Journal of Ecology

Journal of Ecology 2017, **105**, 865–870 doi: 10.1111/1365-2745.12792

MINI-REVIEW: ECOLOGICAL SOLUTIONS TO GLOBAL FOOD SECURITY

Applying plant ecological knowledge to increase agricultural sustainability

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Summary

1. Plant ecological knowledge accumulated over the past 150 years has enormous implications for agriculture, but most of these implications have not been appreciated by ecologists or agronomists. Here, I present several of the most salient examples.

2. Agriculturalists refer to 'improvements', but plant ecologists know that 'trade-offs' represent a better conceptual framework for agricultural production. There is much evidence for trade-offs between yield and resource use efficiency, and between individual fitness and population yield. I argue that there is also a 'limiting trade-off' between short-term yield and sustainability, and it is important to take this into consideration if we are serious about increasing sustainability.

3. At the local level, agricultural sustainability is about maintaining or improving soil fertility, but this is not a priority in most agricultural systems world-wide. Increased biomass density (both living and dead) in the field is the key to increasing sustainability while maintaining high yields, and I present a vision of 'High Biomass Cropping Systems'.

4. Classical and current research in plant community ecology tells us that rotation of crops with different nutritional needs, pests, diseases and weeds can make a major contribution to sustainability. The very limited crop rotations practised in most modern plant production systems are a clear indication that farming practices are usually based on short-term economic and regulatory factors, without much if any consideration for sustainability.

5. *Synthesis*. The modern scientific method tells us how we should test hypotheses, but it says nothing about how hypotheses are generated. We need to address the agricultural research agenda if it is to serve the interests of farmers, consumers and society as a whole, rather than narrow but powerful economic interests.

Key-words: crop rotation, plant production, soil fertility, soil organic matter, trade-offs

Introduction

No human activity is more essential to our species and has greater effects on the environment than agriculture. Agriculture is mankind's most important technology, but it is also the primary source of eutrophication and resultant biodiversity loss, a major source of the greenhouse gases that lead to climate change, and it is undermining its own resource base by promoting soil deterioration and erosion (Lal 2001; Montgomery 2007). Making agricultural production more sustainable is one of the most important challenges facing humanity.

Agriculture can be best understood scientifically as a form of applied ecology: the manipulation of populations, communities and ecosystems to meet human needs (Vandermeer 2011). Most biological problems in agriculture occur at the higher levels of organization: populations, communities and ecosystems (Weiner 2003). Advances in other fields, such as plant molecular genetics, must be placed in this context if they are to contribute to agricultural production.

While most plant ecologists and many agriculturalists would agree in principle that agricultural production is a form of applied ecology, such a conceptual framework is not usually applied in practice within agricultural science, where plant production is still conceptualized in the same way as industrial production: there are inputs and outputs, and environmental effects as well as long-term sustainability, are considered 'externalities', in the same sense that regulations and economic supports are considered externalities. Changing the conceptual framework in which agriculture is seen, analysed and regulated to applied ecology is not just an interesting exercise – it has enormous implications for agricultural practices, research and regulation (Weiner 2003; Vandermeer

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2011; Gliessman 2015; Lescourret *et al.* 2015; Perfecto & Vandermeer 2015).

Here, I address the question 'What does plant ecological knowledge tell us about how to increase agricultural sustainability?'

TAKING SUSTAINABILITY SERIOUSLY

'Sustainability' has become a 'buzz-word', and, as with all buzz-words, it has been overused and misused to promote specific interests. Most of the agricultural methods and practices that are called 'sustainable' would more correctly be referred to as 'slightly less unsustainable' (DeLonge, Miles & Carlisle 2016).

Sustainability is best defined as the ability to continue a defined behaviour indefinitely. Environmental sustainability is the ability to maintain rates of renewable resource harvest, pollution creation and non-renewable resource depletion that can be continued indefinitely (Daly 1990). Most current intensive agricultural systems are not sustainable according to this definition, because they require ever-increasing levels of input such as fertilizers, water and pesticides. Even in cases where input levels are not increasing, the resources being consumed are limited and non-renewable, making such practices unsustainable at a larger scale.

It is often noted and I argue below that more sustainable agriculture means lower yields, but this is only true over the short term. Taken seriously, agricultural sustainability means that yields are maintained or even increase over time without increasing inputs, whereas more intensive, less sustainable agriculture will result in either decreasing yields over time, or ever-increasing inputs, which will degrade local and global resources. Much of the debate about sustainability vs. yield is about the time-scale. Just as in business, the strategy that produces the greatest profit in the short term is not the strategy that produces the highest profit over the longer term. The focus on short-term profit has been considered the main cause of poor business management (Laverty 1996). Similarly, the extreme focus on short-term yield is a primary cause of unsustainable agricultural management.

I deliberately avoid the debate about sustainable vs. organic farming (Wu & Sardo 2010). These two concepts overlap but are very different in concept, and I address only the former. The term 'agroecology' is now more widely used to refer to a socio-political-environmental movement (Altieri & Nicholis 2005; Wezel *et al.* 2009; Gliessman 2015) than to a subfield of ecological science, so I restrict my use of this term to the movement.

Trade-offs, not improvements

Plant breeders like to talk about 'improvements' in crops, and many plant breeding departments in agricultural universities or research centres around the world are named 'Department of Plant Improvement'. Plant ecologists and evolutionary biologists know that what agronomists and plant breeders call 'improvements' can be better understood as 'trade-offs'. A trade-off can certainly represent an improvement under certain conditions, but seeing improvements as trade-offs has major implications for our understanding of plant breeding and agriculture, whereas 'improvement' implies something that is simply better. An automobile produced in 2016 is clearly better than one produced in 1920, but in contrast to 100 years of automobile engineering, millions of years of engineering by natural selection have resulted in organisms in which few pure improvements are possible – only trade-offs remain.

Agricultural research needs to embrace the concept of trade-offs, rather than trying to ignore or overcome them. We obtain high yields by creating a favourable environment for the crop and then develop crop genotypes that can utilize this 'luxury' environment to produce high yields. Sustainability involves doing this in a way that does not reduce the potential to continue this indefinitely at a local or global level.

I present three examples of trade-offs in agriculture, and their implications for sustainability.

YIELD VS. RESOURCE USE EFFICIENCY AND LOSS

The relationship between the level of a resource and a biological process such as the production of yield based on utilization of that resource follows a simple saturation curve: Liebig's 'law of the minimum' (Fig. 1), which is the foundation of some of the most successful theories in ecology (e.g. Tilman 1982; Bloom, Chapin & Mooney 1985). At low levels of a required resource, the resource is limiting, and yield increases linearly with the resource supply level, while at high levels of the resource, the resource is not limiting, so there is no response to further addition of the resource. The efficiency of utilization of the resource is high when the resource level is low and limiting. At high resource supply levels, yield is high but efficiency is low. If the objective is simply to maximize yield, the optimal level of nitrogen fertilization is the lowest level which gives the maximum yield. At this level, N use is not highly efficient, and there will be significant loss of nitrogen, resulting in eutrophication of waterways and nitrates in groundwater. Numerous research projects and agricultural practices, most notably the sowing of 'catch crops' or cover crops to 'catch' the excess nitrogen, have been developed to

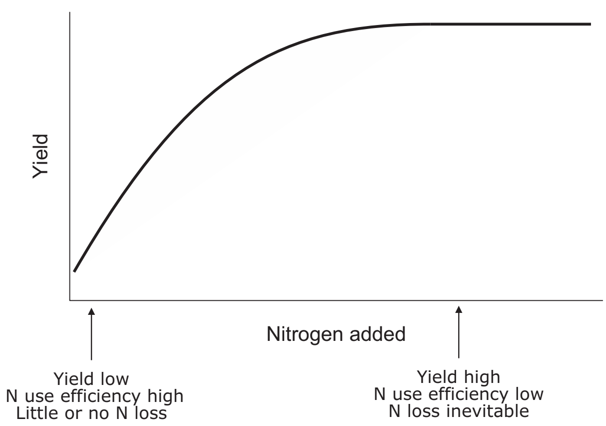

Fig. 1. Nitrogen fertilization, yield and nitrogen efficiency.

eliminate this loss. While this has been successful to some degree, we cannot maximize yield while simultaneously minimizing nitrogen loss. Improved management and technologies mean that we do not need to have low yields to avoid runoff, but we cannot avoid runoff if we maximize short-term yield (Tilman 1999). Even under the best farming practices and improved technologies, we will have to accept a slightly less-than-maximum short-term yield if we are to reduce nitrogen losses. Some farmers in Denmark have successfully lobbied to increase the limits on fertilizer application to obtain higher yields and increase their competitiveness in international markets. Such increases will inevitably result in increased nitrogen loss and eutrophication.

INDIVIDUAL VS. POPULATION YIELD

One of the most interesting trade-offs in plant breeding, which we are just beginning to understand, is that between optimal individual performance and optimal population performance (see paper by Mila in this series; Weiner *et al.* 2010; Denison 2012; Anten & Vermeulen 2016). Darwinian evolution by natural selection operates on individuals, increasing their fitness, but agriculture is about population yield. Fitness is often increased by 'selfish' behaviours that do not benefit the population or the species, so the best performing individuals do not give the best performing populations. High yield is achieved by reducing, not increasing, fitness. It is unlikely that plant breeding or genetic engineering can improve traits that natural selection has been optimizing for thousands or even millions of years, but there may be great unutilized potential in traits that increase crop yield and/or sustainability by decreasing individual fitness, giving us the opportunity to find agricultural solutions that natural selection would never produce (Denison, Kiers & West 2003; Denison 2012). This point has not been understood by researchers working on the genetic engineering of crops. Much effort and money is being put into attempts to improve photosynthesis, a process on which natural selection has been acting for billions of years. The probability that researchers can find solutions that natural selection has not tried and rejected is vanishingly small. But if the objective is different than what natural selection optimizes (e.g. population yield or sustainability), we can do better than nature.

TRADE-OFFS OVER TIME-SCALES: SHORT-TERM YIELD VS. LONG-TERM SUSTAINABILITY

There is much evidence of a 'limiting trade-off' between short-term yield and sustainability (Fig. 2). Research can move or change the shape of this relationship, but it will still be negative. If the potential for research to improve agriculture is as I suggest in Fig. 2, it will be very difficult if not impossible to increase sustainability under the current economic/regulatory environment. If a scientific advance can be used either to increase short-term yield or sustainability, the evidence to date suggests that it is short-term yield, not sustainability, that will be prioritized in practice. It has been argued that the new buzz-word, 'sustainable intensification' is an oxymoron (Lewis-Brown & Lymbery 2012). This may not be correct in theory, but it may be in practice, because 'sustainable intensification' is so weakly and narrowly defined (Loos *et al.* 2014; Norton 2016). To increase sustainability, we need 'ecological intensification' (Bommarco, Kleijn & Potts 2013; Tittonell 2014), in which the emphasis is on long-term productivity rather than short-term yield.

The most important scientific advances in agriculture in the future will not be those that result in higher yields with greater inputs, but those that allow us to maintain high yields while minimizing the yield reductions required to achieve a high degree of sustainability. An example of this is the technique called 'partial root drying' in irrigated agricultural systems, in which one half of the crop's rooting zone is irrigated while the other half is left dry (Kirda *et al.* 2004; Shahnazari *et al.* 2007). The wetted and dry sides are interchanged in subsequent irrigations. Partial root drying can reduce water use greatly, while yields are often equal or very close to those under full irrigation, resulting in a huge increase in water use efficiency. This represents a case in which research does not improve maximum yield, it only reduces resource consumption (arrow a in Fig. 2). Such an approach has much to offer agricultural sustainability.

The importance of improving soil fertility

At the local level, agricultural sustainability is about the maintenance or improvement of soil fertility, as opposed to the continuous depletion of soil fertility we see in most intensive farming systems. Much modern industrial agriculture on highly mineral soils is very similar to hydroponics. Plants are rooted in a

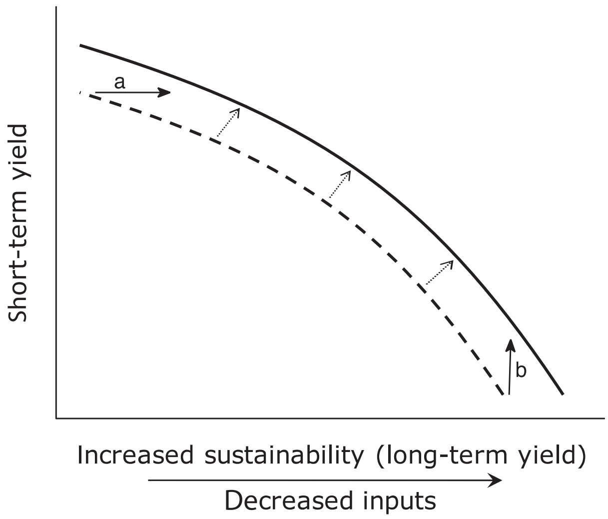

Fig. 2. The limiting relationship between short-term yield and long-term sustainability is negative (dashed line). Agricultural research can shift the relationship in a favourable direction (dotted arrows), giving greater yield at a given level of sustainability (dark line), but the relationship will still be negative. Arrows a and b represent alternative research strategies for increasing sustainability (modified from Weiner 2003).

passive mineral matrix, usually with low cation exchange capacity (CEC) and low water holding capacity. Nutrients, in the form of fertilizers, are added to the soil regularly. Some of these nutrients are taken up by the crop plants, some are consumed in the decomposition of the little organic matter available, and the remainder runs off or volatilizes.

The traditional view within soil science and plant nutrition is that maintaining soil fertility is about the replacement of mineral nutrients removed during harvest or lost in other ways. This is true of course, but soil fertility is not just about the presence and availability of mineral nutrients at one point in time. It is also about the soil's physical and biological properties, e.g. physical structure, water holding capacity, CEC, aeration, microbial activity, etc. In temperate regions, the best way to achieve this is through increased soil organic matter (SOM), which leads to semi-decomposed SOM: humus.

Simply put, increased agricultural sustainability can be achieved through

1. more biomass in the field and
2. improving the chemical, physical composition and biological diversity of this biomass for soil fertility (Lee & Pankhurst 1992).

Most intensively farmed soils are close to a steady state with very little labile, active SOM and low levels of recalcitrant SOM. Before agriculture was introduced, these soils were also in a steady state, but one with much higher levels of dynamic, labile, biologically active, chemically and biologically diverse SOM. Truly sustainable agricultural systems should emulate this aspect of natural ecosystems: high levels of labile OM through high input of plant residues. The continuous decrease in active, labile organic matter from recent plant residues after conversion from natural ecosystems to agriculture is well documented (Haas, Evans & Miles 1957; Hoyle, Baldock & Murphy 2011). Most current agricultural systems result in more output of SOM via decomposition than input via residues (e.g. Manna *et al.* 2005). This process accelerated enormously under industrialization. Already in 1980, Hans Jenny, perhaps the greatest soil scientist, warned against the dangers of removing all plant residues from agricultural fields for energy production (Jenny 1980), pointing out the implications of reduced input of plant residues for soil physical structure as well as water holding and ion-exchange capacities. As it is biomass, living and dead, which fuels the soil ecosystem, we can say that more biomass in the field → more ecosystem → more ecosystem services.

This logic points to a vision of sustainable agriculture I call 'High Biomass Cropping Systems'. Increased plant biomass density in the field is the key to increasing agricultural sustainability, while producing high yields. (i) More standing biomass (and less bare soil) through increased crop density (Weiner *et al.* 2010), intercropping (Vandermeer 1989) or subsidiary crops [cover crops (Wittwer *et al.* 2017) and 'living mulches' (Hartwig & Ammon 2002; Costanzo & Bàrberi 2016)]. Competition among plants in the field should be seen as something to manipulate, not something to avoid. (ii) More dead biomass (input of SOM). We need to exploit currently unutilized potential biomass production to increase living and semi-decomposed biomass for soil protection and improvement. Plant ecology suggests this: In temperate regions, natural ecosystems with the highest sustainable production are those with moderately high levels of standing biomass and high levels of dead, decomposing biomass, not the very early successional systems that current agriculture resembles (Crews *et al.* 2016). Many of the negative environmental impacts of modern agriculture are the results of low quantities of living and dead biomass in the field, but there is no theoretical or empirical basis for the widely held assumption that low standing biomass is a necessary condition for high yields. This emphasis on increased biomass is consistent with our understanding of the development of ecosystems. Later successional ecosystems retain nutrients better than earlier stages because of increased living and dead biomass (Odum 1969; Vitousek & Reiners 1975).

The most radical version of the high biomass approach is the attempt to develop perennial grain crops (Jackson 1985; Glover *et al.* 2010; Van Tassel, DeHaan & Cox 2010; Crews *et al.* 2016). This is an example of strategy b on Fig. 2: start with a system that is highly sustainable, and see how far research can increase yields. The potential for perennial crops is still an open question, but this idea deserves a serious investment in research.

Agricultural community ecology: crop diversification/rotation

The choice of a crop or crops and their rotation is one of the most important decisions the farmer makes (Smith, Gross & Robertson 2008). Crop rotation is to farming what ecological succession is to nature: the sequence of plant communities at one location. The implications of crop diversity, especially the rotation of crops with different nutrient demands, pests and parasites, for sustainability in terms of disease and parasite management, nutrient balance/stoichiometry/soil management, are enormous and well documented (Bullock 1992; Ponisio *et al.* 2015). Nothing demonstrates the huge gap between ecological sustainability and current farming practices than the very restricted rotations we observe in most modern temperate agricultural systems. The fact that rotations are often very limited in their length and the variety of crops involved shows that most farmers' decisions are based primarily if not solely on short-term market factors and economic supports, while long-term sustainability plays little if any role. The most well-known example of this is the continuous production of maize and soybean in the American Midwest, which requires huge chemical inputs. There is increasing awareness that long-term studies of crop rotations should be among the highest priorities in a research agenda to increase agricultural sustainability (e.g. Varvel 2000; Davis *et al.* 2012).

Addressing the agricultural research agenda

Although, as plant ecologists, we want to focus on the scientific basis of agricultural sustainability, it is not possible to address the ecology of agriculture without addressing the political and economic context in which agriculture is practised. Agricultural practices are not primarily determined by agronomic or ecological science, but by markets, regulations and agricultural support programmes, so it would be less than 100% honest not to discuss these. Farmers in the US Midwest do not practice a 'rotation' consisting only of maize and soybeans because of the ecology of these crops, but because the government provides crop failure insurance only for these crops. Making agriculture sustainable requires a food production system that has sustainability as one of its primary goals. This is far from the case at present, where agriculture is a business, like most others, which is primarily driven by the economic interest of large international corporations.

The modern 'hypothetico-deductive' scientific method (Medawar 2013) tells us how to test hypotheses, but it says nothing about how hypotheses are generated. We can test hypotheses about how to increase yields with high inputs, or hypotheses about increasing sustainability. Which we choose is the research agenda. European agriculture is developing in two very different and fundamentally incompatible directions: (i) Industrial agriculture: high intensity, high input, unsustainable industrial farming, driven by large international agrochemical corporations. (ii) A movement, usually referred to as Agroecology, which promotes lower intensity, lower input, more sustainable farming, driven by consumers, environmentalists, public health professionals and some farmers.

A phrase usually associated with debates about agricultural production is 'feeding the world'. This phrase is usually associated with one of these two agendas. Agro-industry's agenda is to continue the development of high input, high cost, non-sustainable agriculture, so farmers will buy more inputs. The agroecological agenda is very different: lower input, lower costs, healthier food and better rural lifestyles, in which farmers buy fewer things.

In the current discussions about 'feeding the world', two objectives are often conflated:

1. Reducing/eliminating starvation and malnutrition.
2. Meeting 'the demand for food'.

These are very different objectives. The former can be defined objectively to a large degree. The second is socially determined and changes over time. We can make an analogy with water resource management. There are at least two possible objectives: (i) Providing enough water for everyone in society to drink and bathe. (ii) The 'demand' for water, which includes the demands of famers in California to raise water-demanding crops in an arid environment, and the demand for water for lawns and golf courses in the desert. In short, 'demand' in the economic sense often has little to do with 'need' in the biological or social sense. The 'demand' for beef has nothing to do with nutrition, health or malnutrition, any more than the 'demand' for diamonds for jewellery. At least diamonds are not harmful to the wearer's health (although they may be to the diamond miner's), whereas beef, consumed in large quantities, as it is in much of the developed world, is damaging both to the health of the consumers and the ecosystems in which it is produced.

Saying that we need more food production to reduce world hunger is like saying that the solution to poverty is printing more money, or that the solution to the housing shortage is producing more bricks (Körner 2015). If we produce more food, it will not go to the hungry – they cannot afford to buy it.

A primary question for ecologists in this context is 'feed the world what?' Basic ecology tells us that we can only feed the world by moving the human diet lower on the food chain. Enormous amounts of high-quality foods that humans can and do consume, such as soybeans, fishmeal and cereals, are fed to animals. We are not only loosing 90% of the energy in this transfer but we are also losing around 70% of the protein (95% for beef; Smil 2002). In a sustainable world, beef would be a luxury product, consumed in small amounts except on special occasions, as we see in the development of sustainable gourmet food by environmentally aware chefs (e.g. Barber 2014).

Conclusions

The good news is that the science of ecology has advanced to a level where we have much of the knowledge necessary to build highly sustainable food production systems that can produce enough food to feed the world's population (Godfray *et al.* 2010). More research will enable us to do this much better, but, to borrow a metaphor from ecological science, the 'limiting factor' for the development of sustainable agricultural systems is not our scientific knowledge, but the political and economic structures within which agriculture is practised. Plant ecology, the subject of this Journal, has much to contribute to the development of sustainable agricultural systems. But this knowledge will only be used if society has sustainability as one of its primary goals.

Acknowledgements

I thank the University of Copenhagen Program of Excellence, European Union FP7 Project no. 289277: OSCAR (Optimising Subsidiary Crop Applications in Rotations), and the Danish Natural Science Research Council (grant number DFF–4181-00064) for support. I also thank Andrea Cavalieri, Tim Crews, David Gibson and an anonymous reviewer for helpful comments on the manuscript. The author declares no conflicts of interests.

Data accessibility

This paper includes no original data.

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Received 14 November 2016; accepted 21 February 2017
Handling Editor: David Gibson