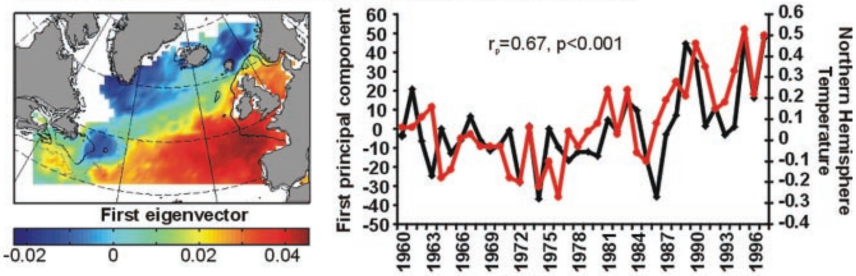
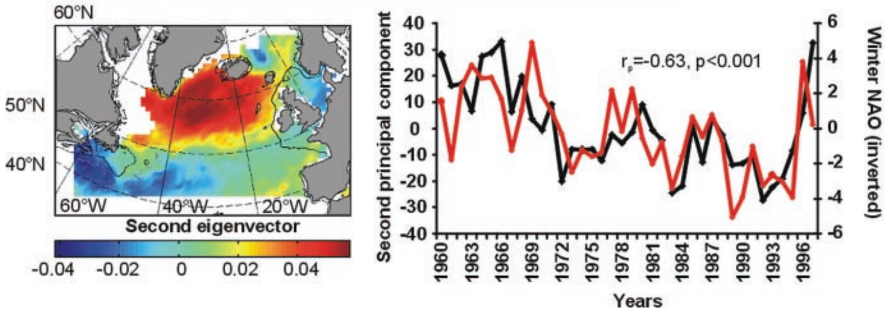
Fig. 2. Principal component analysis of long-term changes in SST in the North Atlantic Ocean. (**A**) First eigenvector and principal component (PC) (in black). Long-term changes in NHT anomalies (in red) and the Pearson correlation coefficient between the first PC and NHT anomalies are indicated. (**B**) Second eigenvector and PC (in black). The long-term changes in the winter NAO (in red) and the Pearson correlation coefficient between the second PC and the NAO index are indicated. The signal displayed by the first PC is highly correlated positively with NHT anomalies [Pearson correlation coefficient (r_P) = 0.67, $P < 0.001$]. In the Subarctic Gyre, the values of the second PC decreased until about 1993 and then increased. The long-term change in the second PC is highly correlated negatively with the NAO index ($r_p = -0.63$, $P < 0.001$). Probability was corrected to account for temporal autocorrelation with the method recommended by Pyper *et al.* (*20*).

A. First eigenvector and principal component (24.35% of the total variability)



B. Second eigenvector and principal component (16.59% of the total variability)



already weakened by overfishing (*18*). Possible mechanisms by which such changes may be manifest are reviewed by Sundby (*19*). Because changes in community structure reflect the adjustment of pelagic ecosystems to modifications in water masses, currents, and/or atmospheric forcing, it is clearly important to continue to monitor plankton associations, which provide us with a valuable means of checking the well-being of marine ecosystems in the North Atlantic Ocean and possibly in other oceanic regions.

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Supporting Online Material

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Materials and Methods
Figs. S1 to S4
References

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Soil Fertility and Biodiversity in Organic Farming

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An understanding of agroecosystems is key to determining effective farming systems. Here we report results from a 21-year study of agronomic and ecological performance of biodynamic, bioorganic, and conventional farming systems in Central Europe. We found crop yields to be 20% lower in the organic systems, although input of fertilizer and energy was reduced by 34 to 53% and pesticide input by 97%. Enhanced soil fertility and higher biodiversity found in organic plots may render these systems less dependent on external inputs.

Intensive agriculture has increased crop yields but also posed severe environmental problems (*1*). Sustainable agriculture would ideally produce good crop yields with minimal impact on ecological factors such as soil fertility (*2*, *3*). A fertile soil provides essential nutrients for crop plant growth, supports a diverse and active biotic community, exhibits a typical soil structure, and allows for an undisturbed decomposition.

Organic farming systems are one alternative to conventional agriculture. In some European countries up to 8% of the agricultural area is managed organically according to European Union Regulation (EEC) No. 2092/91 (*4*). But how sustainable is this production method really? The limited number of long-term trials show some benefits for the environment (*5*, *6*). Here, we present results from

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the 21-year "DOK" system comparison trial (bio-Dynamic, bio-Organic, and "Konventionell"), which is based on a ley rotation. The field experiment was set up in 1978 on a loess soil at Therwil, Switzerland [(*7*) and supporting online material). Two organic farming systems (biodynamic, BIODYN; bioorganic, BIOORG) and two conventional systems (using mineral fertilizer plus farmyard manure: CONFYM; using mineral fertilizer exclusively: CONMIN) are emulated in a replicated field plot experiment (table S1 and fig. S1). Both conventional systems were modified to integrated farming in 1985. Crop rotation, varieties, and tillage were identical in all systems (table S2).

We found nutrient input (N, P, K) in the organic systems to be 34 to 51% lower than in the conventional systems, whereas mean crop yield was only 20% lower over a period of 21 years (Fig. 1, Table 1), indicating an efficient production. In the organic systems, the energy to produce a crop dry matter unit was 20 to 56% lower than in conventional and correspondingly 36 to 53% lower per unit of land area (tables S4 and S5).

Potato yields in the organic systems were 58 to 66% of those in the conventional plots (Fig. 1), mainly due to low potassium supply and the incidence of *Phytophtora infestans.* Winter wheat yields in the third crop rotation period reached an average of 4.1 metric tons per hectare in the organic systems. This corresponds to 90% of the grain harvest of the conventional systems, which is similar to yields of conventional farms in the region (*8*). Differences in grass-clover yields were small.

Cereal crop yields under organic management in Europe typically are 60 to 70% of those under conventional management, whereas grassland yields are in the range of 70 to 100%. Profits of organic farms in Europe are similar to those of comparable conventional farms (*9*). Appropriate plant breeding may further improve cereal yields in organic farming. There were minor differences between the farming systems in food quality (*10*).

The maintenance of soil fertility is important for sustainable land use. In our experimental plots, organically managed soils exhibit greater biological activity than the conventionally managed soils. In contrast, soil chemical and physical parameters show fewer differences (Fig. 2).

Soil aggregate stability as assessed by the percolation method (*11*) and the wet sieving method (*12*) was 10 to 60% higher in the organic plots than in the conventional plots (Fig. 2A). These differences reflect the situation as observed in the field (Fig. 3, A and B), where organic plots had a greater soil stability. We found a positive correlation between aggregate stability and microbial biomass ($r = 0.68$, $P < 0.05$), and between aggregate stability and earthworm biomass ($r = 0.45$, $P < 0.05$).

Soil pH was slightly higher in the organic systems (Fig. 2B). Soluble fractions of phosphorus and potassium were lower in the organic soils than in the conventional soils, whereas calcium and magnesium were higher. However, the flux of phosphorus between the matrix and the soil solution was highest in the BIODYN system (*13*). Soil microorganisms govern the numerous nutrient cycling reactions in soils. Soil microbial biomass increased in the order CONMIN < CONFYM < BIOORG < BIODYN (Fig. 2C). In soils of the organic systems, dehydrogenase, protease, and phosphatase activities were higher than in the conventional systems, indicating a higher overall microbial activity and a higher capacity to cleave protein and organic phosphorus (*12*). Phosphorus flux through the microbial biomass was faster in organic soils, and more phosphorus was bound in the microbial biomass (*14*, *15*). Evidently, nutrients in the organic systems are less dissolved in the soil solution, and microbial transformation processes may contribute to the plants' phosphorus supply.

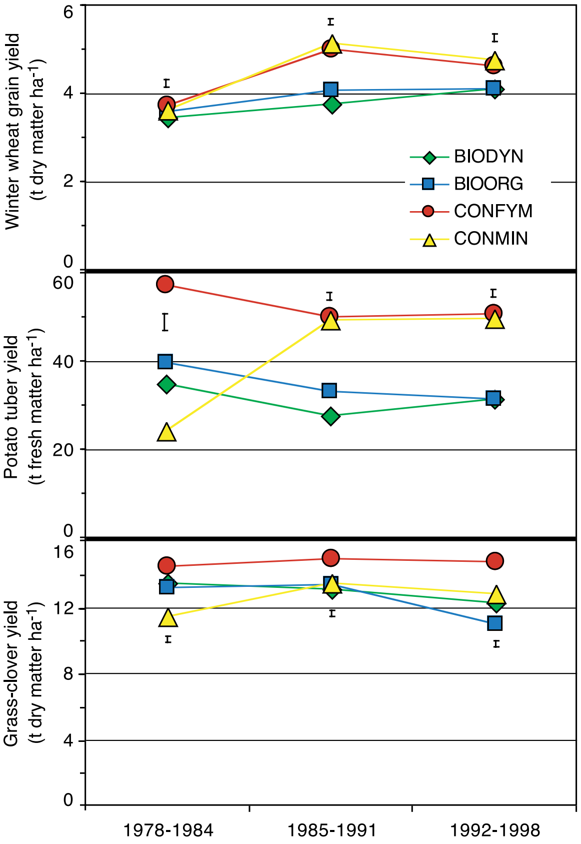

Fig. 1. Yield of winter wheat, potatoes, and grass-clover in the farming systems of the DOK trial. Values are means of six years for winter wheat and grass-clover and three years for potatoes per crop rotation period. Bars represent least significant differences ($P < 0.05$).

Table 1. Input of nutrients, pesticides, and fossil energy to the DOK trial systems. Nutrient input is the average of 1978–1998 for BIODYN, BIOORG, and CONFYM and 1985–1998 for CONMIN. Soluble nitrogen is the sum of NH_4-N and NO_3-N. The input of active ingredients of pesticides was calculated for 1985–1991. Energy for production of machinery and infrastructure, in fuel, and for the production of mineral fertilizer and pesticides has been calculated for 1985–1991.

Farming system	Total nitrogen (kg N ha^{-1} year^{-1})	Soluble nitrogen (kg N ha^{-1} year^{-1})	Phosphorus (kg P ha^{-1} year^{-1})	Potassium (kg K ha^{-1} year^{-1})	Pesticides (kg active ingredients ha^{-1} year^{-1})	Energy (GJ ha^{-1} year^{-1})
BIODYN	99	34	24	158	0	12.8
BIOORG	93	31	28	131	0.21	13.3
CONFYM	149	96	43	268	6	20.9
CONMIN	125	125	42	253	6	24.1

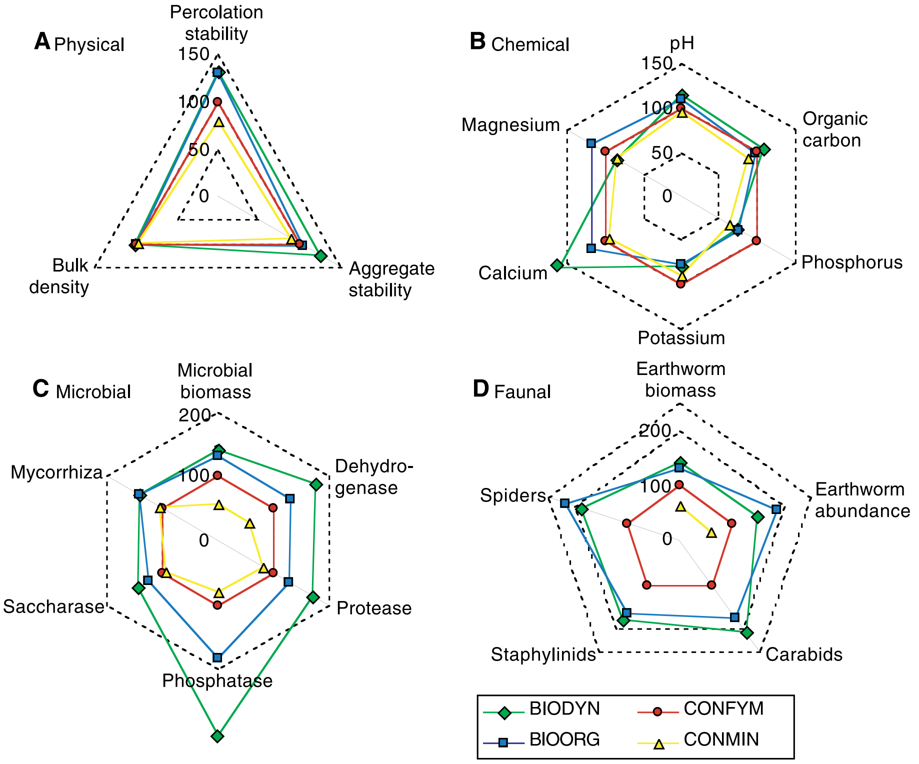

Fig. 2. Physical, chemical, and biological soil properties in soils of the DOK farming systems. Analyses were done within the plough horizon (0 to 20 cm) except for soil fauna. Results are presented relative to CONFYM (= 100%) in four radial graphs. Absolute values for 100% are as follows. (**A**) Percolation stability, 43.3 ml min^{-1}; aggregate stability, 55% stable aggregates > 250 μm; bulk density, 1.23 g cm^{-3}. (**B**) pH(H_2O), 6.0; organic carbon, 15.8 g C_{org} kg^{-1}; phosphorus, 21.4 mg P kg^{-1}; potassium, 97.5 mg K kg^{-1}; calcium, 1.7 g Ca kg^{-1}; magnesium, 125 mg Mg kg^{-1}. (**C**) Microbial biomass, 285 mg C_{mic} kg^{-1}; dehydrogenase activity, 133 mg TPF kg^{-1} h^{-1}; protease activity, 238 mg tyrosine kg^{-1} h^{-1}; alkaline phosphatase, 33 mg phenol kg^{-1} h^{-1}; saccharase, 526 mg reduced sugar kg^{-1} h^{-1}; mycorrhiza, 13.4% root length colonized by mycorrhizal fungi. (**D**) Earthworm biomass, 183 g m^{-2}; earthworm abundance, 247 individuals m^{-2}; carabids, 55 individuals; staphylinids, 23 individuals; spiders, 33 individuals. Arthropods have not been determined in the CONMIN system because of the field trial design. Significant effects were found for all parameters except for bulk density, C_{org}, and potassium (analysis of variance; $P < 0.05$). For methods, see table S3.

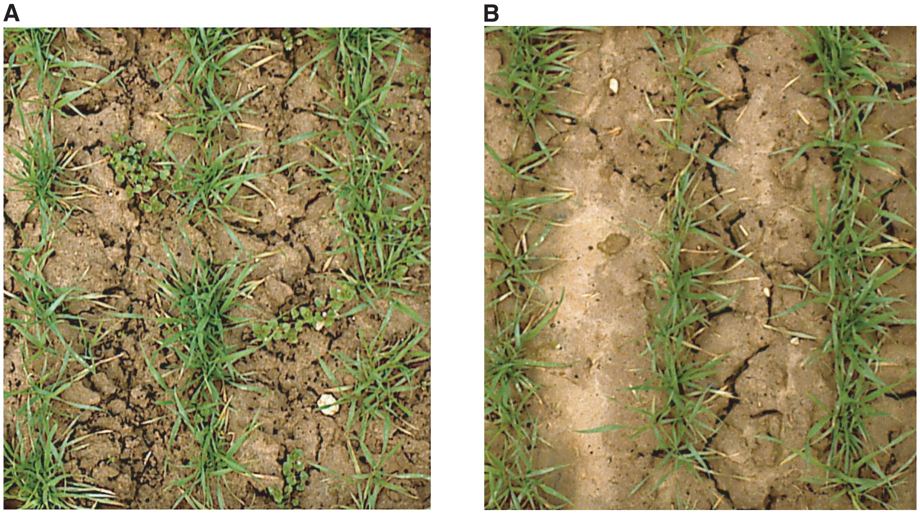

Fig. 3. Biodynamic (**A**) and conventional (**B**) soil surface in winter wheat plots. Earthworm casts and weed seedlings are more frequent in the biodynamic plot. Disaggregation of soil particles in the conventional plots leads to a smoother soil surface. Wheat row distance is 0.167 m. Source: T. Alföldi, Research Institute of Organic Agriculture [Forschungsinstitut für biologischen Landbau (FiBL)].

Mycorrhizae as members of the soil community ameliorate plant mineral nutrition and contribute to soil aggregate formation (*16*). Root length colonized by mycorrhizae in organic farming systems was 40% higher than in conventional systems (*7*) (Fig. 2C).

Biomass and abundance of earthworms were higher by a factor of 1.3 to 3.2 in the organic plots as compared with conventional (*17*) (Fig. 2D). We also investigated epigaeic arthropods that live above ground, because they are important predators and considered sensitive indicators of soil fertility. Average activity density of carabids, staphylinids, and spiders in the organic plots was almost twice that of the conventional plots (*18*) (Fig. 2D).

Healthy ecosystems are characterized by high species diversity. The DOK trial shows that organic farming allows the development of a relatively diverse weed flora. Nine to 11 weed species were found in organically managed wheat plots and one species in conventional plots. Between 28 and 34 carabid species were found in the BIODYN system, 26 to 29 species in the BIOORG system, and 22 to 26 species in the CONFYM system (*18*). Some specialized and endangered species were present only in the two organic systems. Apart from the presence and diversity of weeds, direct effects of pesticides and the density of the wheat crop stand are most likely influencing arthropod activity and diversity.

One of the particularly remarkable findings, presented in Fig. 4, was a strong and significant increase in microbial diversity (BIOLOG Inc., Hayward, CA) in the order CONMIN, CONFYM < BIOORG < BIODYN, and an associated decrease in the metabolic quotient (qCO_2) (*19*). According to Odum's theory on the strategy of ecosystem development, the ratio of total respiration to total biomass decreases during succession in an ecosystem (*20*). This quotient has been adapted to soil organisms (*21*), where CO_2 evolution is a biological process mainly governed by microorganisms. The lower qCO_2 in the organic systems, especially in the BIODYN system, indicates that these communities are able to use organic substances more for growth than for maintenance.

Under controlled conditions, the diverse microbial community of the BIODYN soil decomposed more ^{14}C-labeled plant material than the ones of the conventional soils (*22*). In the field, light fraction particulate organic matter, indicating undecomposed plant material, decayed more completely in organic systems (*23*). Hence, microbial communities

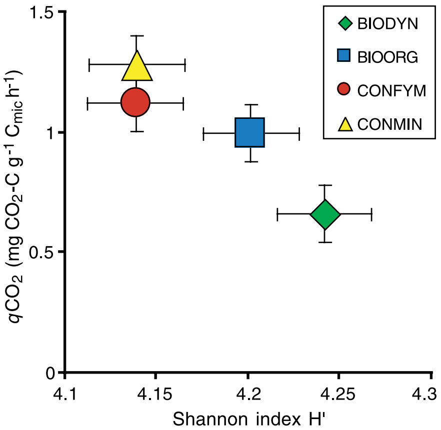

Fig. 4. Soil microbial functional diversity (Shannon index H') and metabolic quotient (qCO$_2$ = soil basal respiration/soil microbial biomass) correlate inversely. A higher diversity in the organic plots is related to a lower qCO$_2$, indicating greater energy efficiency of the more diverse microbial community. The Shannon index is significantly different between both conventional systems (CONFYM, CONMIN) and the BIODYN system, the qCO$_2$, between CONMIN and BIODYN ($P < 0.05$).

with an increased diversity in organic soils transform carbon from organic debris into biomass at lower energy costs, building up a higher microbial biomass. Accordingly, the functional role of diverse plant communities in soil nitrate utilization has been quoted (*24*), as well as the significance of mycorrhizal diversity for phosphorus uptake and plant productivity (*25*). The consistent results of these two studies (*24*, *25*) and our own within the soil-plant system support the hypothesis that a more diverse community is more efficient in resource utilization. The improvement of biological activity and biodiversity below and above ground in initial stages of food webs in the DOK trial is likely to provide a positive contribution toward the development of higher food web levels including birds and larger animals.

The organic systems show efficient resource utilization and enhanced floral and faunal diversity, features typical of mature systems. There is a significant correlation ($r = 0.52$, $P < 0.05$) between above-ground (unit energy per unit crop yield) and below-ground (CO$_2$ evolution per unit soil microbial biomass) system efficiency in the DOK trial. We conclude that organically manured, legume-based crop rotations utilizing organic fertilizers from the farm itself are a realistic alternative to conventional farming systems.

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Supporting Online Material
www.sciencemag.org/cgi/content/full/296/5573/1694/DC1
Materials and Methods
Fig. S1
Tables S1 to S5

21 February 2002; accepted 26 April 2002

Control of Stomatal Distribution on the *Arabidopsis* Leaf Surface

Jeanette A. Nadeau and Fred D. Sack*

Stomata regulate gas exchange and are distributed across the leaf epidermis with characteristic spacing. *Arabidopsis* stomata are produced by asymmetric cell divisions. Mutations in the gene *TOO MANY MOUTHS* (*TMM*) disrupt patterning by randomizing the plane of formative asymmetric divisions and by permitting ectopic divisions. *TMM* encodes a leucine-rich repeat–containing receptor-like protein expressed in proliferative postprotodermal cells. TMM appears to function in a position-dependent signaling pathway that controls the plane of patterning divisions as well as the balance between stem cell renewal and differentiation in stomatal and epidermal development.

Stomata allow gas exchange and thus are key to the survival of land plants, yet the genes controlling stomatal development are poorly understood (*1*, *2*). Both the number and distribution of stomata are regulated during leaf development. Stomata are formed after a series of asymmetric divisions of transiently self-renewing precursors termed meristemoids [fig. S1 (*3*)]. Stomata are continually produced during the mosaic development of the leaf, and many form by division of cells next to preexisting stomata (Fig. 1A). Correct spacing results when the plane of formative asymmetric divisions is oriented so that the new precursor, the satellite meristemoid, does not contact the preexisting stoma or precursor (*1*, *4*). Intercellular signaling provides spatial cues that regulate division orientation and may also block asymmetric division in cells adjacent to two stomata or precursors (*4*). The recessive *too many mouths* (*tmm*) mutation randomizes the plane of asymmetric division in cells next to a single stoma or precursor and permits asymmetric divisions in cells next to two stomata or precursors, thus producing clusters of stomata (Fig. 1, A and C). Also, *tmm* meristemoids divide fewer times before assuming the determinate guard mother cell fate. These phenotypes suggest that TMM is required for cells to respond appropriately to their position during stomatal development and that TMM participates in intercellular signaling.

With the use of positional cloning (*3*), *TMM* was found to encode a leucine-rich repeat (LRR)–containing receptor-like protein of 496 amino acids with a molecular weight of ~54 kD (Fig. 2A). The predicted protein product contains 10 uninterrupted plant-type LRRs (*5*) and a putative COOH-terminal transmembrane domain. *TMM* en-

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