Biodiversity, Food Forests, Food Plants - Annual, Food Plants - Perennial, Plant Systems
by Dr. Mae-Wan Ho September 23, 2008

Sustainable farming *across the world relies on cultivating a diversity of crops and livestock to maximise internal input, and this is in marked contrast to the high external input monoculture of industrial farming, which is proving unsustainable in many respects. Indirect support for the sustainability of agricultural diversity is coming from an unexpected quarter. Academic ecologists are discovering that* ***biodiverse systems*** *are more productive.*

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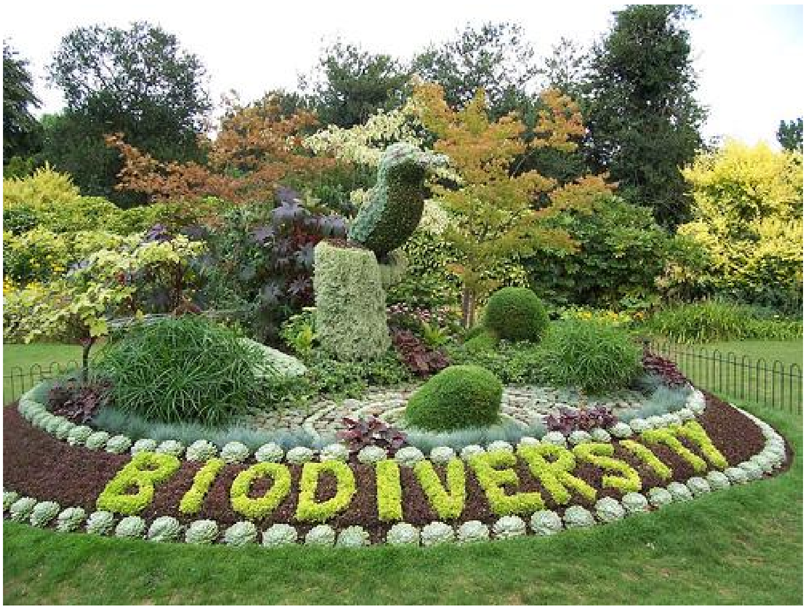

For over three decades, academic ecologists have debated whether complex, species-rich ecosystems are more stable than ones with fewer species. Unfortunately, there are many definitions of complexity, and even more of stability; and so the debate continues.

The question most relevant to agriculture, and also most easily answered, is whether biodiverse systems are more productive. There is growing evidence that biodiverse systems are indeed more productive, although ecologists still disagree as to how that could be explained, and on the number of species needed to sustain an ecosystem, which has large implications also for conservation.

One hypothesis is that there is “niche complementarity” among particular combinations of species, in other words, they have mutually complementary relationships so the more species there are, the greater the chance occurrence of such complementarity. This would be due to both differences in resource requirements over space and time, and positive, symbiotic interactions between the species.

Alternatively, the greater productivity associated with diversity may be due to short-lived or transient effects, caused solely by the presence of some species with high growth rate. Or the effects could simply be experimental artefacts. The species compared may happen to include some with very low-viability, or else with very high, competitive growth rates. These ‘sampling effects’ result from the greater chance of such species being present at higher diversity, and from dynamics that cause a single species to dominate and determine how the ecosystem evolves.

Fortunately, David Tilman and his colleagues in the University of Minnesota, St. Paul, and University of Nebraska, Lincoln, can now address these questions from the results of an experiment they started in May, 1994 and continued to this day [1].

Plots measuring 9m by 9m were seeded with a different number of species. The number of replicate plots with 1, 2, 4, 8, and 16 species were 39, 35, 29, 30 and 35 respectively. The species composition of each plot was chosen at random from a pool of 18 grassland perennials that included four C4 (warm-season) grasses, four C3 (cool-season) grasses, four legumes, four non-legume forbs (broad-leaf flowering herbs), and two woody species. All species occurred in monoculture, and all but three were in at least two monoculture plots, allowing comparison of responses of each species in monoculture to higher-diversity combinations of these same species.

The aboveground living biomass, because it is all produced within a growing season, is an index of primary productivity. In contrast, total biomass (both above and below ground) measures carbon accumulated in living tissues, ie, carbon sequestered from the atmosphere, and hence relevant to reducing CO_2 and global warming, although the authors did not mention it as such.

Both aboveground and total biomass were found to increase highly significantly with species number in every year. The ‘functional group composition’, ie, whether grasses, legumes, forbs or woody species, also had significant influence, especially in the early years. But species number had highly significant positive effects on both above ground and total biomass by 1999 and 2000.

In the early years, there was an increase in aboveground and total biomass with species number that reached a plateau between 4 and 8 species. But, by 2000, there was a sharp jump between 1 and 2 species, and thereafter, a less steep but nonetheless linear increase with species number up to the maximum, 16. In 2000, the 16-species plots had 22% greater aboveground biomass and 27 greater total biomass than 8-species plots. The dependence of biomass on species number and functional group composition became progressively stronger, accounting for one-third of the variation (variance) in 1997 and two-thirds in 2000.

The strengthening of the effect of diversity and the increasingly steep and linear trends in successive years do not support the hypothesis that effects of diversity are short-lived transients. Comparable and significant dependence of total and aboveground biomass on diversity and functional group composition were observed whether one looks at the actual number of planted species in each plot, or the ‘**Shannon diversity index**’, a measure which includes the relative abundance of the species present.

To test the sampling hypothesis that low-viability species were included in the pool, five species that had the least total biomass in monoculture in 2000 were identified, and all plots containing them were excluded from the analysis. Total biomass was still significantly dependent on species number and functional group composition in the remaining 131 plots. Similar results were obtained when plots containing any combinations of the five species with least aboveground biomass in monoculture were excluded. Significant results were also obtained when 30 plots with the lowest total biomass or 31 plots with the lowest aboveground biomass were excluded. Thus the increase in productivity with diversity cannot be due just to sampling effects from low-viability species being included in the pool.

What about the hypothesis that the most competitive species determined the effects of diversity? This was examined by retaining in the analyses of year 2000 only plots containing at least one of the nine species with the highest monoculture total biomass in 2000. Total biomass remained significantly dependent on species number and functional group composition in these 145 plots, and in the subset of 95 plots that contained at least 2 of the nine species. Similar results were obtained for aboveground biomass in 2000. In 1999 and 2000, many high-diversity plots had greater aboveground and total biomass than the best-performing monoculture. The percentage of such plots increased with species number, and about half of the 16-species plots had greater aboveground or total biomass than the best monocultures. Thus, sampling effects from competitive species cannot fully explain the increase in productivity with diversity.

The strong contributions to productivity are species number and complementary relations between the plants. Did complementarity occur among most species? In other words, did most species contribute to increasing community biomass or is there a smaller set of species with complementary interactions, with this set being increasingly likely to co-occur at higher diversity?

Analysis of variance (ANOVA) – a routine, accepted statistical technique – was used to determine the simultaneous effects of the presence or absence of each species on aboveground or total biomass. Three or four species had significant positive effects in most years. Among legumes, Lupinus perennis had significant effects in all nine tests, Lespedeza capitat in six test, and Petalostemum in two tests. Schizachyrium scoparium and Sorghastrum mutans, both C4 grasses were significant in five tests each. These are five of the six most abundant species in mixtures. A rarer forb also had a significant effect. Similarly, when plots were characterized by the presence or absence of functional groups in ANOVAs, in 2000, there were significant positive effects of legumes, forbs and C4 grasses on aboveground biomass, and significant positive effects of legumes and C4 grasses on total biomass. For above ground biomass, the legume x C4 grass interaction was significantly positive (meaning plots that had both of them did better than those with only one), also marginally significantly positive for total biomass.

However, even after controlling for the presence or absence of all functional groups, there were positive effects of species number on both aboveground and total biomass in 2000, indicating that biomass also depended on species number rather than on just functional groups.

In summary, diversity effects on productivity were neither transients nor explained in the long-term solely by sampling effects or by presence of legumes on a low-N soil. Rather discernible complementary relationships among specific species and functional groups contributed significantly as well as species number. Compared with the average of the single best species in monoculture, the 16 species plots had 39% greater aboveground biomass and 42% greater total biomass on average for 1999 and 2000. Moreover, 16-species plots in 1999 and 2000 had 2.7 to 2.9 times greater aboveground and total biomass than the average for all species in monoculture. The positive effects of diversity on productivity strengthen through time.

This is the most comprehensive evidence that biodiverse ecosystems are more productive. As the observed productivity showed no sign of levelling at the highest species number, we do not yet know whether even higher productivity may be reached with further increase in species diversity.

And, by the way, I thought to ask Prof. Tilman whether the plots were organically maintained. He answered,

“They are recently, but were not at the start. We have never used fertilizer of any kind, but did use selective herbicides in some plots the first few years to allow faster and better establishment of the prairie plant species, especially in monocultures. Our high diversity plots are fairly immune to the invasion and growth of weedy species, but the monocultures and low diversity plots are difficult to maintain in that state.”

So, there you have it, biodiverse systems also are less prone to weeds.

References:

1. Tilman D, Reich PB, Knops J, Wedin D, Mielke T and Lehman C. Diversity and productivity in a long-term grassland experiment. Science 2001, 294, 843-5.