other polycultures (Fig 3b). For forage production, PEY was lower than one in polycultures including alfalfa or orchardgrass (Table 5.2b), indicating that these two species were more competitive than wheatgrass.

Weed suppression in polycultures

An entry x year interaction with crossover was present for weed biomass in bundleflower plots managed for seed, so data are presented by year (Table 5.1a). The identity of the companion species in the polyculture had greater effects on weed suppression than did the functional group. The bundleflower monoculture had the highest weed biomass in 2004 and most polycultures had lower weed biomass than the monoculture, except for the mixtures with C4 grasses (Table 5.1a) which were no different than the monoculture. In contrast, in 2005 there were no differences in weed biomass of polycultures versus the monoculture, except the mixtures with alfalfa and orchardgrass (Table 5.1a), which were lower than the monoculture. Similarly, for the forage harvest system, mixtures with alfalfa, white clover, and orchardgrass had lower weed biomass than the monoculture (Table 5.1b). Weed biomass in wheatgrass polycultures managed for seed was no different than that of the monoculture in most cases (Table 5.2a) except for some polycultures including orchardgrass or alfalfa as

companions. For the forage system, all polycultures had lower weed biomass than the monoculture with the exception of the mixtures comprising only bundleflower or eastern gamagrass (Table 5.2b).

The weed community observed in the plots comprised both naturally occurring wild weeds from the soil seed bank (the dominant being horseweed, *Conyza canadensis* [L.] Cronq.; others were *Chenopodium album* [L.], *Taraxacum officinale* G.H. Weber ex Wiggers, and *Setaria* spp.) and voluntary cultivated species from the seed bank or from adjacent plots. These voluntary cultivated species (predominantly alfalfa and orchardgrass) dominated the weed community in most plots, so weed suppression was correlated with our treatments. We could not determine whether plots where alfalfa and orchardgrass were seeded actually suppressed weeds or if the observed low weed biomass was due to the fact that alfalfa and orchardgrass were not counted as weeds in those plots.

Monocultures of perennial grains had both high seed yields and high weed biomass whereas many polycultures had low seed PEY and low weed biomass. This result can probably be explained by the fact that other forage species are more competitive with perennial grains than were the weed species.

Seed yields of perennial grains

Bundleflower seed yields increased from the second to the third year after establishment, which is consistent with the observation that an establishment phase may be needed for bundleflower at northern latitudes (DeHaan et al., 2003). Bundleflower seed yields averaged 72 g m^{-2} year^{-1} across 29 location-year environments from Minnesota to Kansas, in experiments spanning 1-5 years (DeHaan et al., 2003; Kulakow, 1999; Piper, 1993; Piper, 1998), ranging from 3 to 155 g m^{-2} year^{-1} (Piper, 1993). Our results were lower than most published studies but similar to monoculture yields in southern Minnesota (DeHaan et al., 2003). We harvested all seeds at one time when the majority of pods were mature, simulating the harvesting methods that would be done in commercial production. However, bundleflower has a long period of fruiting and maturing, so many seeds that were lost in our process were not in other studies in which seed was harvested seed several times. Two other reasons that may have caused the difference in yields between our study and others are that most other studies harvested seeds from individual spaced plants, which are unrepresentative

of a seeded environment and that most previous studies were weed free, which is not realistic in low input agriculture systems.

Seed yields of wheatgrass comprising 7 locations with experiments spanning 1 to 15 years in Canada (Darwent et al., 1987; Elliott and Howe, 1977; Kruger, 1997), USA (Cornforth et al., 2001; Gardner et al., 1990; Wagoner, 1990), and Germany (Weik et al., 2002a) averaged 35 g m^{-2} year^{-1}, ranging from 17 g m^{-2} year^{-1} in Pennsylvania, USA (Wagoner, 1990) to 98 g m^{-2} year^{-1} in Saskatchewan, Canada (Kruger, 1997). Our wheatgrass seed yields were within the high end of the range of previously published studies. Our results are also consistent with literature that shows maximum wheatgrass yields during the fist two years of establishment (Elliott and Howe, 1977; Wagoner, ; Weik et al., 2002a). However, a severe storm occurred immediately before our wheatgrass harvest in 2005, which may explain the lower seed yields in that year.

Bundleflower in the third year after establishment produced approximately 15% of the average seed yields of commercial soybean in Iowa of 356 g m^{-2} (USDA, 2007) with greater protein content (411 vs. 370 g kg^{-1}). Seed yields for wheatgrass in the second year after establishment were approximately 25% of the average seed yields of oats, 258 g m^{-2} (USDA, 2007) with higher seed protein concentration (150 vs. 110 g kg^{-1} (USDA, 2007). These perennial grain seed yields are low compared to currently grown annual grains, necessitating further breeding and agronomic management research to make them viable crops.

Promising perennial polycultures

The observed complementarity for seed yield (PEY>1) in some polycultures points out to promising systems. The wheatgrass-white clover polyculture is promising because produced highest wheatgrass seed yields, and low growing white clover would not interfere with wheatgrass seed harvest, provides Nitrogen, and good soil cover. The wheatgrass–bundleflower mixture already discussed is also promising for grain production. Bundleflower-C4 grasses polycultures should be investigated in the future to assess the observed complementarity when C4 grasses are better established. No polyculture in our study simultaneously had higher seed yield and greater weed suppression than monocultures. However, wheatgrass-alfalfa mixture and bundleflower-switchgrass-eastern gamagrass polyculture (in 2004) were the few examples of increased weed suppression with no

significant reductions in seed yields. All polycultures had greater total forage yields than the monocultures so perennial grain species are not promising forages per se, but can contribute to mixtures with other high yielding forages. Bundleflower can contribute protein in summer pastures in the Midwest (Fischbach et al., 2005a; Fischbach et al., 2005b) and wheatgrass can improve provide fiber to reduce risk of bloat in ruminants grazing legume dominated pastures. Perennial polyculture systems can be flexible management systems; for instance, in years when weather is unfavorable to seed production, hay or grazing are alternatives to consider.

Future research directions

More research is needed to overcome the challenges to developing successful perennial grain polyculture systems. While protein content of perennial grains is high, seed yields need to be improved in order to reach yields comparable with annual grains. However, these improvements are within the range of yield gains already achieved with annual grains in the last 50 years by agronomic management and plant breeding (see e.g., Duvick, 2005). Apart from increasing yields, breeding efforts should be focused on developing compatible mixtures, with high competitive ability against weeds. Long term trends of yields and species composition of perennial grain polycultures over time may be different from those observed during the establishment years measured in our study, and should be monitored. Also, different results would be expected in situations with better weed control practices. In general, best agronomic management practices for growing these species are needed (e.g., optimal seeding densities for seed, best seeding dates, fertility requirements, and so on).

Table 5.1. Illinois bundleflower performance. a) Seed yield (SY) and proportion of expected yield (PEY), averaged over two years, and weed biomass (WB) under the seed harvest management by year, for monoculture and various polycultures of Illinois bundleflower at one location (Boone) in Iowa. b) IBF forage yield (FY), PEY, and weed biomass (WB) under the forage harvest management (three cuts) for monoculture and various polycultures of bundleflower averaged over two years and two locations (Boone and Ames) in Iowa.

Entry[†]	a) Seed harvest									b) Forage harvest					
	SY		PEY		WB					FY		PEY		WB	
					2004		2005								
	g.m^{-2}				g.m^{-2}					g.m^{-2}				g.m^{-2}	
IBF monoculture	34.3	5.7[‡]			681.0	54.4	224.8	67.8		83.3	14.5			384.0	28.2
IBF-ALF	1.3	L[§]	0.2	L	40.1	L	0.4	L		5.4	L	0.1	L	122.6	L
IBF-WCL	4.4	L	0.3	L	139.2	L	106.3	NS		12.6	L	0.2	L	87.9	L
IBF-OGR	15.1	L	0.6	NS	149.8	L	72.7	L		50.4	L	1.2	NS	138.1	L
IBF-IWG	7.8	L	0.5	NS	163.9	L	134.6	NS		67.1	NS	1.4	NS	310.5	NS
IBF-SWG	32.6	NS[¶]	2.5	NS	220.4	NS	173.7	NS		78.9	NS	1.4	NS	286.9	NS
IBF-EGG	24.4	L	1.2	NS	438.4	NS	236.5	NS		45.9	L	0.9	NS	386.2	NS
IBF-OGR-IWG	5.5	L	0.6	NS	80.7	L	90.1	NS		30.0	L	1.0	NS	137.4	L
IBF-SWG-EGG	18.3	NS	1.9	NS	166.5	L	227.9	NS		65.2	NS	1.9	NS	311.0	NS
IBF-OGR-SWG	13.4	L	1.3	NS	129.9	L	110.3	NS		37.1	L	1.1	NS	200.2	L
IBF-IWG-EGG	13.9	L	0.9	NS	62.4	L	47.0	NS		44.3	L	1.2	NS	101.2	L

[†]IBF=Illinois bundleflower, IWG= intermediate wheatgrass, SWG=Switchgrass, EGG=eastern gamagrass, OGR= orchardgrass, ALF=alfalfa, WCL=white clover

[‡] Standard error for monoculture means.

[§] Means lower than the monoculture means or PEY lower than 1 (P<0.05).

[¶] Means no different than the monoculture or PEY equal to 1 (P>0.05).

Table 5.2. Intermediate wheatgrass performance. a) Seed yield (SY), proportion of expected yield (PEY), and weed biomass (WB) under the seed harvest management, for monoculture and various polycultures of intermediate wheatgrass averaged over two years and two locations (Boone and Ames) in Iowa. b) IWG forage yield (FY), PEY, and weed biomass (WB) under the forage harvest management (three cuts) for monoculture and various polycultures of wheatgrass averaged over two years and two locations (Boone and Ames) in Iowa.

Entry[†]	a) Seed harvest						b) Forage harvest					
	SY $g.m^{-2}$		PEY		WB $g.m^{-2}$		FY $g.m^{-2}$		PEY		WB $g.m^{-2}$	
IWG monoculture	46.9	4.8[‡]			88.1	26.7	239.8	20.1			272.9	21.5
IWG-ALF	29.7	NS[§]	1.2	NS	4.7	L	81.6	L	0.5	L	79.1	L
IWG-WCL	48.8	NS	2.0	H[#]	131.3	NS	135.5	L	0.9	NS	82.1	L
IWG-IBF	41.2	NS	1.8	H	128.2	NS	152.8	NS	1.0	NS	310.5	NS
IWG-OGR	18.7	L[¶]	0.7	NS	63.6	NS	48.1	L	0.3	L	167.6	L
IWG-EGG	25.6	NS	0.8	NS	65.2	NS	147.5	L	1.0	NS	244.2	NS
IWG-ALF-OGR	11.4	L	0.6	NS	1.7	L	46.8	L	0.5	L	15.5	L
IWG-WCL-OGR	12.2	L	0.6	NS	14.2	L	32.5	L	0.3	L	50.6	L
IWG-IBF-OGR	13.8	L	0.6	NS	62.9	NS	72.7	L	0.7	L	137.4	L
IWG-ALF-EGG	17.4	L	0.9	NS	38.9	L	76.7	L	0.8	NS	71.7	L
IWG-WCL-EGG	36.4	NS	2.2	H	94.4	NS	136.0	L	1.4	NS	63.8	L
IWG-IBF-EGG	36.1	NS	2.1	H	93.6	NS	224.6	NS	2.1	H	200.2	NS

[†]IBF=Illinois bundleflower, IWG= intermediate wheatgrass, SWG=Switchgrass, EGG=eastern gamagrass, OGR= orchardgrass, ALF=alfalfa, WCL=white clover

[‡] Standard error for monoculture means.

[§] Means no different than the monoculture or PEY equal to 1 (P>0.05).

[¶] Means lower than the monoculture means or PEY lower than 1 (P<0.05).
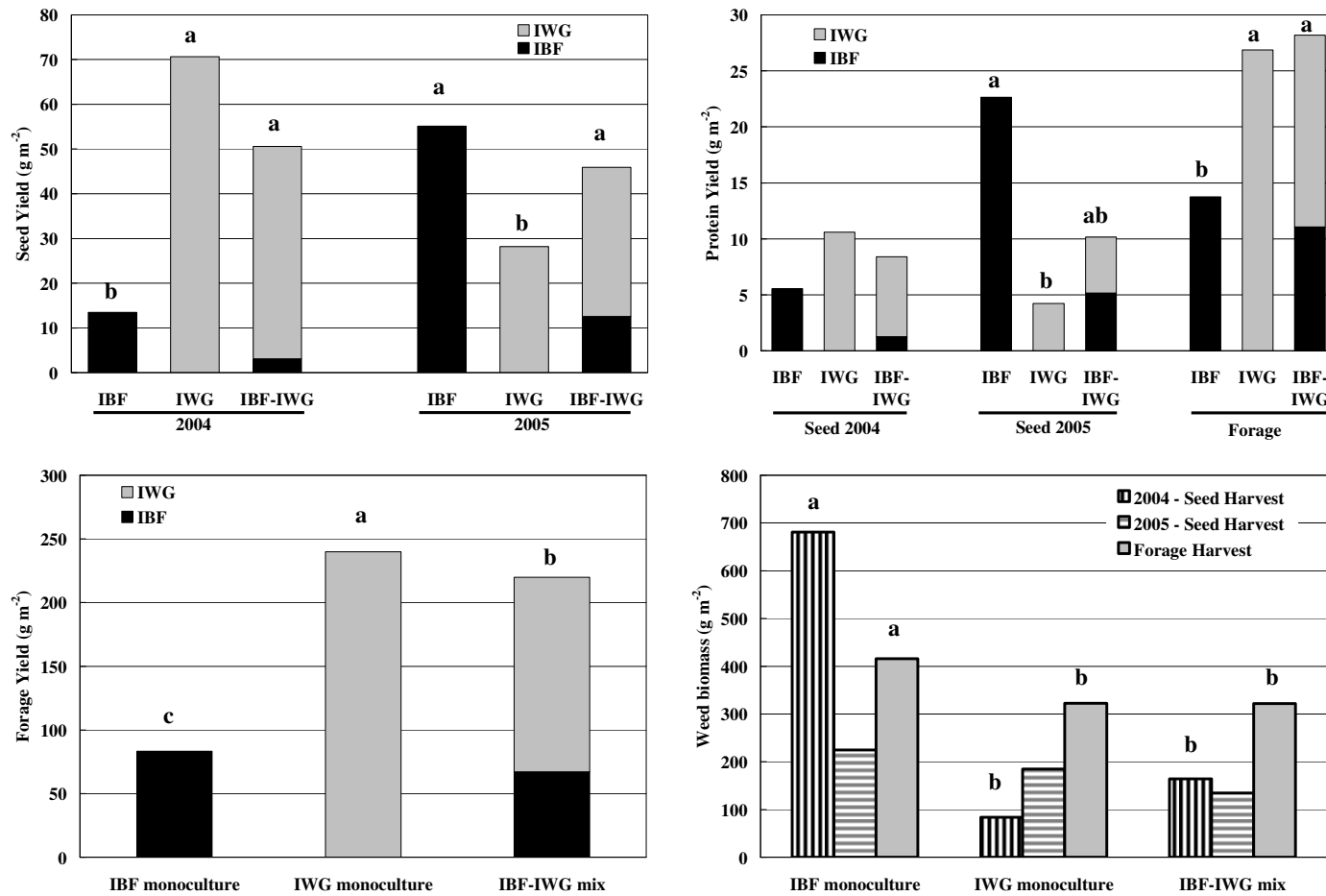
[#] PEY higher than 1 (P<0.05).

Figure 5.1. A comparison between Illinois bundleflower and intermediate wheatgrass monoculture and binary mixture: a) seed yield by year at one location, b) forage yield averaged over two years and two locations, c) Seed protein yield by year for one location and forage protein yield averaged over two years and two locations, and d) weed biomass averaged over two locations in Iowa by year for the seed harvest regime and averaged over two years for the forage harvest regime. Means with the same letters within years or managements are not different at the 5% probability level. IBF=Illinois bundleflower, IWG= intermediate wheatgrass.
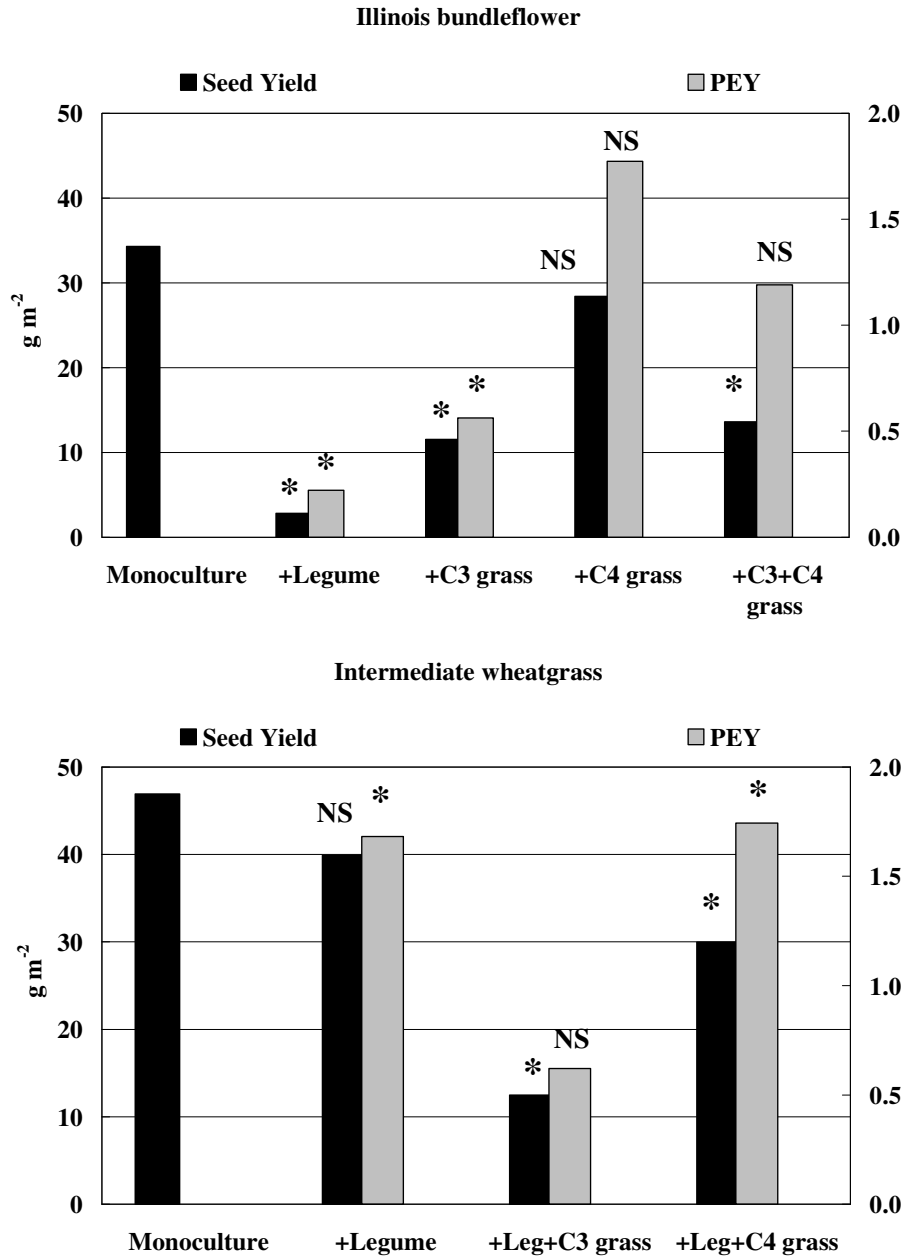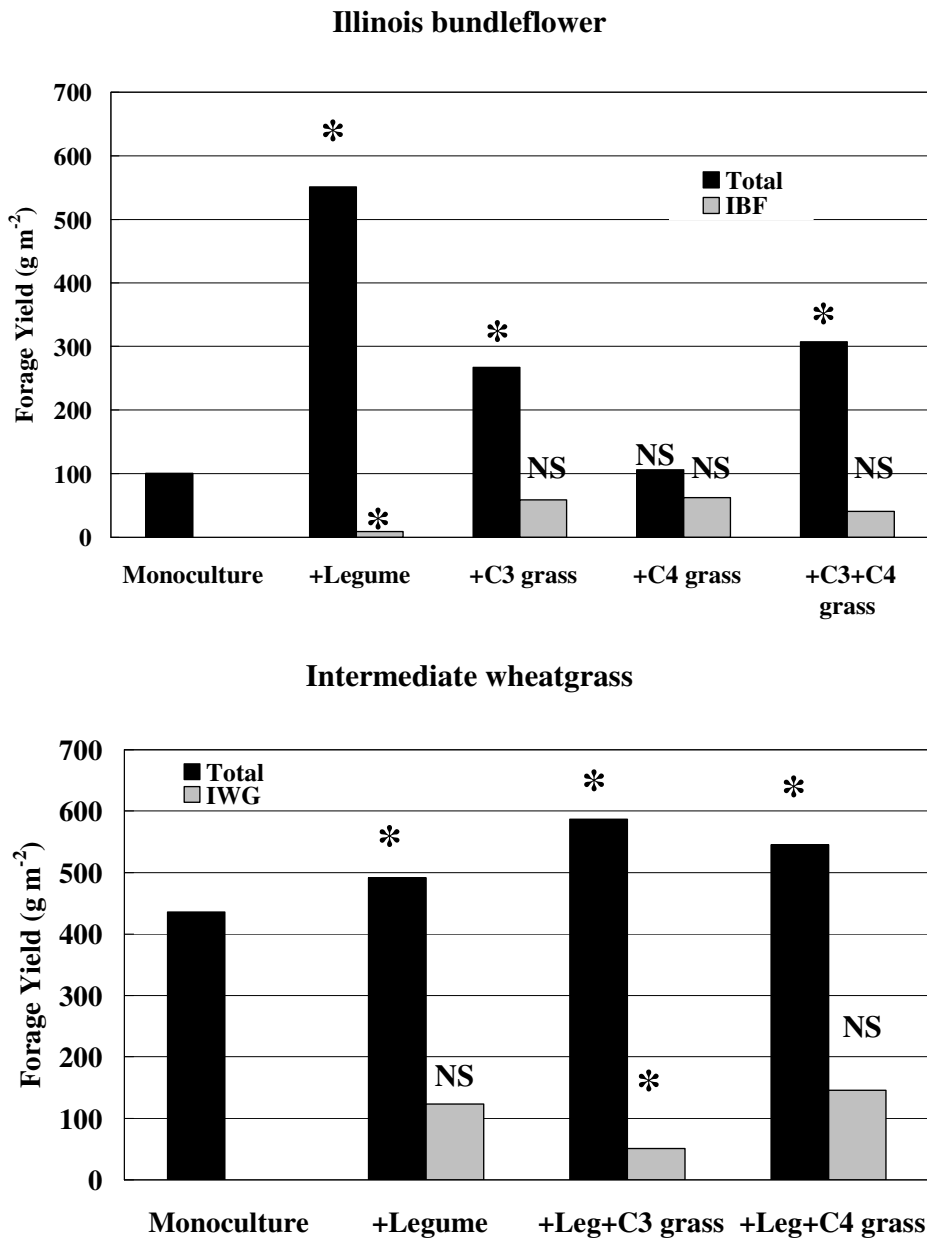
Illinois bundleflower

Intermediate wheatgrass

*Figure 5.2. Seed yield and proportion of expected seed yield (PEY) for monocultures and polycultures of different functional group composition of a)Illinois bundleflower averaged over two years at one location, and b)intermediate wheatgrass averaged over two years and two locations in Iowa. Seed yields from polycultures different from monoculture, and PEY values different from 1, are denoted with * (P<0.05).*

Illinois bundleflower

Intermediate wheatgrass

*Figure 5.3. Total forage yield and species (IBF or IWG) forage yield for monocultures and polycultures of different functional group composition of a)Illinois bundleflower and b)intermediate wheatgrass, averaged over two years and two locations (Ames and Boone) in Iowa. Forage yields from polycultures different from the monoculture are denoted with * (P<0.05).*

CHAPTER VI. GENERAL CONCLUSIONS

This research provided insight into the agronomic characteristics of perennial herbaceous polycultures as alternatives for forage, grain, and biomass production. It also documented the contribution of plant species richness to biomass and seed productivity, weed suppression, and stability. The central contribution of this research was to begin merging Ecology and Agriculture as a basis for better understanding and designing sustainable production systems. The key findings of this research were:

1. Average biomass productivity consistently increased in establishing perennial polyculture agroecosystems with increasing seeded plant species richness across two locations, three years, and two harvest management regimes.

2. In most situations, polycultures were more productive than the average of monocultures, but not more productive than the best adapted species in monoculture for each environment; i.e., non transgressive overyielding was usually observed. Alfalfa under multiple harvest management and intermediate wheatgrass under single harvest management were the highest yielding species in monoculture.

3. The observed polyculture overyielding was due to complementarity among species in the community rather than to selection effects of individual species at all richness levels across environments and was likely explained by legume-grass facilitation.

4. Polycultures with high richness had lower variability in yield (i.e., greater stability) than the highest yielding monocultures. Stability analyses used in plant breeding may help interpret the results of polyculture experiments.

5. Intermediate wheatgrass produced up to 65.8 ± 6.5 g m^{-2} of seed and Illinois bundleflower up to 55.0 ± 8.1 g m^{-2}. With plant breeding and better agronomic management these yields can likely be improved in the near future to be practical for production situations.

6. The mixture comprising both perennial grains (intermediate wheatgrass and Illinois bundleflower) produced as much seed as the best yielding monoculture each year (non transgressive overyielding was observed). Polycultures of Illinois bundleflower with C4 grasses and polycultures of intermediate wheatgrass with legumes produced as much seed as

the monocultures. If the companion species in the polyculture produced harvestable grain transgressive overyielding may be achievable.

7. Weed biomass decreased exponentially with seeded species richness in all environments. Most polycultures exerted greater weed suppression than perennial grain monocultures but also they had reduced seed yields. Breeding and management of crop mixtures to optimize the trade-off between seed yield and weed suppression is a central challenge for the development of perennial polyculture systems.

This research was intended to test a number of hypotheses. We did it, and therefore this work is completed. The main limitation of our conclusions is temporal: the four initial years of perennial plant communities. Longer term studies could reveal different results, so maintaining our perennial polyculture experiment could be valuable. Scientific inquiry always opens new questions, and here are some of those that could be studied over the longer term:

1. Do the richness effects measured during the first three years become stronger or disappear in the long term (in terms of forage biomass, seed production, weed invasion)?

2. How do complementarity and selection effects change over time? Is transgressive overyielding more frequent in the long term?

3. How does seed yield of perennial grain species in monoculture and polyculture change over the long term?

4. Does plant species richness affect soil properties like organic matter content or nutrient pools in perennial polycultures over the long term?

5. How does associated biodiversity respond to changes in planned diversity in perennial polycultures (insects, pathogens, soil microorganisms)?

6. What is the relative importance of species composition, dominance, and diversity in controlling invasions in perennial plant communities over time? Can spatial representation and analyses techniques help understand the dispersal of weeds and seeded species in the experimental polyculture plots?

7. How do different competition and overyielding indices correlate for the species included in the experiment? How do they change over time in perennial plant communities?

Perennial herbaceous polycultures offer tremendous opportunities for the design of sustainable agroecosystems but the research devoted to these is minimal compared to the potential benefits. Future generations of ecologists, agronomists, and agroecologists are needed to meet this research needs. Hopefully this dissertation will help engage other spirits and minds to this important task.

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