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Review

The utility of crop genetic diversity in maintaining ecosystem services

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Abstract

Few studies have addressed the relationship between genetic diversity and provision of ecosystem services in agroecosystems. In this review, we argue that the contribution of biological diversity to ecosystem functioning in agricultural production systems is variable, but can be substantial, and occurs at the genetic, as well as species, level in arable systems. In particular, we look at the potential benefits of crop genetic diversity in enhancing agroecosystem functioning and the provision of services, both directly and indirectly. Increasing crop genetic diversity has shown to be useful in pest and disease management, and has the potential to enhance pollination services and soil processes in specific situations. By contributing to the long-term stability of agroecosystems and helping to provide continuous biomass cover, crop genetic diversity also aids the ecosystem to sequester carbon, and helps in preventing soil erosion.

Keywords: Agroecosystem; Carbon sequestration; Crop genetic diversity; Ecosystem services; Pest and disease; Pollination

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1. Introduction

The relationship between diversity and ecosystem functioning has engendered much debate (Diaz and Cabido, 2001; Hooper and Vitousek, 1997; Loreau et al., 2001; Schwartz et al., 2000). There is a growing consensus that functional diversity, the value and range of species traits rather than just species numbers, is important to short-term ecosystem resource dynamics and long-term ecosystem stability, as it increases positive interactions or complementary functions (Diaz and Cabido, 2001; Wilby and Thomas, 2007). Norberg et al. (2001) further suggest that phenotypic variance, rather than a species diversity metric, may be a more appropriate measure of diversity when attempting to relate diversity to ecosystem functioning. Additional contributions stress functional traits and interactions, on genetic as well as species levels. Tilman et al. (1997) theorize that ecosystem productivity in diverse systems is enhanced by niche-complementarity, where a community of species whose niches complement one another is more efficient in using resources in a multi-species system; increased diversity increases the chances of having better competitors thus maximizing nutrient use, which in turn increases biomass (Tilman et al., 1997; Wilby and Thomas, 2007). Mulder et al. (2001) point to facilitative interactions, rather than niche complementarity, in aiding productivity in a bryophyte community, theorizing that differing architectures among plants leads to favorable humidity conditions during drought.

In placing the emphasis on the number of individual traits rather than species interactions, Tilman et al. (1997) also point to the importance of the ‘‘sampling effect’’ in diverse mixtures. Engelhardt and Ritchie (2001) experimentally show that increased richness of macrophyte species resulted in higher algal and total plant biomass, due to the increased likelihood of the presence of an influential species. Hooper and Vitousek (1997) show a similar richness–biomass relationship, but also underline the importance of plant community *composition*, as opposed to just the number of functional groups, for production and nitrogen dynamics. Mulder et al. (2001) suggest that the ‘‘insurance hypothesis’’ – having a variety of species and/or greater genetic diversity to ensure an ecosystem against declines in its functioning in the face of a range of environmental upsets – can also be seen as a complex sampling effect. This focuses on the importance of individual traits that may be useful at a later time (Norberg et al., 2001; Yachi and Loreau, 1999). Hughes and Stachowicz (2004) comment that genetic diversity may be more likely to affect the resistance of ecosystems to perturbation than to affect ecosystem processes under normal conditions. Reusch et al. (2005) suggest that genetic diversity, through genotypic complementarity, can buffer against extreme climatic events, replacing the role of species diversity in a species-poor coastal ecosystem. Studies of this sort are limited, and there are still little known about how the reduction of diversity within single species can impact ecosystem functioning (Madritch and Hunter, 2003).

Despite the extensive debate on species diversity and ecosystem functioning, and links to the importance of genetic diversity, it is difficult to extrapolate this debate to agroecosystems because most experiments in the species debate are not very representative of the crop diversity and rotations of agricultural systems (Ceroni et al., 2007). The last two decades have provided substantial documentation that considerable local crop genetic diversity continues to be maintained in farmers' fields in the form of traditional varieties (Bellon et al., 1997; Brush, 2004; Jarvis et al., 2004, 2007a,b), and this diversity has constituted an important element of farmers' livelihood strategies (Smale, 2006). Planting a diversity of varieties has allowed the farmer to be more readily responsive to changing market demands or environmental variations that might affect crop production (Vandermeer, 1995; Brush and Meng, 1998; Gauchan and Smale, 2007), to reduce the application of pesticides (Zhu et al., 2000), to receive price premiums for high-quality traditional varieties that compensate for lower yields (Smale et al., 2004), to respond to social and cultural obligations (Rana et al., in press; Latournerie-Moreno et al., 2006), and to improve dietary diversity and ensure nutritional well being (Johns and Sthapit, 2004). With a fairly comprehensive documentation of crop diversity and crop-associated species interactions (e.g., pollinators and below-ground organisms), agricultural ecosystems should provide a data-rich area for testing the assumptions of the ecosystem services debate. Crop environments provide the opportunity to examine the relationship between diversity at the genetic level and ecosystem functions and services, yet few studies have addressed this.

In this review, we argue that the contribution of biological diversity to ecosystem functioning in agricultural production systems is variable, but can be substantial, and occurs at the genetic, as well as species, level in cropping systems. In particular, we identify the potential benefits of crop genetic diversity in enhancing agroecosystem functioning and the provision of services, both directly and indirectly. Two hypotheses are presented. The first is that crop genetic diversity has a direct effect on the maintenance of ecosystem services by providing both: (i) increased numbers of functional traits and (ii) facilitative interactions that maintain above and below ground associated biodiversity. Second, we propose that crop genetic diversity, by increasing long-term stability of the ecosystem in the face of biotic and abiotic stresses and socio-economic variability, promotes the continuous maintenance of biomass and the ecosystem services it provides. Fig. 1 provides a schematic diagram on how these hypotheses are related, and provides the framework of the potential for crop genetic diversity to enhance specific ecosystem functions: (i) pollination efficiency, (ii) pest and disease control, (iii) soil processes (nutrient cycling, decomposition and erosion control), and (iv) carbon sequestration.

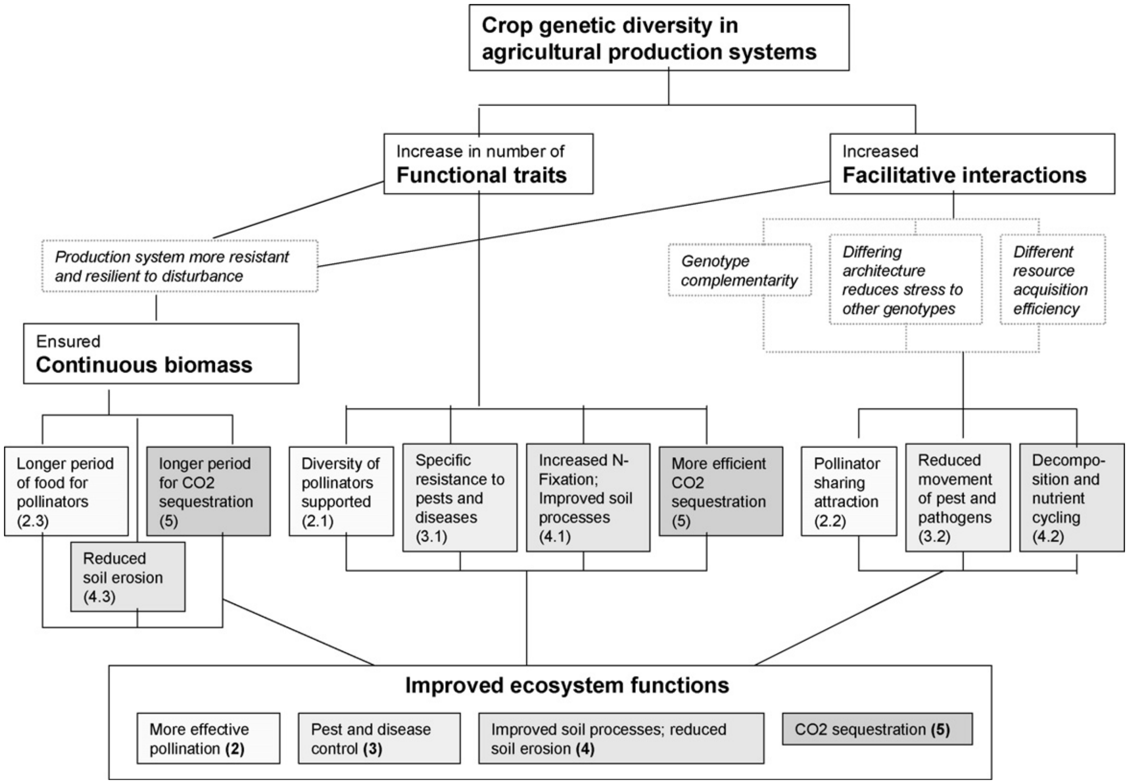

Fig. 1. The potential benefits of crop genetic diversity in directly (increased number of functional traits and increased facilitative interactions) and indirectly (ensured continuous biomass) enhancing agroecosystem functioning and provision of services [Numbers in the figure refer to numbered sections in the text; text within the dotted boxes is provided to clarify the aspects of direct and indirect effects considered in the figure and text.].

2. Pollination

It is argued that the loss of biodiversity in agroecosystems resulting from agricultural intensification and habitat loss negatively affects the maintenance of pollination systems and causes the loss of pollinators world-wide (Kearns et al., 1998; Kremen and Ricketts, 2000; Kremen et al., 2002; Richards, 2001; Ricketts, 2004). Richards (2001) reviews well-documented cases where low fruit or seed set of crops and the resulting reduction in crop yield has been clearly assigned to pollinator impoverishment.

In general, most plants are pollinated by variable suites of flower visitors, varying significantly in both their abundance and their ability to effectuate pollination. While it is rare that plants have single pollinators (Kearns et al., 1998), fig trees provide an important exception to this; each of the 750 *Ficus* species is associated with a distinct species of pollinating wasp, possibly attracted to the unique proportions of volatile compounds in species-specific floral scents (Grison-Pige et al., 2002). Yet, even for those plants with several pollinators, a diversity of native pollinators is essential for sustaining pollination services because of year-to-year climatic and environmental variation (Kremen et al., 2002). In the face of pollinator losses world-wide due to intensive agricultural practices, would enhancement of crop genetic diversity in agroecosystems be an effective intervention for pollinator maintenance? This would be a plausible intervention if it were shown that an increase in crop genetic diversity could indeed sustain greater pollinator diversity, temporally or at a local or landscape scale.

2.1. Functional traits

Pollinator-attracting genotypes of certain crops have been explored as a management strategy to enhance pollination services (Jackson and Clarke, 1991; Suso et al., 1996), as genetic polymorphisms in reproductive characters of flowering plants can influence pollinator foraging (Cane and Schiffhauer, 2001). In many cases, pollinators favor one variety over another, despite the close proximity of different varieties. Jackson and Clarke (1991) show this to be the case in an almond orchard where honey bees visit one variety mostly, but not the commercially desirable variety. Nectarless cultivars of melon have little attraction for pollinators, and need to be planted in fields with cultivars providing nectar in order to achieve sufficient pollination (Bohn and Mann, 1960). Male-sterile cultivars of a number of crops (for example, carrot, cotton or safflowers) produce little or no floral rewards and consequently receive diminished pollination services from visiting insects (Free, 1993). Studies show that strategic plantings, alternating different varieties in a checkerboard pattern for example, can optimize effective pollination visits to two varieties of different attractiveness, and at the same time promote cross-hybridization and better fruit production (Kubisova and Haslbachova, 1991).

However, genetic polymorphisms in reproductive characters that may affect pollination services are specific to some crops and not others: with turnip rape, nectar secretion is quantitatively and qualitatively similar among varieties (Brunel et al., 1994) and Galetto et al. (1998) find no correlation between the nectar sugar ratio or flower morphology and the kinds of pollinating visitors, after testing a number of *Lycium* species and varieties.

2.2. Facilitative interactions

Few have looked at the possibility of facilitative *interactions* among genotypes in the pollination network that can positively affect pollination services. A species-level study of *Clarkia* has shown facilitative interactions, via pollinator sharing among congeners that jointly attract pollinators, increase pollinator availability and lower pollen limitation of reproduction compared to populations occurring alone (Moeller, 2004). Facilitative interactions may occur as well between pollinating species, resulting in more effective pollination. Sunflowers are generally planted in alternating rows of male fertile and male sterile plants. Honeybee foragers tend to specialize as nectar or pollen gatherers, and thus are not inclined to cross between rows. The presence of other native bees, collecting both pollen and nectar, has been shown to facilitate cross pollination and also alter the behavior of honeybees, ‘‘chasing’’ them into visiting more frequently across rows as they try to avoid contact with other species of bees (Greenleaf and Kremen, 2006).

2.3. Continuous biomass

One could speculate that staggered flowering times among crop varieties would prolong season-long visitation throughout the protracted flowering season (thus increasing the chances of pollinator population survival to the next growing season), as well as increasing the types of pollinators visiting at different times during the season, since several bee species are sensitive to climatic variation (Kremen et al., 2002; Willmer et al., 1994). This management strategy is used with maize varieties in the Yucatan, Mexico, where short-cycle maize and the more popular long-cycle maize are planted together in order to supply bees with pollen during the wet season and sustain the bee population until the next floral season (Tuxill, 2005). At the species level, anecdotal evidence in one system points to similar interactions, where the existence of winter wildflowers in California are thought to help build up pollinator populations for the early spring mass blooming period of almond trees (McGregor, 1976). Recent investigations of pollination webs have mapped facilitative interactions of pollinators and host plants (Vasquez, 2004; Memmott, 1999), and changes in such interactions with the introduction of alien species (Memmott and Waser, 2002) in a diversity of ecosystems. However, such analytical approaches need to be applied to agroecosystems (including facilitative interactions between crop cultivars) if this is to be considered a viable management strategy for pollinator conservation.

In contrast, increasing landscape heterogeneity is currently receiving considerable attention as an effective intervention for pollinator maintenance. It has been repeatedly shown that size of, and distance from, natural habitat is a primary factor in maintaining pollination services in an agricultural landscape (Kremen et al., 2002; Richards, 2001; Ricketts, 2004; Steffan-Dewenter et al., 2002; Steffan-Dewenter and Tscharntke, 1999). With native, unmanaged bee communities in California, pollination services are positively related to proportion of upland natural habitat, rather than farmer type, insecticide usage, field size or honey bee abundance (Kremen et al., 2002). Increasing isolation of habitat islands among agricultural fields results in both decreased abundance and species richness of flower-visiting bees for both mustard and radish crops in Germany, and the number of seeds per fruit and per plant decreases significantly with increasing distance from the nearest grassland for both crops (Steffan-Dewenter and Tscharntke, 1999). Studies show that distance from nests or ‘‘safe sites’’ may be the main cause of decreased pollinator services due to habitat loss (Richards, 2001). With coffee crops in Costa Rica, native pollinator richness, overall visitation rate and pollen disposition rates are all significantly higher in sites within 100 m of forest fragments (Ricketts, 2004). Habitat loss has also selected for large-bodied pollinators able to forage over long distances (Richards, 2001). Introduced honey bee, *Apis mellifera*, visitation rates, however, are less affected by the distance to natural habitat when compared to native bees (Ricketts, 2004; Steffan-Dewenter et al., 2002), but also show the highest yearly variability (Ricketts, 2004). This indicates the importance of having a diverse set of pollinators within a pollinator network.

Proximity to natural habitats is not a management intervention that farmers can easily change. But experimental work has shown the value of deliberately manipulating plant communities’ on-farm, essentially bringing natural environments closer to crops. These crop-associated plant communities, such as those found in flower-rich field margins, set asides, strip crops, agroforestry crops and permanent hedgerows can provide additional forage (pollen and nectar) and nesting resources for pollinators (Dover, 1997; Carvell et al., 2004). Abundance and composition of pollinators can be influenced, and presumably managed, by the purposeful use of crop-associated companion plantings (Gurr et al., 2004; Pywell et al., 2005). Annual communities of weeds can also support the persistence of pollinators on farms (Morandin and Winston, 2006; Gemmill and Ochieng, in submission).

3. Pest and disease control

Diversity, in the form of crop genetic diversity, polycultures, and landscape heterogeneity, each at various temporal scales, has been effectively used to control the spread of and damage caused by pests and diseases in agroecosystems. Mechanisms of how diversity can be employed in a field or landscape for pest and disease control are well studied, as summarized below.

3.1. Functional traits

The use of single resistance genes in a monoculture is a source of strong selective pressure for pathogen races capable of overcoming the resistance, thus these resistances are often short lived (de Vallavieille-Pope, 2004). It is therefore intuitive to spread the risk of total infection and crop loss by planting varieties with differing resistances, so that if one resistant trait is overcome, the entire field of crops is not lost. Furthermore, with increased diversity in resistance mechanisms, there is less selective pressure on the pathogen to overcome any single resistance. Jarvis et al. (2007a,b) discuss two conflicting hypotheses that explore the utility of on-farm genetic diversity: the diversity-benefit (Mundt, 1991) and diversity-hazard (Kolmer et al., 1991) hypotheses, with the latter stating that diverse systems accelerate the evolution of super races of pathogens. On-farm observation and empirical evidence point to traditional genetically diverse systems selecting for stability and low aggressiveness of pathogens rather than super-races and instability (Lannou and Mundt, 1996).

Varietal mixtures also have an advantage over multilines (mixtures of genetically similar lines or varieties that mainly differ only in their resistances to different pathotypes) in that the heterogeneity of other traits are more efficient in addressing abiotic stresses, and less time and resources are lost in multiline breeding (Wolfe, 1985).

3.2. Facilitative interactions

A principal purpose of the use of genetic mixtures for disease management is to slow the pathogen's spread by slowing the rate and incidence of infection (Mundt, 2002), provided the components differ in their susceptibility (Wolfe, 1985). Mechanisms involved include: increasing the distance between susceptible cultivars; creating a physical barrier to spore dispersal; decreasing the proportion of susceptible plant tissue; overcoming selection pressure for pathogens to surmount valuable forms of disease resistance; increasing selection in host population for more competitive or more resistant genotypes; increasing competitive interactions among pathogen populations and inducing resistance in the host for subsequent infection (de Vallavieille-Pope, 2004; Finckh et al., 2000; Garrett and Mundt, 1999; Jarvis et al., 2007a,b). Mixtures have reduced disease severity by 40–80% in the cases of cereal rusts and powdery mildew (Wolfe, 1985). The success of barley mixtures in reducing disease and thus increasing yield have led to the proposed use of mixed soft wheat varieties for energy-efficient feedstock for a possible bioethanol industry in the UK (Swanston and Newton, 2005). Other successful examples of the use of varietal mixtures in Europe, North America, Asia, and South America are reviewed in de Vallavieille-Pope (2004).

However, a review by Finckh et al. (1999) shows that there is high variation in results. With two-way cultivar mixes, disease reduction on susceptible cultivars varies between 33 and 71% across the years (Finckh et al., 1999). Neither densities of Malawian bean flies nor their rates of parasitism changes significantly by diversifying the field with non-host plants or with varietal mixtures (Letourneau, 1995). Polycultures do not provide any advantage to natural enemy populations when compared with monocultures of corn in Ohio (Tonhasca and Stinner, 1991).

Predictability of the utility of crop genetic diversity is an important factor in deciding on management options. Crop genetic diversity will not work in every situation, and each situation in which it does work, options will have to be tailored to the specific case by manipulating the selection of crop genetic diversity, the field size and position, the spatial arrangement of crop genetic diversity within a field, and temporal variables (Trutman, 2005). Garrett and Mundt (1999) suggest that the following conditions would increase the probability of host diversity reducing disease: smaller plants; flatter dispersal gradients; smaller lesions; shorter generation times; and greater specialization of pathogen populations. However, weighting of the factors is still unclear, and overall predictably could be limited due to environmental variation (Garrett and Mundt, 1999). The number of plant genotypes, the planting density and arrangement within a field, and the spatial and temporal scales at which diversity is to be deployed will likely be situation- and crop-dependent. Holt and Chancellor (1999) provided an example of how diversity management can be used to control the *tungro* virus disease in rice. In this specific situation of long-term disease incidence in a dynamic cropping system, they suggest that resistant crop deployment be spatially random, and that relatively large proportions of fields be sown with resistant varieties in order to have sufficient area-wide impact to reduce disease incidence in fields of susceptible varieties (Holt and Chancellor, 1999). From their models, they further suggest the concentration of resistant varieties deployment in the season of greatest disease spread, rather than pre-empting it, and in terms of scale, to deploy small genotype units in random patterns to maximize area-wide strategic impact, or large units and concentrated deployment to protect individual fields (Holt and Chancellor, 1999). Although effects of polycultures on microbial pathogens are not consistently evident or predictable (Matson et al., 1997; Schlapfer and Schmid, 1999), genetic diversity, either with multilines or mixtures, can significantly reduce fungal pathogen impacts (Matson et al., 1997). Incidence of viruses transmitted by insects is more predictably lowered in polycultures (Matson et al., 1997).

Using crop diversity and crop genetic diversity for pest and disease management confers a number of indirect benefits as well, besides the increase in productivity. The reduced needs for chemical pesticides reduces the negative effects that they have on associated biodiversity, such as pollinators and soil biodiversity (Kearns et al., 1998), as well as the risk of harmful effects on the health of farm workers and the pollution of nearby water sources.

4. Soil nutrient dynamics

Soil organisms perform a number of vital functions that regulate the soil ecosystem, including: decomposition of litter and cycling of nutrients; converting atmospheric nitrogen to an organic form, and reconverting this to gaseous nitrogen; and altering soil structure (Altieri, 1999). Some authors say that the reduction in the diversity of soil biota under agricultural practice may profoundly alter decomposition and nutrient availability in soils (Matson et al., 1997), as well as reduce the soil community's resilience and resistance to stress (Griffiths et al., 2000). However, there is a lack of consensus on the effects of diversity (above-ground and soil biota) on soil dynamics, due to the high redundancy in soil systems, thus it is difficult to draw general conclusions. Some of the debate on the utility of diversity in ensuring soil ecosystem processes is reviewed here.

4.1. Functional traits

Some well-defined microbial processes such as nitrification and methane oxidation are carried out by a limited microbial subset, thus such processes may be more sensitive to changes in diversity (Griffiths et al., 2000). However, the effect of diversity on decomposition of plant litter has engendered debate. Many studies support the idea that there is no predictable effect of increasing species richness of plant litter, reporting both positive and negative effects on soil biological activity and decomposition rates (Bardgett and Shine, 1999). Some examples of this debate include Wardle et al. (1997) providing experimental evidence which does not support the hypothesis that enhanced species richness improves ecosystem function, while Hansen and Coleman (1998) observe that diverse assemblages of Oribatid mites have significantly faster litter decomposition rates in mixed-species litters. Barlocher and Graça (2002) report redundancy in the decomposer community; while riparian vegetation diversity affects stream fungal community diversity, litter decay rates do not differ between the fungal communities (Barlocher and Graça, 2002).

The importance of species diversity in soil dynamics seems to be situation-dependent. As Wardle et al. (1997) state, the varied nature of effects of each added species is also likely to be related to its functional characteristics, rather than diversity *per se*. But what of genetic diversity? Does genetic diversity play a role in decomposition and nutrient cycling? The concept of the extended phenotype (*sensu* Dawkins, 1982), that genes can be important in determining ecosystem-level processes, has been explored repeatedly in this context. Schweitzer et al. (2004) show a tight coupling of plant polyphenols to rates of nitrogen cycling and decomposition. Polyphenols are known to influence the quality of plant litter substrate for microbial decomposition (Schweitzer et al., 2004), and Schweitzer et al. (2004) report that tannin concentrations, which correlate with genetic composition of plant litter, are the best predictors of soil net nitrogen mineralization. The ratio of condensed tannin to total nitrogen is also the best predictor of decomposition (Schweitzer et al., 2004). Treseder and Vitousek (2001) show that a small degree of genetic divergence causing varying nitrogen and lignin concentrations among populations of *Metrosideros polymorpha* (the Ohia lehua native shrub or tree of Hawaii) affects decomposition rates of senescent leaves, related positively to nitrogen concentration and negatively to lignin concentration.

The specific genotypes to be used to enhance soil fertility and nitrogen fixation can be a central factor to consider. A study by Wolde-meskel et al. (2004) suggests the existence of intraspecific variation in nodulation and rhizobial affinity among *Acacia* populations; this is species-specific, as some *Acacia* species are promiscuous for nodulation (Wolde-meskel et al., 2004). Intentional introduction of soil organisms to increase soil biodiversity and aid in nutrient dynamics is a common practice (Altieri, 1999). However, effectiveness of this management option may depend on varieties present, as there can be considerable variation in the effectiveness of the plant-mycorrhizae association within plant species. Many studies show that cultivars of various crops do not respond similarly, physiologically or morphologically, to inoculation with vesicular–arbuscular mycorrhizae (Jun and Allen, 1991; Krishna et al., 1985; Ronsheim and Anderson, 2001).

4.2. Facilitative interactions

Having seen that genotype can be important in influencing soil dynamics, the next step is to see if genotypic *diversity*, *per se*, plays a role. Few studies have explored this.

A series of studies by Madritch and Hunter (2002) on *Quercus laevis* show non-additive effects of mixed litter on soil carbon and nitrogen content, where mixed-litter treatments differed significantly from single phenotype treatments. Soil respiration also increased with intraspecific litter diversity, especially in areas of high nitrogen deposition (Madritch and Hunter, 2003). They suggest that more diverse litters may provide substrate for a more diverse assemblage of metabolic pathways, which may lead to an increase in respiration, and also suggest that other studies may have failed to find an effect of diversity on respiration due to nitrogen limitation, thus being unable to take advantage of the diverse litter substrate (Madritch and Hunter, 2003, 2005). This points to a niche-complementarity explanation, when nutrients are not limited.

While these examples do not come from agroecosystems, it is important to note that studies have highlighted that there is a potential role for above-ground genetic diversity to play in soil ecosystem processes that should be investigated further, particularly in light of the ability to alter nitrogen levels as needed for optimal nutrient cycling.

Nitrogen fixation, on the other hand, is a soil agroecosystem process that has received considerable attention in the diversity debate. The inclusion of legumes and/or fibrous rooted crops in crop rotations (Altieri, 1999), and species mixtures and with legume and non-legume combinations are oft used techniques to increase yield stability in nitrogen-limited environments (Schlapfer and Schmid, 1999), without having to employ costly and water-polluting fertilizers.

However, few studies have explored the utility of genetic *diversity* for this ecosystem process. One can imagine the use of multiple varieties, including ones that respond well to inoculation, if trying to maximize this service with other desirable characteristics. The use of genetic diversity will be plant-specific, as results will likely vary depending on specific biological needs and circumstances. One example where intraspecific plant diversity has been demonstrated to be *detrimental* is with wild garlic: Ronsheim and Anderson (2001) demonstrate that plants have a relatively greater benefit from the mycorrhizal association if their neighbors are genetically identical or from the same population than from a different population. It is hypothesized that genotypically similar plants benefit from the sharing of a more effective hyphal network (Ronsheim and Anderson, 2001).

4.3. Continuous biomass

Crop genetic diversity has the potential to enhance an ecosystem's capacity to sustain biomass levels, through improving the agricultural ecosystem's resilience and resistance to environmental variability. High levels of crop genetic diversity occur most commonly in areas where the production environment itself is extremely variable (Brush, 1991; Brush and Meng, 1998; Aguirre et al., 2000). Environmental stresses can influence the generation and maintenance of intraspecific diversity for increased portfolio of types to cope with multiple stresses and changing conditions, ensuring a more stable vegetation cover under less predictable environments. Brown and Rieseberg (2006) discuss the importance of determining whether local landraces in extreme habitats possess specialized tolerant genotypes rather than those genotypes that are broadly adapted and cope by phenotypic plasticity when developing a strategy to ensure sustainable production in harsh environments and continuous biomass coverage.

Soil, water and nutrient availability, and consequent yield biomass, is a management issue that has the potential to be addressed through crop genetic diversity. Sawadogo et al. (2005) show that farmers in Burkina Faso cope with unpredictable rainfall by managing a high number of varieties of sorghum, millet and cowpea, which allow the option of planting either or both late and early maturing varieties. Farmers in Chiapas, Mexico plant local maize varieties in areas with poor soil quality and improved varieties in higher soil quality (Bellon and Taylor, 1993), allowing for maximum biomass production on their land and in turn preventing soil erosion in areas of poor soil quality. In Nepal, farmers typically plant several varieties of rice to match land types, soil, moisture and other micro-ecological conditions in upland, lowland and swamp environments, often all found on the same farm; in total, more than twice the number of rice varieties are found in the hills (which are generally more prone to erosion) than in the lowlands (Gauchan and Smale, 2007). Farming on slopes tends to be associated with greater diversity in both crops and varieties (Gauchan and Smale, 2007). In these cases, tolerant varieties are planted where there would otherwise be no vegetative cover, and multiple varieties are planted to best match soil type. This provides for a more continuous planted biomass, avoiding or decreasing soil erosion (and also enhancing the soil's ability to sequester carbon—see following section).

5. Carbon sequestration

Carbon sequestration markets are fast emerging to place monetary value on a service long provided by ecosystems for free. However, plant diversity has rarely been seen as enhancing carbon sequestration. A recent study by Bunker et al. (2005) show that carbon storage is very species-specific, and depends on wood density, diameter, basal area, and maximal wood volume, thus diversity *per se* does not play an important role. Many studies have focused on plant biomass as the main determinant of rates of carbon sequestration, and some suggest that carbon assimilation is not affected by diversity (Stocker et al., 1999). However, models show that species diversity may provide increased biological insurance in the face of species loss due to reduced precipitation (Bunker et al., 2005), which in turn ensures that the service in question will continue to be provided, even in the face of drought.

Agricultural practices that reduce soil degradation and desertification help retain soil organic matter in the surface layer, and thus enhance the soil's ability to sequester carbon (Batjes and Sombroek, 1997). Slowing soil degradation and impeding desertification could conserve up to 0.5–1.5 Pg C annually (Dixon et al., 1994). Practices that return large quantities of biomass and increase soil organic matter inputs to the agroecosystem also enhance carbon sequestration.

Thus, practices that increase species and genetic diversity, at various time scales, and help increase productivity year-round, can indirectly increase the ecosystem's ability to sequester carbon. This includes enhancing soil fertility with practices such as multiple cropping and agroforestry, enhancing crop rotation complexity, adding cover crops year-round, using improved crops or varieties, and planting deep-rooted crops or varieties (Lal and Kimble, 1997; West and Post, 2002). As explored in the previous sections, using species or varietal mixtures for pest and disease management and enhanced pollination services, as well as for ensuring the agroecosystem against abiotic stresses, can also increase productivity and long-term stability of the system.

6. Maximizing multiple services

From the examples elaborated above, it is not with an overwhelming consensus that one can say that genetic diversity is essential for the provision of ecosystem services in an agroecosystem. Increasing genetic diversity, or the number of varieties planted, has shown to be very useful in pest and disease management, but so has landscape heterogeneity and species diversity. In the other three services addressed, a link has been made to the importance of the genetic level, calling for more work on the use of diversity at the genetic level in specific situations. But with a range of management options to choose from, addressing genetic diversity alone may not be the single most successful solution in providing any one ecosystem service.

However, our review has stressed the interactive and combined effects of diversity. Addressing only one ecosystem service at a time is not a practical approach. As illustrated in Fig. 1, the many direct and indirect effects of crop genetic diversity work through various aspects of agroecosystems, and can improve multiple ecosystem functions. Such a holistic framework should be incorporated when evaluating the contribution of crop genetic diversity to the ecosystem services that underpin sustainable agriculture. Relative trade-offs between the role of crop genetic diversity in the provisioning of ecosystem services and identification of complementarities and synergies are critical to such evaluations. For instance, planting herbivore-resistant varieties only may drive away pollinators; in one study pollinators spent significantly more time per flower on *Brassica rapa* plants with lower resistance to flea beetle herbivores (Strauss et al., 1999). As this review has indicated, genetic diversity may play an important role in enhancing the provision of many services concurrently in multifunctional and sustainable agriculture.

7. Future ecosystem service value

Appreciation of the future utility of genetic resources is apparent both from the hundreds of thousands of accessions of genetic resources in gene banks worldwide, and from the continuous maintenance of a significant amount of local genetic resources by small-scale farmers worldwide. Crop breeders and small-scale farmers alike depend on crop genetic diversity to ensure continued and improved productivity and resilience of their system in the face of variability. Yet an important and often forgotten benefit of conserving genetic diversity is the additional delivery of current and future ecosystem services. Therefore, in addition to calculating future production values of improved varieties, we could be calculating the value of improved delivery of ecosystem services by crop genetic diversity in agricultural ecosystems. For example, varieties that are drought-tolerant would not only be valued for increasing productivity in areas suffering drought, their planting would also prevent soil erosion and desertification, increase soil organic matter and thus soil carbon sequestration, and possibly stabilize slopes and maintain watersheds.

Although it may not yet be entirely apparent that genetic diversity is important for present-day delivery of valuable ecosystem services from our agricultural ecosystems, the conservation of this diversity stabilizes ecosystem functioning in the long-run, and thus ensures delivery of ecosystem services in the future.

References

Aguirre, J.A., Bellon, M.R., Smale, M., 2000. A regional analysis of maize biological diversity in Southeastern Guanajuato, Mexico. Econ. Bot. 54, 60–72.

Altieri, M., 1999. The ecological role of biodiversity in agroecosystems. Agric. Ecosyst. Environ. 74, 19–31.

Bardgett, R., Shine, A., 1999. Linkages between plant litter diversity, soil microbial biomass and ecosystem function in temperate grasslands. Soil Biol. Biochem. 31, 317–321.

Barlocher, F., Graça, M., 2002. Exotic riparian vegetation lowers fungal diversity but not leaf decomposition in Portuguese streams. Freshwater Biol. 47, 1123–1135.

Batjes, N., Sombroek, W., 1997. Possibilities for carbon sequestration in tropical and subtropical soils. Global Change Biol. 3, 161–173.

Bellon, M.R., Pham, J.-L., Jackson, M.T., 1997. Genetic conservation: a role for rice farmers. In: Maxted, N., Ford-Lloyd, B.V., Hawkes, J.G. (Eds.), Plant Genetic Conservation: The In Situ Approach. Chapman and Hall, London, pp. 261–289.

Bellon, M.R., Taylor, J.E., 1993. ''Folk'' soil taxonomy and partial adoption of new seed varieties. Econ. Dev. Cultur. Change 41, 763–786.

Bohn, G.W., Mann, L.K., 1960. Nectarless, a yield-reducing mutant character in the muskmelon. Proc. Am. Soc. Hortic. Sci. 76, 455–459.

Brown, A.H.D. Rieseberg, L., 2006. Genetic features of populations from stress-prone environments, In: Jarvis, D., Mar, I., Sears, L., (Eds.), Enhancing the Use of Crop Genetic Diversity to Manage Abiotic Stress in Agricultural Production Systems. Proceedings of a Workshop, May 23–27, 2005, Budapest, Hungary. International Plant Genetic Resources Institute, Rome, Italy, pp. 2–10.

Brunel, E., Mesquida, J., Renard, M., Tanguy, X., 1994. Distribution of pollinating entomofauna on rapeseed (*Brassica napus* L) and turnip rape (*Brassica campestris* L) flowers- the effect of the turnip rapes apetalous character. Apidologie 25, 12–20.

Brush, S., 1991. A farmer-based approach to conserving crop germplasm. Econ. Bot. 45, 153–165.

Brush, S.B., Meng, E., 1998. Farmer's valuation and conservation of crop genetic resources. Genet. Resour. Crop Evol. 45, 139–150.

Brush, S.B., 2004. Farmers' Bounty: Locating Crop Diversity in the Contemporary World. Yale University Press, New Haven.

Bunker, D., DeClerck, F., Bradford, J., Colwell, R., Perfecto, I., Phillips, O., Sankaran, M., Naeem, S., 2005. Species loss and aboveground carbon storage in a tropical forest. Sciencexpress 310, 1029–1031.

Cane, J., Schiffhauer, D., 2001. Pollinator genetics and pollination: do honey bee colonies selected for pollen-hoarding field better pollinators of cranberry *Vaccinium macrocarpon*. Ecol. Entomol. 26, 117–123.

Carvell, C., Meek, W.R., Pywell, R.P., Nowakowski, M., 2004. The response of foraging bumblebees to successional changes in newly created arable field margins. Biol. Conserv. 118, 327–339.

Ceroni, M., Liu, S., Costanza, R., 2007. The ecological and economic roles of biodiversity in agroecosystems. In: Jarvis, D., Padoch, C., Cooper, D. (Eds.), Managing Biodiversity in Agricultural Ecosystems. Rome, Columbia University Press and International Plant Genetics Resources Institute, New York, pp. 446–473.

Dawkins, R., 1982. The Extended Phenotype. New York, Oxford University Press, New York.

de Vallavieille-Pope, C., 2004. Management of disease resistance diversity of cultivars of a species in single fields: controlling epidemics. Compte Rendus Biol. 327, 611–620.

Diaz, S., Cabido, S., 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16, 646–655.

Dixon, R., Winjum, J., Andrask, K., Lee, J., Schroeder, P., 1994. Integrated land-use systems: assessment of promising agroforest and alternative land-use practices to enhance carbon conservation and sequestration. Climatic Change 27, 71–92.

Dover, J.W., 1997. Conservation headlands: effects on butterfly distribution and behaviour. Agric. Ecosyst. Environ. 63, 31–49.

Engelhardt, K., Ritchie, M., 2001. Effects of macrophyte species richness on wetland ecosystem functioning and services. Nature 411, 687–689.

Finckh, M., Gacek, E., Czembor, H., Wolfe, M., 1999. Host frequency and density effects on powdery mildew and yield in mixtures of barley cultivars. Plant Pathol. 10, 807–816.

Finckh, M., Gacek, E., Goyeau, H., Lannou, C., Merz, U., Mundt, C., Munk, L., Nadziak, J., Newton, A., de Vallavieille-Pope, C., Wolfe, M., 2000. Cereal variety and species mixtures in practice, with emphasis on disease resistance. Agronomie 20, 813–837.

Free, J.B., 1993. Insect Pollination of Crops. Academic Press, London.

Garrett, K., Mundt, C., 1999. Epidemiology in mixed host populations. Phytopathology 89, 984–990.

Galetto, L., Bernardello, G., Sosa, C.A., 1998. The relationship between floral nectar composition and visitors in *Lycium* (Solanaceae) from Argentina and Chile: what does it reflect? Flora 193, 303–314.

Gauchan, D., Smale, M., 2007. Comparing the choices of farmers and breeders: the value of rice landraces in Nepal. In: Jarvis, D., Padoch, C., Cooper, H.D. (Eds.), Managing Biodiversity in Agricultural Ecosystems. New York, Rome, Columbia University Press and Bioversity International, pp. 407–425.

Greenleaf, S.S., Kremen, C., 2006. Wild bees enhance honey bees pollination of hybrid sunflower. Proc. Natl. Acad. Sci. U.S.A. 103, 13890–13895.

Griffiths, B., Ritz, K., Bardgett, R., Cook, R., Christensen, S., Edelund, F., Sorensen, S., Baath, E., Bloem, J., de Ruiter, P., Dolfing, J., Nicolardot, B., 2000. Ecosystem response of pasture soil communities to fumigation-induced microbial diversity reductions: an examination of the biodiversity-ecosystem function relationship. Oikos 90, 279–294.

Grison-Pige, L., Bessiere, J., Hossaert-McKey, M., 2002. Specific attraction of fig-pollinating wasps: role of volatile compounds released by tropical figs. J. Chem. Ecol. 28, 283–295.

Gurr, G.M., Wratten, S.D., Altieri, M. (Eds.), 2004. Ecological Engineering for Pest Management: Advances in Habitat Manipulation Management. CSIRO Publishing, Melbourne.

Hansen, R.A., Coleman, D.C., 1998. Litter complexity and composition are determinants of the diversity and species composition of oribatid mites (Acari: Oribatida) in litterbags. Appl. Soil Ecol. 9, 17–23.

Holt, J., Chancellor, T., 1999. Modeling the spatio-temporal deployment of resistant varieties to reduce the incidence of rice tungro disease in a dynamic cropping system. Plant Pathol. 48, 453–461.

Hooper, D., Vitousek, P., 1997. The effects of plant composition and diversity on ecosystem processes. Science 277, 1302–1305.

Hughes, A., Stachowicz, J., 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. Proc. Natl. Acad. Sci. 101, 8998–9002.

Jackson, J., Clarke, G., 1991. Gene flow in an almond orchard. Theor. Appl. Genet. 82, 1432–2242.

Jarvis, D.I., Padoch, C., Cooper, H.D., 2007a. Managing Biodiversity in Agricultural Ecosystems. Rome, Columbia University Press and Bioversity International, New York.

Jarvis, D., Brown, A., Imbruce, V., Ochoa, J., Sadiki, M., Karamura, E., Trutmann, P., Finckh, M., 2007b. Managing crop disease in traditional agroecosystems: the benefits and hazards of genetic diversity. In: Jarvis, D.I., Padoch, C., Cooper, H.D. (Eds.), Managing Biodiversity in Agricultural Ecosystems. Rome, Columbia University Press and Bioversity International, New York, pp. 292–319.

Jarvis, D., Zoes, V., Nares, D., Hodgkin, T., 2004. On-farm management of crop genetic diversity and the convention on biological diversity programme of work on agricultural biodiversity. Plant Genet. Resour. Newslett. 138, 5–17.

Johns, T., Sthapit, B.R., 2004. Biocultural diversity in the sustainability of developing country food systems. Food Nutr. Bull. 25, 143–155.

Jun, D., Allen, E.B., 1991. Physiological responses of 6 wheatgrass cultivars to mycorrhize. J. Range Manage. 44, 336–341.

Kearns, C., Inouye, D., Waser, N., 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. Annu. Rev. Ecol. Evol. Syst. 29, 83–112.

Kolmer, J.A., Dyck, P.L., Roelfs, A.P., 1991. An appraisal of stem rust resistance in North American hard red spring wheats and the probability of multiple mutations to virulence in populations of cereal rust fungi. Phytopathology 81, 237–239.

Kremen, C., Ricketts, T., 2000. Global perspectives on pollination disruptions. Conserv. Biol. 14, 1226–1228.

Kremen, C., Williams, N., Thorp, R., 2002. Crop pollination from native bees at risk from agricultural intensification. Proc. Natl. Acad. Sci. 99, 16812–16816.

Krishna, K., Shetty, K., Dart, P., Andrews, D., 1985. Genotype dependent variation in mycorrhizal colonization and response to inoculation of pearl millet. Plant Soil 86, 113–125.

Kubisova, S., Haslbachova, H., 1991. Pollination of male-sterile green pepper line (Capsicum annuum L.) by honeybees. Acta Horticulturae 288.

Lal, R., Kimble, J., 1997. Conservation tillage for carbon sequestration. Nutr. Cycl. Agroecosyst. 49, 243–253.

Lannou, C., Mundt, C.C., 1996. Evolution of pathogen population in host mixtures: Simple race-complex race competition. Plant Pathol. 45, 440–453.

Latournerie-Moreno, L., Tuxill, J., Yupit-Moo, E., Arias-Reyes, L., Cristobal-Alejo, J., Jarvis, D.I., 2006. Traditional maize storage methods of Mayan farmers in Yucatan, Mexico: implications for seed selection and crop diversity. Biodivers. Conserv. 15, 1771–1795.

Letourneau, D., 1995. Associational susceptibility: effects of cropping pattern and fertilizer on Malawian bean fly levels. Ecol. Appl. 5, 823–829.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J., Hector, A., Hooper, D., Huston, M., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808.

Madritch, M., Hunter, M., 2002. Phenotypic diversity influences ecosystem functioning in an oak sandhills community. Ecology 83, 2084–2090.

Madritch, M., Hunter, M., 2003. Intraspecific litter diversity and nitrogen deposition affect nutrient dynamics and soil respiration. Oecologia 136, 124–128.

Madritch, M., Hunter, M., 2005. Phenotypic variation in oak litter influences short- and long-term nutrient cycling through litter chemistry. Soil Biol. Biochem. 37, 319–327.

Matson, P., Parton, W., Power, A., Swift, M., 1997. Agricultural intensification and ecosystem properties. Science 277, 504–509.

McGregor, S.E., 1976. Insect Pollination of Cultivated Crop Plants. Published on the internet at: http://gears.tucson.ars.ag.gov/book/index.html.

Memmott, J., 1999. The structure of a plant-pollinator food web. Ecol. Lett. 2, 276–280.

Memmott, J., Waser, N.M., 2002. Integration of alien plants into a native flower-pollinator visitation web. Proc. Roy. Soc. Lond. B: Biol. Sci. 269, 2395–2399.

Moeller, D., 2004. Facilitative interactions among plants via shared pollinators. Ecology 85, 3289–3301.

Morandin, L., Winston, M., 2006. Pollinators provide economic incentive to preserve natural land in agroecosystems. Agric. Ecosyst. Environ. 116, 289–292.

Mulder, C., Uliassi, D., Doak, D., 2001. Physical stress and diversity-productivity relationships: the role of positive interactions. Proc. Natl. Acad. Sci. 98, 6704–6708.

Mundt, C.C., 1991. Probability of mutation to multiple virulence and durability of resistance gene pyramids; further comments. Phytopathology 81, 240–242.

Mundt, C.C., 2002. Use of multiline cultivars and cultivar mixtures for disease management. Annu. Rev. Phytopathol. 40, 381–410.

Norberg, J., Swaney, D.P., Dushoff, J., Casagrandi, R., Levin, S.A., 2001. Phenotypic diversity and ecosystem functioning in changing environments: A theoretical framework. Proc. Nat. Acad. Sci. 98, 11376–11381.

Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., 2005. Providing foraging resources for bumblebees in intensively farmed landscapes. Biol. Conserv. 121, 479–494.

Rana, R., Garfield, C., Sthapit, B.R., Jarvis, D., in press. Influence of socio-economic and cultural factors in rice varietal diversity management on-farm in Nepal. Agric. Human Values.

Reusch, T., Ehlers, A., Hammerli, A., Worm, B., 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. Proc. Natl. Acad. Sci. 102, 2826–2831.

Richards, A., 2001. Does low biodiversity resulting from modern agricultural practice affect crop pollination and yield? Ann. Bot. 88, 165–172.

Ricketts, T., 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. Conserv. Biol. 18, 1262–1271.

Ronsheim, M., Anderson, S., 2001. Population-level specificity in the plant-mycorrhizae association alters intraspecific interactions among neighboring plants. Oecologia 128.

Sawadogo, M., Ouedraogo, J., Belem, M., Balma, D., Dossou, B., Jarvis, D.I., 2005. Components of the ecosystem as instruments of cultural practices in the in situ conservation of agricultural biodiversity. Plant Genet. Resour. Newslett. 141, 19–25.

Schlapfer, F., Schmid, B., 1999. Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. Ecol. Appl. 9, 893–912.

Schwartz, M., Brigham, C., Hoeksema, J., Lyons, K., Mills, M., van Mantgem, P., 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. Oecologia 122, 297–305.

Schweitzer, J., Bailey, J., Rehill, B., Martinsen, G., Hart, S., Lindroth, R., Keim, P., Whitham, T., 2004. Genetically based trait in a dominant tree affects ecosystem processes. Ecol. Lett. 7, 127–134.

Smale, M., 2006. Valuing Crop Biodiversity: On-farm Genetic Resources and Economic Change. Oxfordshire, CABI Publishing.

Smale, M., Bellon, M.R., Jarvis, D., Sthapit, B., 2004. Economic concepts for designing policies to conserve crop genetic resources on-farms. Genet. Resour. Crop Evol. 51, 121–135.

Steffan-Dewenter, I., Tscharntke, T., 1999. Effects of habitat isolation on pollinator communities and seed set. Oecologia 121, 432–440.

Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., Tscharntke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83, 1421–1432.

Stocker, R., Komer, C., Schmid, B., Niklaus, P., Leadley, P., 1999. A field study of the effects of elevated CO_2 and plant species diversity on ecosytem-level gas exchange in a planted calcareous grassland. Global Change Biol. 5, 95–105.

Strauss, S., Siemens, D., Decher, M., Mitchell-Olds, T., 1999. Ecological costs of plant resistance to herbivores in the currency of pollination. Evolution 53, 1105–1113.

Suso, M., Moreno, M., Mondragao-Rodrigues, F., Cubero, J., 1996. Reproductive biology of *Vicia faba*: role of pollination conditions. Field Crops Res. 46, 81–91.

Swanston, J., Newton, A., 2005. Mixtures of UK wheat as an efficient and environmentally friendly source for bioethanol. J. Ind. Ecol. 9, 109–126.

Tilman, D., Lehman, C., Thomson, K., 1997. Plant diversity and ecosystem productivity: Theoretical considerations. Proc. Natl. Acad. Sci. 94, 1857–1861.

Tonhasca, A., Stinner, B., 1991. Effects of strip intercopping and no-tillage on some pests and beneficial invertebrates of corn in Ohio. Environ. Entomol. 20, 1251–1258.

Treseder, K., Vitousek, P., 2001. Potential ecosystem-level effects of genetic variation among populations of *Metrosideros polymorpha* from a soil fertility gradient in Hawaii. Oecologia 126, 266–275.

Tuxill, J., 2005. Agrarian change and crop diversity in Mayan milpas of Yucatan, Mexico: Implications for on-farm conservation. PhD Thesis, Yale University, New Haven.

Vandermeer, J., 1995. The ecological basis of alternative agriculture. Annu. Rev. Ecol. Syst. 26, 201–224.

Vasquez, D.P., 2004. Indirect effects of an introduced ungulate on pollination and reproduction. Ecol. Monogr. 74, 281–308.

Wardle, D., Bonner, K., Nicholson, K., 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. Oikos 79, 247–258.

West, T., Post, W., 2002. Soil organic carbon sequestration rates by tillage and crop rotation: a global data analysis. Soil Soc. Am. J. 66, 1930–1946.

Wilby, A., Thomas, M., 2007. Diversity and pest management in agroecosystems some perspectives from ecology. In: Jarvis, D., Padoch, C., Cooper, H.D. (Eds.), Managing Biodiversity in Agricultural Ecosystems. Rome, Columbia University Press and Bioversity International, New York, pp. 269–291.

Willmer, P., Bataw, A., Hughes, J., 1994. The superiority of bumblebee to honeybees as pollinators-insect visits to raspberry flowers. Ecol. Entomol. 19, 271–284.

Wolde-meskel, E., Berg, T., Peters, N., Frostegard, A., 2004. Nodulation status of native woody legumes and phenotypic characteristics of associated rhizobia in soils of southern Ethiopia. Biol. Fertil. Soils 40, 55–66.

Wolfe, M., 1985. The current status and prospects of multiline cultivars and variety mixtures for disease resistance. Annu. Rev. Phytopathol. 23, 251–273.

Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proc. Natl. Acad. Sci. 96, 1463–1468.

Zhu, Y.Y., Chen, H.R., Fan, J.H., Wang, Y.Y., Li, Y., Chen, J.B., Fan, J.X., Yang, S.S., Hu, L.P., Leung, H., Mew, T.W., Teng, P.S., Wang, Z.H., Mundt, C.C., 2000. Genetic diversity and disease control in rice. Nature 406, 718–722.