Basic and Applied Ecology **8** (2007) 199—208

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Basic and Applied Ecology

www.elsevier.de/baae

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The diversity–biomass–productivity relationships in grassland management and restoration

Qinfeng Guo*

US Geological Survey, Northern Prairie WRC, 8711 37th St. SE, Jamestown, ND 58401, USA

Received 8 June 2005; accepted 7 February 2006

KEYWORDS
Burning;
Grazing;
Planting;
Seeding;
Unified approach

Summary

Diversity, biomass, and productivity, the three key community/ecosystem variables, are interrelated and pose reciprocal influences on each other. The relationships among the three variables have been a central focus in ecology and formed two schools of fundamentally different nature with two related applications: (1) management – how biomass manipulation (e.g., grazing, burning) affects diversity and productivity, and (2) restoration – how diversity manipulation (e.g., seeding, planting) affects biomass and productivity. In the past, the two apparently related aspects have been studied intensively but separately in basic research and the reciprocal effects of the three variables and applied aspects have not been jointly addressed. In most cases, optimal management often involves regulating biomass so that high diversity and productivity or other preferred habitat characteristics can be achieved and maintained, while restoration usually involves planting/seeding a certain number and/or combination of native species so that the native structure and function of the habitat can be restored and degraded ecosystems can recover faster. This article attempts to unify these two schools and discusses the significance and implications of the diversity–biomass–productivity relationships in practice, with particular emphasis on grassland ecosystems.

Zusammenfassung

Diversität, Biomasse und Produktivität, die drei Lebensgemeinschafts-/Ökosystem-Schlüsselvariablen, sind miteinander verknüpft und haben wechselseitige Einflüsse aufeinander. Die Beziehungen zwischen den drei Variablen waren ein zentraler Fokus der Ökologie und formten zwei Lehrmeinungen fundamental unterschiedlicher Natur, die zwei miteinander verbundene Anwendungen hatte: (1) Management – wie beeinflusst die Manipulation der Biomasse (z. B. Beweidung, Brände) die Diversität und Produktivität, und (2) Restauration – wie beeinflusst die Manipulation der

*Tel.: +1 701 253 5565; fax: +1 701 253 5553.
E-mail address: qguo@usgs.gov.

1439-1791/$ - see front matter
doi:10.1016/j.baae.2006.02.005

Diversität (z. B. säen, pflanzen) die Biomasse und Produktion. In der Vergangenheit wurden die zwei offensichtlich miteinander in Beziehung stehenden Aspekte intensiv aber getrennt voneinander in der Grundlagenforschung untersucht und die wechselseitigen Effekte der drei Variablen sowie die Aspekte der Anwendung wurden nicht in zusammenwirkend untersucht. In den meisten Fällen beinhaltet ein optimales Management häufig die Regulation der Biomasse, damit eine große Diversität und Produktivität oder andere bevorzugte Habitateigenschaften erreicht und erhalten werden können. Die Restauration beinhaltet dagegen normalerweise das Pflanzen bzw. Säen einer bestimmten Anzahl und/oder einer Kombination natürlicher Arten, so dass die natürliche Struktur und Funktion der Habitate wieder hergestellt wird und degradierte Ökosysteme sich schneller erholen. Dieser Artikel versucht diese beiden Lehrmeinungen zu vereinen und diskutiert die Bedeutung und Implikationen der Diversitäts-Biomasse-Produktivitäts-Beziehungen in der Praxis mit einem besonderen Schwerpunkt auf Grünland-Ökosystemen.

Introduction

The effects of biomass on species diversity and the effects of diversity on ecosystem productivity are two closely linked foci in recent research which have generated considerable debates and insights on the role of diversity in ecosystem performance (Aarssen, 2001; Grime, 2002; Huston, 1997; Loreau, Naeem, & Inchausti, 2002). However, most related studies so far have dealt with these two issues separately and their practical implications have not been given enough attention. As human population and demands rapidly grow, managers face increased frequency and intensity of human disturbances of natural habitats. Meanwhile, as many once highly diverse natural habitats have been transformed into species-poor habitats such as croplands, the need to restore biodiversity becomes increasingly urgent. This is especially the case in grasslands, which once occupied larger but still occupy vast areas of many parts of the world. Both ecologists and land managers face an increasingly difficulty or dilemma balancing between the protection of grassland biodiversity and sustainable productivity (Aber et al., 2000; Watkinson & Ormerod, 2001). In many situations, the results of management are unsatisfactory and restoration is unsustainable, especially in ecosystems invaded by non-native species (SER, 2004). This could be at least in part due to the lack of communication between the advances in basic ecological research and timely and proper application (Palmer, Ambrose, & Poff, 1997).

The areas of study in community and ecosystem ecology that have the greatest potential to improve the results of management and restoration are the interrelations among diversity, biomass, and productivity (Grime, 2002; Guo, 2003a, b; Roy, 2001). Studies to date on their relationships are of two types: (1) observations examining the effects of preexisting or manipulated biomass on diversity and productivity (Grace, 1999; Guo & Berry, 1998; Noy-Meir, 1975) and (2) experiments examining the influences of diversity (seeding, planting) on annual biomass production (i.e., productivity; e.g., Hooper et al., 2005; Spehn et al., 2005). Although the importance of these types of ecological studies is widely recognized, their influence on management and restoration techniques has not been sufficiently addressed. It is important that we are able to predict the effects of biomass on diversity, and diversity on biomass, productivity, and product quality in various ecosystems in order to determine if enhanced biomass can further increase or decrease diversity and productivity. Managers and restorers need to know the practical significance and implications of these relationships as well as the role of succession after they are applied in the field (Harper, 1987).

Some of the factors that jointly control local and regional species diversity and productivity (i.e., climate, topography, light, latitude; Grace, 1999; Grime, 1979) are almost completely beyond human control. However, some manipulative factors such as fire, grazing, nutrient addition, and seeding are also important for ecosystem performance and compose critical elements in management and restoration (Bradshaw, 1987; Cottam, 1987; Hodgson & Illius, 1996). Early efforts have discussed the conservation implications of the studies on biodiversity and ecosystem functioning (Hector, Joshi, Lawler, Spehn, & Wilby, 2001). Here, I first briefly describe some frequently reported general relationships between diversity, biomass, and productivity, and then discuss how managers and restorers can use this information in the field.

Relations among diversity, biomass, and productivity

Diversity, biomass, and productivity are three key variables in community and ecosystem ecology. These variables have been measured in different ways under different circumstances. Here, for simplicity and comparability with most other studies, species diversity is defined as the number of species (or species richness), biomass is defined as the above-ground dry organic materials produced per unit of area (e.g., $g\,m^{-2}$), and productivity is defined as the biomass production (primary production) per area and per time unit (e.g., $g\,m^{-2}\,yr^{-1}$; Noy-Meir, 1975; Newman, 1993).

The hump-shaped (or unimodal) relationships between biomass and diversity (see reviews by Grace, 1999; Mittelbach et al., 2001; Roy, 2001; Waide et al., 1999) have been frequently observed in mature vegetation (Fig. 1). Most recent experiments show positive log-linear or curve-linear relations (asymptotic) relationships between species diversity and productivity in newly seeded grassland communities (Hooper et al., 2005; Spehn et al., 2005). Long-term observations reveal hump-shaped relationships between existing biomass and habitat productivity (Fig. 2; Noy-Meir, 1975). The mechanisms behind these relationships have been mainly discussed in terms of species facilitation and competition; i.e., when biomass is relatively low, diversity and productivity increase due to interspecific facilitation; whereas when biomass accumulates to a certain level, competition leads to lower diversity and productivity (Weiner, 2001). In experimental communities, facilitation, species selection, complementary effects, and insurance have been proposed to account for the diversity–productivity relationships (see next section). For detailed discussions and other alternative hypotheses, see Noy-Meir (1975), Waide et al. (1999), and Loreau et al. (2002).

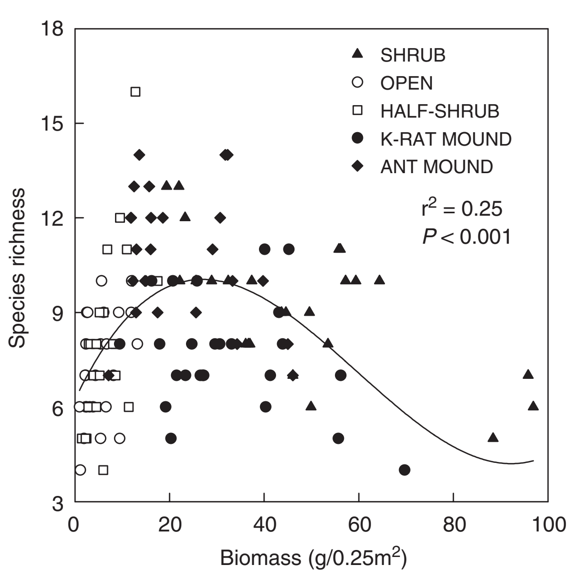

Figure 1. An example of the hump-shaped relationship between biomass and diversity (species richness). Data were collected from five major types of microhabitats at a permanent experimental study site near Portal, Arizona, USA (modified from Guo & Berry, 1998; see also Grime, 1979).

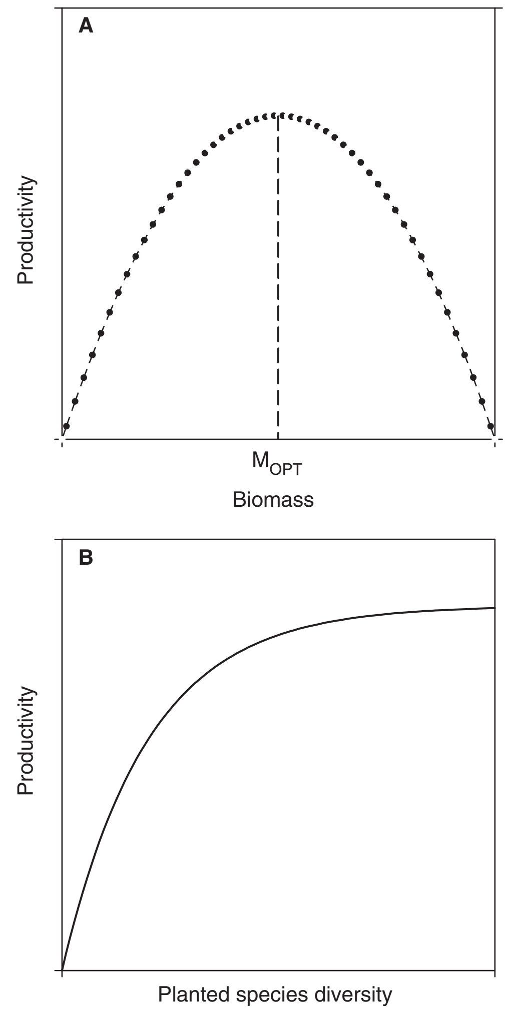

Figure 2. (A) The hump-shaped biomass-productivity following Noy-Meir (1975). The dashed vertical line indicates the optimal biomass level (M_{OPT}; modified from Guo, 2003b). (B) A positive relationship between planted species diversity and productivity in newly seeded communities (following Hooper et al., 2005; Loreau et al., 2002; Spehn et al., 2005). Note that the number of species to be seeded should not exceed the highest level in surrounding natural grassland communities. The actual shape of the relationship may be linear or curvilinear reflecting the combined result of both the number of species and the species composition (i.e., species identity effects).

It would be important to point out that a critical condition underlying the relationships among diversity, biomass, and productivity described above is the inclusion of the full range of the independent variable, i.e., from zero to the highest possible level; otherwise, various or no relationships may emerge. For example, in a frequently disturbed habitat, the biomass may not reach its highest possible level and may thus only show positive relationships with diversity or productivity (Guo, 2003b; Guo & Berry, 1998). Therefore, managers and restorers need to know how to carefully and wisely apply the widely recognized relationships described above to their field techniques and practices. At the same time, basic studies should describe exceptional patterns and identify the underlying causes related to the local or regional ecological conditions and unique disturbance histories.

Management — effects of biomass on diversity and productivity

Some management and restoration may have specific goals. For example, in certain man-made grasslands such as those in Botanic Gardens, golf courses, and campuses, the management focus may be landscape 'beauty', tourism or entertainment, rather than diversity and productivity. Such management issues are beyond the scope of this paper (as the title indicates) and therefore are not discussed here. In most natural and managed (including restored) grasslands, however, a common management goal is to maintain diversity and productivity. Although in some rangelands the management goal is often perceived as increasing productivity only in order to meet increasing human demands and diversity maybe of less concern, this perception is now changing as more people also recognize the importance of nutritional diversity and forage quality. Therefore, rangeland management may be about more than just production: farmers need to provide their livestock with forage of the right palatability and nutritional quality hence the diversity of component species is also indeed a major concern (Marriott, Fothergill, Jeangros, Scotton, & Frédérique Louault, 2004; Parton & Risser, 1979). Besides, high diversity also have many other benefits for overall ecosystem health including higher nutrient use efficiency, better habitat and product quality (Parton & Risser, 1979, but see Smith & Allcock, 1985 and White, Barker, & Moore, 2004), higher carbon sequestration rate (CO_2 uptake), reductions in nutrient leaching (Scherer-Lorenzen, Palmborg, Prinz, & Schulze, 2003), higher litter decomposition rate (Hector, Beale, Minns, Otway, & Lawton, 2000), and greater community/ecosystem stability (Loreau et al., 2002; Fig. 3).

Grassland ecosystem management mainly includes grazing, burning, haying, irrigation, fertilizing, chemical treatment, and biocontrol agent release targeted at noxious weeds. However, the optimal frequency and intensity of some of these activities such as grazing or burning in various habitats for maintaining diversity and habitat productivity are often debated. It is now widely accepted that varying the frequency, intensity, and timing of burning, grazing, or combinations of fire and herbivory can often increase habitat productivity and species diversity by periodically removing above-ground biomass (i.e., reducing competitive exclusion; Dyer, Turner, & Seastedt, 1991) and by compensatory growth (Oba, Mengistu, & Stenseth, 2000). This is especially important when the

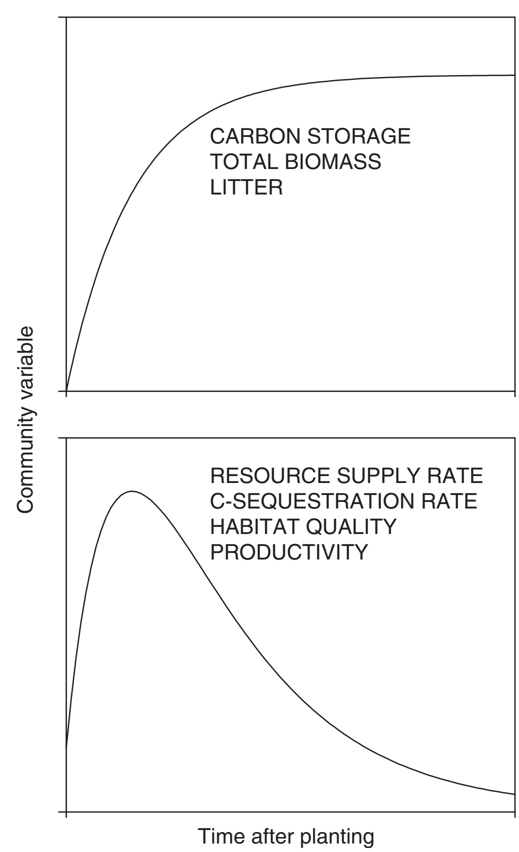

Figure 3. Projected temporal changes in several key community/ecosystem variables in generalized environments after planting (i.e., no major disturbance during ecosystem development). For simplicity, only one curve is presented to show the general trends in several community variables.

management and conservation efforts involve protecting rare and threatened species that only emerge in early successional stages or areas where these species have been greatly reduced by shading or other competitive factors (Kessler, 1999). Using the established relationships among the three key community variables described above, we may be able to identify the optimal (i.e., intermediate) level of biomass to help us reach our management goals.

The intermediate disturbance hypothesis (IDH; Connell, 1978; Grime, 1979; Huston, 1979) that predicts the highest diversity at the intermediate level of disturbance has been used to explain some commonly observed patterns in species diversity. Yet, it is often difficult to quantitatively define "intermediate disturbance" and the issue has rarely been examined or discussed in the same context with biomass control or manipulation. Community biomass should have direct links with the level of disturbance, but does intermediate disturbance also indicate moderate levels of community biomass? Field observations and experimental studies showing diversity to be highest at the intermediate level of both disturbance and biomass (i.e., the hump-shaped curve) suggest so. If this relationship can be further confirmed, the intermediate disturbance can be indirectly interpreted by moderate biomass levels, and could be much more easily measured and controlled in the field. In practice, the best way to identify the optimal (moderate) level of biomass for a particular habitat (type) would be to study the full range of biomass supported by the habitat, from zero (right after a highly destructive disturbance) to the steady-state (or equilibrium) values along a complete seasonal, successional or spatial biomass gradient (Bischoff, Auge, & Mahn, 2005; Guo, 2003b, 2005).

Three additional related issues are attracting increasing attention from both ecologists and managers. First, some abiotic factors such as climate can greatly alter the consequences of any biotic manipulation such as grazing and burning. Therefore, management and restoration should be practiced based on the best information we can obtain from experiences in the past and future projections. Second, biological invasion is now a growing concern because it affects ecosystem functions and processes including the diversity–-biomass–productivity patterns (Pfisterer, Joshi, Schmid, & Fischer, 2004). Invasive species appear to be highly productive and competitive and therefore may threaten many native species. The effects of these invasives seem to be scale-dependent. On a small scale when the habitat is relatively homogenous, invasives may form persistent pure stands which therefore lead to local extinction of natives; over a larger scale, natives are likely to find favorable habitats where invasives cannot invade, persist, or compete, therefore, extinction of natives is not likely to occur. However, the long-term consequences of the effects of biological invasion on native species survival or extinction still need to be monitored because this may influence our management decisions. Thirdly, to a large extent, below-ground biomass governs ecosystem processes and should be considered in our management plans. Related questions to be addressed include: (1) what is the relation between above- and below-ground biomass in a particular habitat? (2) what is the role of below-ground biomass? and (3) how can we also manipulate below-ground biomass and measure changes in it (Wardle, 2002)?

In short, in management practices, biomass is the most easily and frequently manipulated variable. To ensure the expected results to be achieved, the relationships described above suggest that intensive management using grazing or fire to periodically remove some of the accumulated above-ground biomass in the grassland is indispensable (an example of homeostasis; Richards, Possingham, & Tizard, 1999;Watt, 1968). In habitats invaded by non-native species, when total elimination of invasives is not yet feasible, techniques that can effectively remove their biomass should be developed. In management with goals of higher productivity and biodiversity, protecting rare or endangered species seems to benefit from protecting overall diversity because the number of rare or endangered species sustainable in a particular community is likely to be positively related to overall community diversity.

Restoration – effects of planted species richness on productivity and restoration rate

Recent biodiversity experiments show that, in newly seeded communities, biomass production rate is higher on species-rich plots than on species-poor plots. It is argued that habitat productivity increases with species diversity mainly through facilitation, niche complementarity, and the possibility of including more productive species (Huston, 1997). Habitat quality, carbon sequestration rate, and resource supply rate likely follow the productivity curve during experimental community development or restoration, as described in Fig. 3

(Possingham, Lindenmayer, & Tuck, 2002) but exceptions do exist and must be treated separately.

Although seeding experiments have limitations such as random species extinction and sampling effects (Lepš, 2004), they offer valuable information regarding the effects of biodiversity on ecosystem processes (Schmid & Hector, 2004). They also raise an interesting question: will further increases in the above- and below-ground biomasses of high-diversity plantings in turn affect diversity? In other words, is the higher species richness obtained by planting sustainable over a longer time period (Fig. 4)? Also, the relationships among diversity, biomass and productivity are likely to vary when management practice changes or in community development (or restoration) or during biotic invasion (Pfisterer et al., 2004). For these reasons, it is necessary to conduct long-term experiments, i.e., ideally longer than the life spans of the dominant planted species or the native species in the surrounding habitats or the length of the entire successional cycle, from planting to maturity, when biomass stabilizes. Succession studies in the Great Plains grasslands suggest that a whole successional cycle (indicated by the existence of mature individuals of dominant species, or by the maximum community biomass) may take more than 15 years (Gibson & Hulbert, 1987).

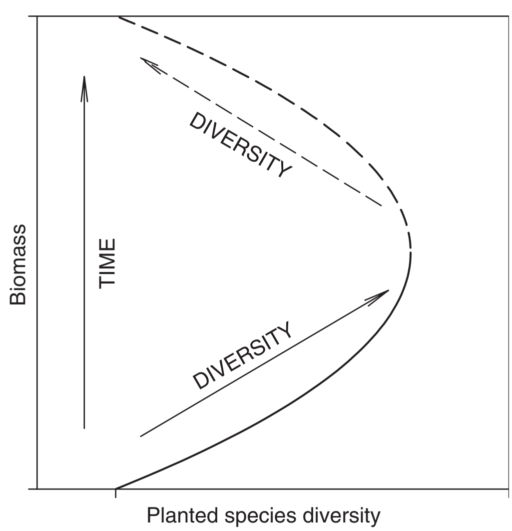

Figure 4. More complete picture of temporal changes in diversity and biomass after planting indicating what might happen (in diversity) if there is no appropriate continuing management after restoration. The difference between experiments and field observation is that in experiments, above-ground biomass is removed for measuring productivity (but below-ground biomass continues to accumulate) so the time needed for the hump-shaped curve to occur would be longer than natural settings where both above- and below-ground biomass is allowed to accumulate. Arrows indicate changes in community variables with time. The solid part of the curve indicates what has been observed in most previous short-term experiments and the dashed part indicates what might happen in the future when biomass continues to increase (see also Schmid & Hector, 2004).

Recent experimental studies have also shown that biomass increases at higher rates on species-rich plots than on species-poor plots, suggesting that these plots might mature earlier given similar initial conditions across all plots. However, as biomass and the biomass accumulation rate (i.e., productivity) continue to increase on species-rich plots, competition eliminates the less competitive species. Therefore, it would be reasonable to argue that species diversity will decline in plots with a higher initial species richness and biomass accumulation rate when biomass reaches a certain level (Fig. 4; Schmid & Hector, 2004). In species-poor plots, however, other species in the regional species pool may invade, and thus, increase diversity, because on these plots, both initial biomass and the biomass accumulation rate are low (assuming the initial ecological conditions such as resource levels were very similar across all plots). So, over the long-term, a commonly reported, hump-shaped diversity–biomass relationship may appear (Fig. 4; Grace, 1999; Guo & Berry, 1998). Such a scenario may occur whether the set of field plots are kept as a closed system (i.e., no species immigration) or as an open system with possibilities of species immigration from the regional species pool.

The time required for a hump-shaped curve (i.e., the relation between diversity and biomass) to emerge would depend on the initial species richness and biomass in the native grasslands relative to the richness, biomass accumulation rate, and lifespans of the planted species. Species richness in mature native grasslands on the same scale may tell whether all the species planted can be sustained when biomass reaches a comparable level to that of mature native grasslands. However, it is clear that long-term studies are needed to more fully understand the planting-to-mature grassland community dynamics and the corresponding diversity–biomass relationships.

Although virtually all experiments attempting to measure relationships between diversity and productivity on seeded plots have suffered from small plot size (but see Roscher et al., 2005) and time constraints (short-term), these studies do offer some significant insights on actual restorations of larger areas and for longer time periods. Restoration may be called "enforced succession" in which a maximum rate of biomass yield is one of the major practical goals. Unlike natural succession, during which species emerge or invade naturally, slowly, and sometimes stochastically, restorationists often plant multiple species at one time (Bradshaw, 1987). However, in a specific area, exactly how many species should be planted and will the planted species richness be sustained over the long-term? This question may be partly answered by the species–area relationship curve generated from native natural habitats, although the actual number of species to be planted should be higher because some unfitted species might be included in planting. The consequences of planting different numbers or combinations of species over the long run are unknown and vary greatly among ecosystems. Empirical data from actual restoration is particularly lacking due to the short observational period and many other limitations. However, theoretically, planting diverse native species may have some important benefits:

Support and maintenance of high community species diversity

It is likely that not every species in any multispecies seeding can germinate and establish. Therefore, planting greater numbers of native species may lead to high diversity and restoration rate as measured by biomass accumulation. In other words, diverse species planting can ensure that the niches in the habitat could be fully occupied in case of failures among the most productive species, especially in early stages of restoration when the habitat is quite open or when the targeted habitat is quite heterogeneous. Optimal high diversity planting can increase the chances that rare or endangered species resided in the original natural habitats may be included (Hector et al., 2001).

Identifying most successful native species

By planting diverse species, we can identify the species that are most successful and persistent and those that are least competitive and might disappear in subsequent years. At the same time, we would not miss other potentially adaptive and productive native species in the restored habitats. Historical vegetation data can help identify highly productive species but might not be enough, because disturbance regimes and other factors such as climate might have changed substantially.

Greater resistance to biological invasions through niche occupation and a high rate of biomass accumulation

Habitat invasibility is likely to be affected by existing species richness and biomass levels, among other factors (Dukes, 2001). Therefore, if more species are planted and they accumulate higher biomass, the planted area would be better protected from increased biomass of existing exotic species or immigration of other invasive species (Tracy, Renne, Gerrish, & Sanderson, 2004; Bakker & Wilson, 2005). Another advantage of diverse plantings is that it allows the identification of species that may be most competitive with existing invasive species in surrounding habitats (e.g., sister or congeneric native species). This can help guide future massive, large-scale plantings, where the habitats may or may not have been invaded. If designed and practiced correctly, the restoration process could offer us one of the rare chances to effectively avoid or reduce biological invasions.

Forming diverse seed banks

It is likely that after the community biomass reaches a certain level, some of the planted species will be competitively excluded. An optimal high diversity planting may also have a greater chance of preserving the species with persistent seed banks. The diverse seed banks formed by the reproduction of planted species would help protect the area from the effects of further disturbances and by ensuring that species important for early succession stages are present in the seed banks. According to general succession theory, species that disappear in later stages are usually those that are critically important in early stages of restoration because they usually germinate earlier, and establish and grow faster after the initial planting.

Although diverse planting has many ecological benefits, several related issues must be taken into account during restoration planting. First, one must be careful not to plant too many species in a given area as it may have adverse effects on the germination and performance of most suitable species. Second, total seed density and the proportion of each species to be planted need to be carefully calibrated. A frequently neglected issue is that restoration should also consider the evolutionary context of the species to be planted. Logical plantation and management regimes should follow the evolutionary forces that favored the initial success, e.g., best adaptation to fire (or other disturbance) and/or the inter-annual climate variability (or global climate change). Such considerations and practice would enhance the ecosystem's resilience or stability. In reality, however, such logical considerations may be limited by the availability and the costs of the seeds of the species chosen for planting.

Several studies also address the effects of species composition or identities of planted species and such effects have been further confirmed by recent studies (Grime, 2002 and literature therein). In a recent experimental testing of the diversity-function relations conducted at a restoration site, Callaway, Sullivan, and Zedler (2003) concluded that, even after some of the most productive species were excluded from planting, the species-richness effects persisted. This indicates that, in restoration potential bias caused by the species identity can, at least partially, be offset by (1) planting a large number of species so that the most productive (or nitrogen fixing) species can be included, and (2) randomly drawing species from the local-regional species pool, or alternatively when seed sources for most species in the regional pool are limited. On the other hand, selecting and planting the most dominant species that formerly characterized the natural or surrounding native habitat, to speed up the restoration rate. Most experimental studies examining the relationships between diversity and productivity have not specifically manipulated or studied other associated factors that may also strongly affect restoration success.

Future work – unifying the two schools

A synthesis of early studies suggests that, diversity, biomass, and productivity show reciprocal effects on each other and, in practice, management and restoration often go hand in hand. For example, to preserve habitat diversity and productivity during restoration, intensive management such as periodic burning, grazing, and haying (to reduce biomass and competition) are needed after the germination and establishment of the seeded species (usually when standing biomass reaches the "optimal" point; Figs. 1, 2). Otherwise, restored habitats may return to unwanted conditions in which aggressive invasive species that are available nearby can easily reinvade and become dominants. For example, without an appropriate control of stream water inflows, a restored sedge meadow in Madison, Wisconsin, converted to cattails (*Typha* spp.) after about 5 years (Zedler, 2003).

Theoretically, the diversity–biomass–productivity relationships should also apply to other systems (e.g., forest), but all may operate at different spatial and temporal scales, where the primary operative factors may vary from one to another. To evaluate the universal applicability of the diversity–biomass–productivity relationships, studies in other ecosystems are needed. Special focus should be on the specific spatial-temporal scales on which certain relations exist in order to determine the optimal magnitude and frequency of disturbance that would benefit the whole system. In doing so, however, it would be equally critical to realize that inconsistencies exist in the relations that may actually be due to other factors such as scale or continuous human alterations, rather than the system's emergent properties. Identifying such factors and examining how such factors may alter the relations would be helpful for reaching the goals of ecosystem management and restoration (Hobbs & Norton, 1996).

Although intermediate levels of biomass or disturbance are needed for most systems to maintain biodiversity, catastrophic events and long-term stable conditions are also needed to allow very early or late stage species to regenerate. In other words, such extreme events are necessary for the system to complete its full successional cycle but should occur at a very low frequency. In grasslands, complete burns may occur every few years, while in forests, complete burns may not occur for several hundreds of years. Accident, large scale, complete forest fires under human conditions can be avoided by more prescribed flash understory burns which can also protect overall species diversity.

The optimal level of biomass and planting richness can be estimated by historical (or successional) vegetation data with spatial data as reference. With an increasing frequency and intensity of disturbance associated with human activities and recent efforts in restorations, increasingly large areas of land are in early stages of succession, and may never complete the full successional cycles. Future experimental studies that simultaneously examine long-term reciprocal effects between diversity and biomass for specific habitats would be most insightful.

Conclusions

While the potential effects of physical factors on the relationships among diversity, biomass, and productivity described here need yet to be further evaluated, management that keeps biomass at certain levels and for certain periods of time would promote species diversity and productivity. In restoration, initial planting of optimal level of species richness would help achieve and maintain habitat productivity, product (e.g., nutritional) quality, and a desirable restoration rate. Niche preoccupation and a high rate of biomass production by initial high diversity planting may also increase habitat resistance to biological invasion by non-native species. Future studies must recognize and emphasize the fundamentally different nature between the two schools of study examining the influences of diversity, biomass, and productivity on each other. Management and (particularly) restoration, when conducted jointly following the diversity–biomass–productivity relationships, can serve as efficient ways of achieving optimal results as well as studying biodiversity and ecosystem functioning. Incorporating these two schools of thought in the same theoretical and practical context in application would greatly benefit our management/restoration efforts and basic ecological research.

Acknowledgements

I thank M. Duchscher, R. Gleason, B. Jamison, D. Jorde, H. Kantrud, D. Losure, K. Smith, J. Zedler, and A. Zimmerman for helpful comments on an early version of the manuscript. Partially supported by the US Geological Survey.

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