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Towards an agroecological approach to crop health: reducing pest incidence through synergies between plant diversity and soil microbial ecology

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Given environmental, economic, and social costs of unilateral chemical and biotechnological interventions to control pests, there is an urgent need to transition towards a knowledge-intensive holistic approach emphasizing agroecosystem design and management. The focus will be on what makes agroecosystems susceptible and vulnerable to insect pests, pathogens and weeds, in order to design diversified agroecosystems that prevent and suppress insect pest, pathogen and weed problems. We propose a plant health model applicable to agroecosystems that feature biodiversity enhanced designs and soils rich in organic matter and microbial life, managed with low chemical loads. In such diversified farming systems, the general protection of the plant is a consequence of mutualistic above and below ground relationships between plants, insects, and soil microbial communities. From a practical standpoint, the approach involves (a) restoring plant diversity at the landscape and field level, with spatial and temporal crop combinations that deter pests and/or enhance natural enemies and (b) increasing soil organic matter through green or animal manures, compost and other amendments, which enhance antagonists that control soilborne pathogens. Polycultures promote a complex root exudate chemistry which plays an important role in recruitment of plant-beneficial microbes, some of which enhance plants' innate immune system. Unleashing biotic interactions between plant diversity and increased microbial ecological activity generate conditions for the establishment of a diverse and active beneficial arthropod and microbial community above and below ground, essential for pest/disease regulation.

The Integrated Pest Management (IPM) concept arose in the early 1970s in response to concerns about impacts of pesticides on human health and the environment[1]. By providing an alternative to the chemical control strategy, it was envisioned that ecological theory should provide a basis for predicting how specific changes in production practices and inputs might affect pest problems, and thus aid in the design of agricultural systems less vulnerable to pest outbreaks[2]. In such systems pesticides would serve strictly as back-ups of natural regulation processes. Unfortunately, most IPM programs failed to put ecologically based theory into practice and deviated to advocate for "silver bullet" schemes to control pests, emphasizing unilateral interventions based on agrochemicals, pheromones and transgenic crops, at the expense of more desirable cultural practices and biological control regulation processes[3].

In the last two decades, calls for more holistic approaches to management of diseases[4] insects[5] and weeds[6] have resurfaced in the literature, urging for a shift from a responsive, symptom-based, linear approach relying on biocides to a proactive, knowledge-intensive holistic approach emphasizing agroecosystem design and management based on cultural and biological controls. The focus is still on the pest organisms: understanding their biology and why herbivores quickly adapt and succeed in agroecosystems, in order to identify weak links in their life cycles and thus refine control measures. Despite these new perspectives, there is a need to rethink

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the concept of crop protection for plant health using principles of the field of agroecology[7], which focuses more on what makes agroecosystems susceptible and vulnerable to insect pests, pathogens and weeds, in order to design agroecosystems that prevent pest problems.

The old disease/pest triangle model predicts that for a disease to manifest, a susceptible host, a virulent pathogen and a favorable environment must occur simultaneously[8]. The lack of plant diversity and biologically poor soils of monocultures, plus pesticide applications create a "perfect storm" for pest infestations. A new plant health model needs to evolve applicable to agroecosystems that feature biodiversity enhanced designs managed with low chemical loads. In such diversified farming systems, the general protection of the plant is a consequence of mutualistic above and below ground relationships between plants, insects, soil microbial communities[9].

An agroecologically based plant health approach considers that if the cause and appearance of a pest or disease is understood as imbalance, then the goal of treatments should be to restore balance and resilience of the agroecosystem. The focus of this approach is on the causes of pest and disease outbreaks-not treating symptoms (suppressing pests and diseases), which does not necessarily lead to plant health. Pest resilient agroecosystems can be achieved by restructuring and managing farm systems in ways that maximize the array of "built-in" preventive mechanisms and restore core regulatory systems, such as immune (biological pest regulation mechanisms) and metabolic (soil biological activity, organic matter dynamics and nutritionally balanced crops) functions. This preventative strategy relies on poorly explored synergies between plant diversity and the soil microbial community which are set in motion by polycultural patterns and addition of organic matter, key practices in the design of pest resilient and healthy agroecosystems[10].

Why are agroecosystems vulnerable to pest and disease infestations?

Industrial agriculture has advanced at the expense of native vegetation leading to landscape simplification, by reducing habitat and food resources available to natural enemies of insect pests; this simplification reduces ecological services such as biological pest control. An emblematic example of these phenomena is biofuel-driven growth monoculture plantings in the US Midwest. The huge corn expansion has resulted in lower landscape diversity, altering the supply of aphid natural enemies, reducing biocontrol services by 24%. This soil use change cost soybean producers in these States an estimated \$58 million year^{-1}, in reduced yield and increased pesticide use[11].

A reduction of crop diversity was registered in the USA from 1978 to 2012, parallel to the intensification of the industrial agriculture mode, increasing possibilities for catastrophic insect pest outbreaks[12]. Deploying one variety across vast agrolandscapes results in low genetic diversity, increasing the vulnerability of crops to diseases[13]. Insecticide applications create secondary insect pest outbreaks and/or resurgence due to elimination of natural enemies or creation of resistance[14]. More than 550 arthropod species have resistance to at least one insecticide and many pathogens have evolved resistance to fungicides within two years of use, highlighting the limits of the chemical control strategy[15].

The efficacy of insect-resistant genetically modified organisms (GMO) crops, expressing δ-endotoxin genes from *Bacillus thuringiensis* (BT) has been questioned because of the potential for pest populations to evolve resistance[16]. There are also documented negative impacts on predators at higher trophic levels thus potentially affecting biological control processes[17,18]. In addition, due to lower insecticide applications in BT crops, secondary pests that are not susceptible to the expressed toxin are becoming an increasing concern[19]. Moreover, many studies have demonstrated that the introduction of GMO crops have not reached the desired reduction of pesticides use, especially herbicide resistant crops, thereby not resulting in substantial environmental benefits[20,21].

Worldwide use of inorganic fertilizers significantly increased between 1990 and 2020 to about 200 million tons, representing a 46% increase since 1990. Nitrogen fertilizers contribute 56% (113 million tons) of the total, phosphorus fertilizers 24% (48 million tons) and potassium fertilizers the remaining 20% (39 million tons)[22]. Over-fertilizing crops can actually worsen pest problems as increasing soluble nitrogen levels in plants can decrease their resistance to pests, resulting in higher disease incidence and pest density and consequently crop damage[23]. The nitrogen contents of crops grown on organic farms are often lower than those of conventional systems[24], suggesting that the lower foliar content of NO_3–N of organic crops may be a key factor in determining lower insect damage on crops fertilized with organic amendments. Apparently organic crops that are nitrogen-limited are often less attractive to herbivores potentially linked to the lower pest pressure often observed in organic systems[25]. These findings have been also previously explained according to the *trophobiosis* theory[26,27] which postulates that heavy applications of soluble nitrogen (N) fertilizers (and also certain pesticides) increase the cellular amounts of N, ammonia and amino acids, faster than the rate at which plants synthesize them for proteins. These reductions in the rate of protein synthesis result in temporary accumulation of free N, sugars and soluble amino acids in the foliage which boost growth and reproduction by insect herbivores and plant pathogens.

On the other hand, low soil organic matter content induces poor soil microbial communities and low populations of antagonists and mycorrhizal fungi, which exert suppressive effects on many soil borne pathogens[28]. Also lack of crop diversity leads to poor root complexity and thus lower production of primary metabolites and exudates that play a key role in recruitment of plant-beneficial microbes[29].

Restoring plant diversity in agroecosystems

A central question in agroecology has been on how to manage biodiversity in cropping systems to influence agroecosystem function, particularly enhanced pest and disease regulation. Bolstering plant genetic and species diversity has been a cornerstone strategy of agroecosystem redesign to promote higher diversity of above and below ground-associated biota which in turn leads to more effective pest control and disease suppression[30].

Over the last 40 years, many studies have evaluated the effects of crop diversity on the abundance of insect pests. Results from 209 studies involving 287 pest species found that, compared with monocultures, the population of pest insects was lower in 52% of the studies, and higher in 15% of the studies. Of the 149 pest species exhibiting lower densities in intercropping systems, 60% were monophagous and 28% polyphagous species[31]. A meta-analysis involving 148 comparisons found out that farms with species-rich vegetational schemes exhibited a 44% increase in abundance of natural enemies, a 54% increase in pest mortality, and consequently a 23% reduction in crop damage when compared to monoculture farms[32]. Unequivocally, recent reviews and meta-analyses suggest that crop diversification strategies promote a combination of ecological mechanisms that lead to synergies and tradeoffs between natural enemy enhancement, reduction of insect pest densities, and reduced crop damage[33–35].

Various mechanisms have been offered to explain how intercropping leads to insect pest regulation: (1) individual plants are less apparent and are more difficult to find because they are dispersed in intercropped systems; (2) certain intercrop species will disrupt the ability of a pest to attack the main crop, or some crops might have a repellent effect on herbivores; (3) a more attractive intercrop draws the pest away from the main crop and (4) natural enemies are more abundant and efficient in diverse than in simple cropping systems[30,33,36]. The functional push-pull system involving the intercropping of maize with a repellent plant and an attractive trap plant as a border crop, to control stemborers in Africa, adds a new dimension to the existing hypothesis[37]. The regulation of pests was mediated by chemically mediated interactions involving release of attractant semiochemicals from the trap and repellent plants from the intercrops[38].

Plant pathologists have also observed that mixed crop systems can decrease pathogen incidence by slowing down the rate of disease development by host dilution, interception of propagules and spore deposition by the nonhost crop, alteration of wind velocity, direction, turbulence, or creating environmental conditions less favorable to the spread of certain pathogens[39–41]. Intercropping significantly reduces wind-borne fungal pathogens disease in comparison to monocultures, as it has been reported for *Uromyces appendiculatus*, the cause of bean rust, in mixed intercropping with maize (causing 51–25% reductions)[42], or for *Alternaria solani* in tomatoes canopy, when intercropped with marigold (causing 64–73% reductions) or pigweed (causing 27–38% reductions)[39]. Lower disease contributes to less crop damage and higher yields in mixed crops compared to corresponding monocultures.

Increasing genetic diversity leads to lower disease incidence, particularly rusts and powdery mildews of small grain crops, such as wheat[43]. Crop variety mixtures restrict the spread of a disease relative to the mean of their components, provided that the components differ in their susceptibility, such as in the case of *Septoria nodorum*, a non-specialized and splash-dispersed pathogen and the powdery mildew pathogen, *Erysiphe graminis*, in wheat mixtures[44,45].

Temporal diversification through rotations decreases severity and damage of several fungal and nematodal root rot pathogens[46]. Declines in pathogen abundances usually occur when non-host crops are included in the rotation. Rotation of beans with grain crops such as corn, wheat, barley, rye, or oat resulted in reduced root rot severity and increased yield. A minimum of 3-year rotation with barley was needed in fields with a history of severe potato root rot incidence[47]. Similar effects were observed in Kidney beans plots that were planted to oats in the previous three seasons[48]. In addition to granting enhanced nutrient provisioning to plants, improvement of soil physical properties, increases in soil C, rotations can increase soil microbial composition activity, responsible for suppressing the growth of certain plant pathogens[48].

Crop rotation strategies cut off or disturb population cycles of many low dispersal insect pests which overwinter in the host crop fields. Multilayer rotations significantly reduced numbers of pests such as southern corn rootworm, *Diabrotica virgifera virgifera* LeConte, and the European corn borer, *Ostrinia nubilalis* Hübner, compared with no-rotations[49,50]. Coincidentally, multi-year rotation systems showed higher populations of predators than short (2 years) rotation systems[51].

Biodiversity enhancement at the landscape level is key to avoid loss of ecological service-providing organisms such as beneficial insects and soil biota components. New research shows that landscape configuration (spatial arrangement), in addition to composition, strongly affects natural enemy and pest populations. Natural enemies tend to be more abundant in fine-grained landscapes (comprised of smaller fields and habitat patches) and are influenced by the connectivity of crop fields to other habitat types[52]. Similarly soil bacterial and fungal communities, associated with sclerophyllous forests, can influence soil microbial composition of adjacent organic vineyards[53].

Restoring biological activity in soils

Copious additions of organic matter via green manures, compost, litter residues, etc., improve soil quality but also increase soil microbial populations including microorganisms, such as mycorrhizal fungi, species of *Pseudomonas*, *Fusarium*, *Trichoderma*, *Streptomyces*, and *Actinomyces*, known for their disease suppressiveness[54]. Organic amendments, such as animal and green manure and composts can control diseases caused by soilborne pathogen species of *Rhizoctonia, Verticillium, Fusarium, Phytophthora*, *Pythium*, *Sclerotinia*, etc.[55]. Antibiotics, antagonism via secondary metabolite production, iron-chelating siderophores, hyperparasitism, lytic enzymes, competition for space and nutrients are all likely to be responsible for disease suppression by these microbes[56]. *Pseudomonas* spp. employ antibiosis and have been shown to suppress soil-borne diseases through production of antibiotic compounds such as 2,4-diacetyl phloroglucinol, phenazines, cyclic lipopeptides, and cyanides[56]. Some plant-beneficial microbes suppress diseases via nutrient competition, particularly plant growth-promoting rhizobacteria (PGPR), which have evolved high-affinity siderophores that can suppress soil-borne pathogens through iron competition[57].

Another mechanism by which rhizobia, mycorrhizal fungi, and several plant growth-promoting rhizobacteria/fungi can suppress plant diseases is through enhancing the defensive capacity of the plant innate immune system, a phenomenon commonly known as induced systemic resistance (ISR)[58]. Rhizobacteria of the genera *Pseudomonas* and *Bacillus* are well known for their antagonistic effects and their ability to induce resistance, mainly through the salicylic acid-dependent SAR pathway[59]. Several resistance-inducing inoculants are being formulated and tested for more efficient disease biocontrol strategies[60]. The application of such natural formulations represents an input substitution strategy which should be used, if necessary, to suppress certain pathogens during the agroecological transition, while assessing the risks that this may entail to agroecosystem functional biodiversity.

Root exudate chemistry (amino acids, simple organic acids and complex secondary metabolites) plays an important role in recruitment of plant-beneficial microbes. For example, benzoxazinoid metabolites in root exudates of maize are key in the recruitment of ISR-eliciting *Pseudomonas putida* bacteria[61]. Several researchers are elucidating ways to increase the ability of several cereal varieties to exude sufficient quantities of chemicals responsible for recruitment of ISR-eliciting PGPR[62].

Although soil microbial effects on soil-borne pathogens are well known, soil microbial communities also play a role in depressing insect pest populations through changes in plant resistance. Root colonization by beneficial microbes can induce biosynthesis of plant defense-related compounds (flavonoids, lignin, and other secondary metabolites) against a variety of leaf-chewing as well as phloem-feeding insects through various plant hormonal signaling pathways[63]. Organic management practices can alter soil microbial communities and plant defense potentials, for example through changes in salicylic acid (SA) levels and influence settling and performance of various insect pests. Tomatoes grown using conventional management are preferentially settled by leafhopper pests and have lower SA levels, compared to tomatoes grown using organic management[64].

Ecological weed suppression

Although weeds biologically interfere with crops in different ways than insects and pathogens, similar strategies of soil management and plant diversification are used to prevent and/or reduce their germination, growth and seed production.

Intercrops are often superior to monocultures in weed suppression, as crop combinations exploit resources more efficiently than sole crops, thus suppressing the growth of weeds more effectively through greater pre-emptive use of resources. Examples abound in the literature where various intercropping designs (fodder legumes/maize, cotton/sesame or sorghum, wheat/red clover, sorghum/cowpea, etc.) were effective to reduce densities of different narrow- and broad-leaved weed species[65,66].

Temporal designs also exert suppressive effects on weeds and many studies have shown that various crop × rotation combinations reduce weed plant and seed densities. The mechanisms responsible for the greater weed suppression in crop rotations is linked to the continuous soil disturbance which disrupts weed growth and through stimulation of germination, eventually depleting the soil weed seed bank[67]. When cover crops or green manures are used in rotations for weed suppression, it is important to select species that exhibit high initial growth and establishment rates so that they rapidly develop a close dense canopy to cover the ground completely to smother and shade out weed species[68].

Another approach utilized in weed management systems is through the manipulation of allelopathic cover crop residues in annual and perennial cropping systems[69]. Rye, sorghum, rice, sunflower, rape seed, vetch and wheat residues have been documented as having allelopathic effects affecting germination of small seeded weeds. After maturity, the residues of the mowed or rolled cover crops remain on the soil surface, and as they decompose release allelochemicals which suppress weeds[70]. When crop residues like sorghum are left as a mulch, toxins are released onto the soil and diffuse only 2–3 cm in the soil profile. Small seeded crops and weeds planted into this toxic layer will not germinate due to the presence of

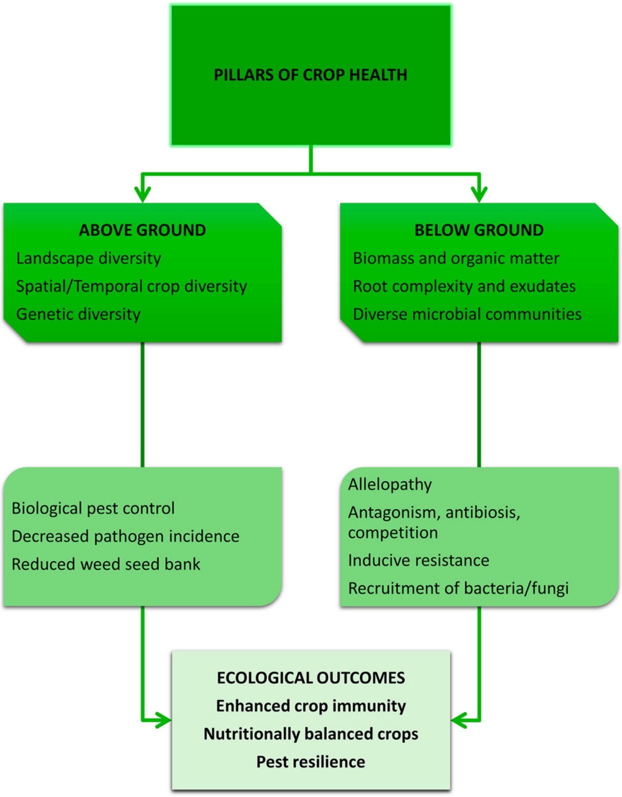

Fig. 1 | The pillars of plant health in agroecosystems. Exploiting the synergies between plant diversity and microbial community ecological activity.

allelochemical compounds such as sorgoleone, dhurrin, and other compounds[71]. This is why farmers traditionally plant their large-seeded crops (corn, beans, etc.) deeper and thus germination and root growth occur in a less toxic environment[72]. Many farmers in Brazil transplant vegetables such as tomatoes, onions and others through the in situ mulch. The mulch hinders weed seed germination and seedling emergence, often for several weeks, sufficiently delaying the onset of weed growth until after the crop's minimum weed-free period, making post plant cultivation, herbicides or hand weeding unnecessary, yet main crops exhibit acceptable crop yields[73].

Many weed species are more effective and faster than crops in capturing nutrients applied in fertilizers, and thus increases in soil fertility may benefit growth canopy development with negative effects on crop yields. Reducing applications of chemical N fertilizers may reduce populations of weeds that are responsive to fertilization[74]. Organic farming systems rely upon the use of organic fertilizers and amendments that typically release nutrients (especially N) at a slower rate compared with mineral fertilizers. Slower nutrient release from organic sources usually results in decreased weed competitive ability, but effects depend on crop and weed species, plant densities, critical period of weed competition and other factors[75].

Conclusions

Agroecosystems experience multiple disturbances each growing season (plowing, irrigation, pesticide, and fertilizer applications, harvesting, etc.) creating conditions for rapid colonization by insect pests, weeds and pathogens which are opportunist species, with high dispersal ability and rapid growth. In addition, low crop diversity and soils poor in organic matter lead to an impoverished community of co-existing beneficial organisms, reducing crop plants' resilience to tolerate stress. The goal of agroecology is to create ecologically vigorous agroecosystems, which are adaptable, and diverse enough to tolerate stress. This implies agroecosystem redesign, involving two main pillars: (a) establishment of a diversified plant ecological infrastructure which leads to suppression of pests via 'top-down' enhancement of natural enemy populations or via resource concentration and other 'bottom-up' effects acting directly on the colonization of pests and pathogens and (b) management of soils rich in organic matter that harbor diverse soil microbial communities integrally involved in antagonism, promotion of plant growth and induced resistance (Fig. 1). The approach exploits the synergies between greater plant diversity and increased microbial community biomass and ecological activity. These two pillars generate conditions for the establishment of a diverse and active beneficial arthropod and microbial community above and below ground, essential for provisioning pest/disease regulation. Despite the importance of agroecosystem biodiversity in promoting plant health, IPM programs often do not sufficiently consider its enhancement, as this approach is knowledge rather than input intensive. Agroecological design promotes interactions that set in motion ecological processes such as biological control, and this is complicated to attain via technological recipes or input prescriptions common to IPM schemes.

An agroecological approach to plant health is definitely knowledge intensive and requires in-depth, context-specific insights of each agroecosystem in question, including soil ecology, biology of target pathogens and herbivores and their antagonists, and the effects of vegetation and soil management practices on ecological processes at the farm and landscape levels.

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Author contributions

M.A.A. and C.I.N. co-conceived the idea. M.A.A. wrote the initial draft of this manuscript. C.I.N., G.D. and L.N. brought major elements to the discussion. M.A.A. and L.N. put together the core literature for the conception of the paper. M.A.A., C.I.N., G.D. and L.N. have reviewed and commented on the final version of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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