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NET PRIMARY PRODUCTION, NET ECOSYSTEM PRODUCTION, AND NUTRIENT AVAILABILITY*

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ABSTRACT

It is doubtful that net primary production (NPP) of crop plants on a specific site can be predicted from net primary production of natural vegetation on that site prior to clearing for two reasons: 1) clearing changes the amounts of various resources (particularly nitrogen) available for plant use; and 2) crop plants generally have different resource demands and resource use efficiencies than do plants dominating natural ecosystems. Possibly we can link the rate of NPP in a natural ecosystem to the nitrogen availability of that system, and in turn, link nitrogen availability to crop demand and thus the magnitude of crop NPP that a site can support.

Ecosystem maintenance involves two tasks: 1) keeping the system's carbon and nutrient stocks organized; and 2) minimizing net losses of carbon and nutrients from the system. Both tasks require energy investments in the system. A useful relative index of the magnitude of this investment in maintenance appears to be net ecosystem production (NEP). Net ecosystem production refers to the net change in organic matter stocks in the system for some defined period of time. For agricultural systems NEP is the sum of NPP and organic matter inputs (associated with manuring) minus the sum of heterotrophic respiration plus organic matter outputs (associated with harvest and erosion). If NEP is negative, then the system is probably losing nutrients. The optimum rate of NPP in agricultural systems is that where a sufficient fraction of the NPP is invested to maintain NEP equal to or greater than zero. Agriculturalists should be "caretakers" or "builders" and not "miners".

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RESUMEN

Es poco probable que la producción primaria neta (PPN) de las plantas cultivadas en un lugar específico pueda predecirse a partir de la producción primaria neta de la vegetación natural de dicho lugar, antes de su aclareo, por dos razones: 1) el aclareo cambia las cantidades de diversos recursos (particularmente el nitrógeno) disponibles para su utilización por la planta, y 2) las plantas cultivadas tienen, en general, demandas y eficacia de utilización de los recursos diferentes a las de plantas dominantes en los ecosistemas naturales. Quizá podamos asociar el nivel de PPN de un ecosistema natural a su disponibilidad de nitrógeno y, a su vez, asociar esta disponibilidad de nitrógeno a la demanda del cultivo y, por tanto, a la magnitud de PPN del cultivo que dicho lugar puede mantener.

La conservación de los ecosistemas implica dos tareas: 1) mantener organizados los stocks de carbono y nutrientes del sistema, y 2) minimizar las pérdidas netas de carbono y nutrientes del sistema. Ambas tareas requieren una inversión de energía en el sistema. La producción neta del ecosistema (PNE) parece ser un índice relativo útil de la magnitud de esta inversión en mantenimiento. La producción neta del ecosistema se refiere al cambio neto en los stocks de materia orgánica del sistema durante un período definido. Para los sistemas agrícolas, la PNE es la suma de la PPN y los inputs de materia orgánica (asociados con el abono), menos la suma de la respiración heterotrófica más los outputs de materia orgánica (asocidos con la cosecha y la erosión). Si la PNE es negativa, el sistema está probablemente perdiendo nutrientes. El nivel óptimo de la PPN en los sistemas agrícolas es aquél en que se invierte una fracción suficiente de la PPN para mantener la PNE igual o mayor que cero. Los técnicos agrícolas debieran ser "guardianes" o "constructores" del sistema, no "minadores".

OVERVIEW

The objective of this paper is to consider two central questions to be discussed in the Zaragoza workshop. The two questions are:

1) Can the rate of agricultural production on a site be predicted from the rate of organic production of the site's natural vegetation?
2) What is the optimum rate of agricultural production on a site for minimizing ecosystem degradation? Is it equal to the rate of organic production of the site's natural vegetation?

In answering the first question we contrast resource-use strategies of crop plants and natural vegetation. We also discuss how the conversion of natural ecosystems to agricultural ecosystems alters resource availability. Based on these considerations we conclude that it may be difficult to predict agricultural production from the rate of organic production of the site's natural vegetation. However, it may be possible to link the rate of organic production of the site's natural vegetation with nitrogen availability in the system and in turn link nitrogen availability to the nutrient demand of the proposed crop system.

In answering the second question we argue that net ecosystem production is a better index than net primary production for defining the relationship between ecosystem metabolism and the maintenance of ecosystem resources. Natural ecosystems function such that most of the time (except immediately following disturbance) a large fraction of the annual net primary production is invested in long-term ecosystem growth (net ecosystem production) and / or ecosystem maintenance. On the other hand, agricultural ecosystems are managed such that a large fraction of the annual net primary production is removed during harvest, and so only a small amount of the annual net primary production (if any at all) is invested in long-term ecosystem growth (net ecosystem production) and / or ecosystem maintenance. This small investment in ecosystem growth and maintenance combined with repeated soil distrurbance, an integral part of planting, weed control and harvest in many agricultural ecosystems, cause many agricultural ecosystems to have negative net ecosystem production rates. Based on experience with both natural and agricultural ecosystems, we know that an ecosystem with a negative net ecosystem production rate (indicating a reduction in the system's carbon stock), is usually a system in which nutrient stocks are being reduced. If we keep in mind the fact that nutrient depletion of one system indicates nutrient loading of another, a system with a negative net ecosystem production must be recognized as a "pollution" source. This type of reasoning leads us to the conclusion that the optimum rate of agricultural production on a site for minimizing ecosystem degradation should allow for the investment of a sufficient fraction of annual net primary production to maintain the site's net ecosystem production equal to or greater than zero.

PREDICTING NET PRIMARY PRODUCTION OF AGRICULTURAL ECOSYSTEMS FROM NET PRIMARY PRODUCTION OF NATURAL ECOSYSTEMS

The net primary production of any ecosystem is controlled by the availability of a variety of resources including light, water and nutrients, and the strategy of the plants for using those resources. While the conversion of a natural ecosystem to an agricultural ecosystem will not dramatically alter the solar energy or precipitation inputs to a site, it will dramatically change the nutrient availability. With the conversion of a natural ecosystem to an agricultural ecosystem, there is also a dramatic change in the way the plants use resources. These changes in resource availability and resource use must be considered as we review the idea that the rate of agricultural production on a site can be predicted from the rate of organic production of the site's natural vegetation.

Changes in Nutrient Availability Following Conversion

Recognition of the effects of disturbance on element cycling and loss in terrestrial ecosystems has increased in recent years. In part, this emphasis represents the continuation of a long-standing concern among ecologists and soil scientists over the possibility that forest clearing causes nutrient losses which could affect the long-term productivity of a site (cf. Hesselman, 1917a, b in Stalfelt, 1960; Romell, 1935; Likens *et al.*, 1978, Leaf, 1979). More recently, practical concern has also focused on the effects of disturbance on downstream water quality (Likens and Bormann, 1974; Sollins *et al.*, 1981). Element losses following disturbance have also been used to characterize the degree of homeostasis of terrestrial biogeochemical cycles (Bormann and Likens, 1979; Swank and Waide, 1980), and they have been suggested as a useful measure of ecosystem-level stability (O'Neill *et al.*, 1977).

Studies of nutrient cycling and loss following disturbance in natural ecosystems have emphasized nitrogen for several reasons:

1) Nitrogen is the element most often limiting to plant growth, and substantial losses following disturbance could slow future plant growth.
2) Following disturbance, losses of nitrogen (especially nitrate) often increase more than do losses of other nutrient elements (Likens *et al.*, 1970; Vitousek *et al.*, 1979).
3) The increased production and loss of nitrate in disturbed ecosystems can cause increased solution losses of cations, since the supply of mobile anions controls cation leaching (Nye and Greenland, 1960; Likens *et al.*, 1969; Johnson and Cole, 1980).
4) Increased nitrification can either directly (Bremner and Blackmer, 1978) or indirectly (Firestone *et al.*, 1980) increase rates of nitrous oxide production and volatilization.
5) Increased nitrate losses to ground water and streams can be a health hazard (Magee, 1977).

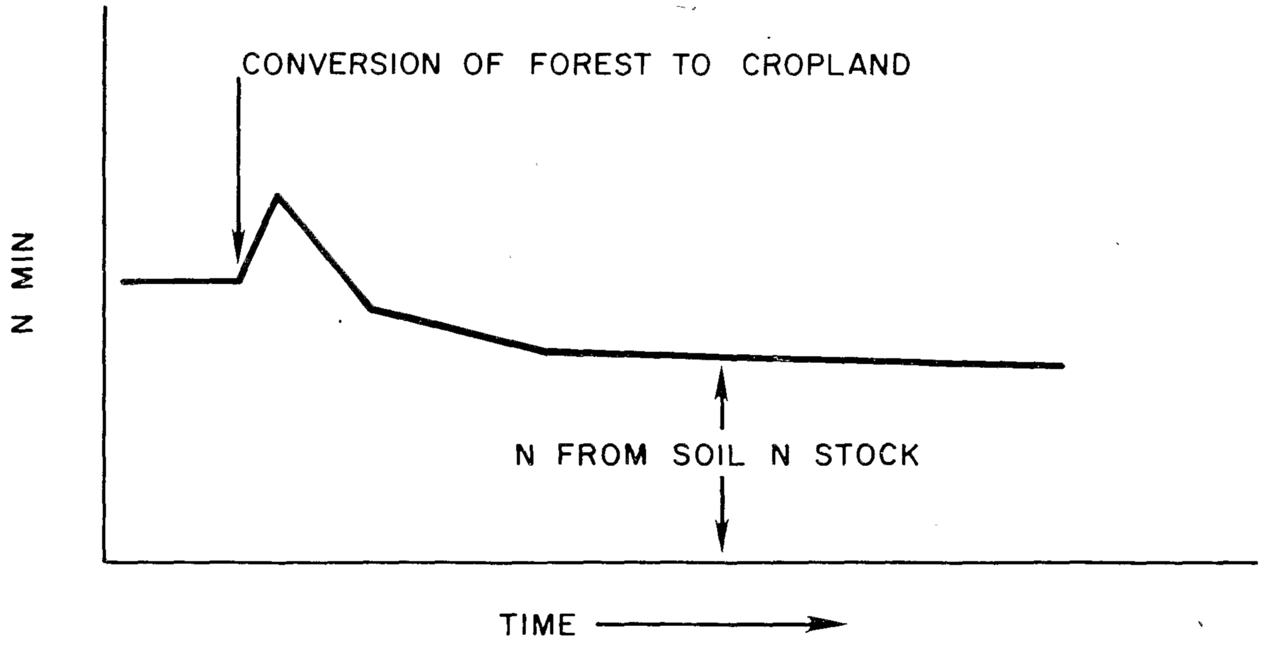
Since nitrogen often plays the role of a limiting element in crop production we will focus in this section on how the conversion of natural ecosystems to agricultural ecosystems will alter the availability of this resource.

Based on our understanding of the relationship between forest disturbance and nitrogen cycling and our knowledge of nitrogen stocks and fluxes in agricultural soils, we can predict that the rate of nitrogen turnover is related to the time since the last disturbance and the type of vegetation on the site following disturbance. The general pattern of nitrogen turnover (in the absence of fertilization) on a site converted from a forest to cropland is given in Figure 1. In the graph we plot net nitrogen mineralization (NMIN) as a function of time. Net nitrogen mineralization is defined as the fraction of the inorganic nitrogen produced (from the soil, organic nitrogen pool) that exceeds the microbial demand for nitrogen. The nitrogen (the amount of NMIN) represents the amount that can be taken up by plants or that can be lost from the system via leaching or gaseous flux.

Immediately following clearing, the NMIN at the site is increased above that occurring at the site just prior to the clearing. This disturbance-related elevation of NMIN is a function of changes in soil microclimate (the soil becomes warmer and often wetter) and changes in the structure of soil aggregates (shielded substrate may become vulnerable to enzyme attack, and inactive ("trapped") enzymes may be rendered active again).

The easily metabolized components of the soil nitrogen pool eventually are exhausted due to the continual removal of nitrogen from the site through harvest, leaching and erosion. The loss

Figure 1. The general pattern of nitrogen turnover (in the absence of fertilization) in a site converted from forest to cropland plotted as a function of time. NMIN is net nitrogen mineralization, the fraction of inorganic nitrogen produced (from the soil organic nitrogen pool) that exceeds the microbial demand for nitrogen.



of easily metabolized soil nitrogen is reflected in a drop in NMIN. In time, NMIN drops below what it was in the natural ecosystem that occupied the site prior to the conversion.

Thus we have a pattern of constantly changing nitrogen availability at the site following conversion. The change in nitrogen availability will certainly be reflected in the NPP of any crop on the site since crop plants have high nitrogen demands. High nitrogen demands have been a characteristic of most crop plants since domestication.

Crop Plants and High Nitrogen Availability: Roots in History

Many of our agricultural plants were developed from wild plants growing on sites characterized by frequent soil disturbances and high nutrient availabilities. These relationships are particularly clear for the New World species, and have been reviewed by Sauer (1969). The principal New World crop species of *Zea, Manihot, Solanum, Lycopersicum, Cucurbita, Ipomoea, Dioscorea, Amaranthus, Nicotiana, Gossypium,* and *Phaseolus* all apparently had their origin in northern and western South America (Peru, Ecuador, Columbia and Venezuela) or in Middle America (Mexico, Guatemala, Honduras, Nicaragua, and Costa Rica). The southern and Caribbean extensions from these origins initially emphasized vegetative propagation of the root and tuber crops followed by sown cultures of *Amaranthus* and *Phaseolus.* The northern extensions emphasized seed crops, principally *Zea, Phaseolus* and *Cucurbita.*

Initially man was attracted to the carbohydrate crops, particularly roots and tubers. These species were found growing wild in hill and mountain lands in the margins between forests and grasslands. These margins were sites of frequent soil disturbance due to natural events such as windthrow and later to man's wood harvesting activities.

As we noted earlier, soil disturbance promotes increased nutrient availability, particularly increased nitrogen availability. The ability of present-day crop plants to respond to nitrogen availability with rapid growth, fits with a presumed original adaptation as weedy species to disturbed soils in the forest boundary. Root and tuber harvest and seed sowing both involve soil disturbance and thus increased nitrogen availability. It is logical that weedy growth characteristics would be selected among progeny in both instances (Loomis and Gerakis, 1975).

Comparison of Physiological Characteristics of Crop Plants and Plants Dominating Natural Ecosystems

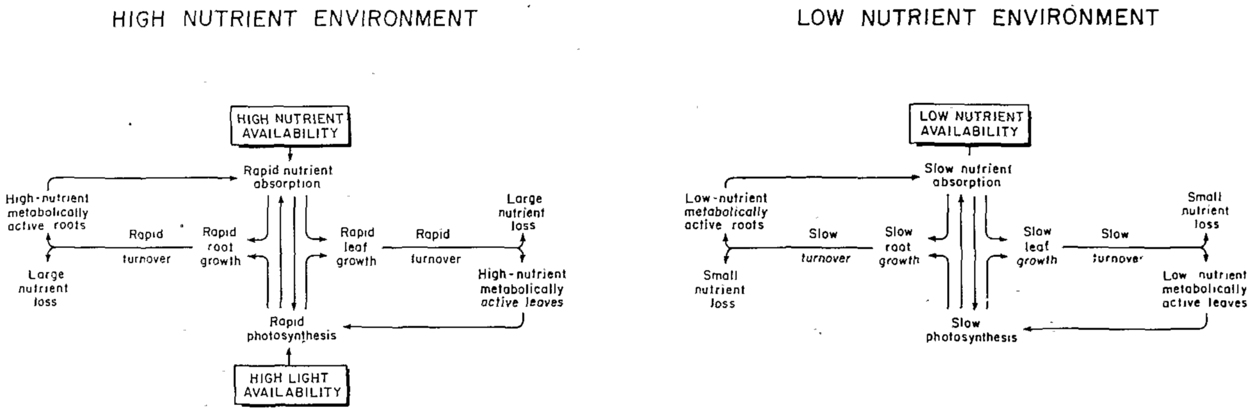
The high nitrogen demands of crop plants appear to be linked to physiological characteristics that enable these plants to exploit resource-rich environments. In this section we make a comparison between the general physiological characteristics of crop plants where resources are plentiful and plants from natural environments where resources are often in short supply. Again we will focus on nutrients, particularly nitrogen.

Chapin (1980) has compared the physiological characteristics of plants in high nutrient environments (e. g. crop plants) with those in low to intermediate nutrient environments (plants dominating most natural ecosystems). The results of his comparison are summarized in Figure 2.

Habitats of high fertility are most effectively exploited by plants which have high relative growth rates. The root absorption capacity of these plants is high, particularly at high external nutrient concentrations, and this provides the minerals necessary for rapid growth. The high root absorption capacity is sensitive to and depends upon a high photosynthetic rate because (a) plants in fertile soils have low mobile carbohydrate reserves, and (b) these species have high root respiration rates. The plants also have a high photosynthetic rate, which provides the carbon and energy for their rapid growth. This photosynthetic rate is, however, quite responsive to leaf nitrogen (and in some cases phosphorus) concentration, so that, if nutrient absorption is not maintained at high rates, photosynthetic and growth rates decline. The photosynthetic rate declines with leaf age and the nutrient absorption capacity declines with root age, so that maintenance of both processes depends upon rapid (perhaps subannual) turnover of both leaves and roots. These high rates of tissue turnover entail substantial nutrient loss in senesced tissues because of the inherent inefficiency of nutrient retranslocation. The litter has a narrow C/N ratio and low lignin concentration so that it decomposes rapidly. The rapid decay in turn is essential to maintain high site fertility and rapid carbon acquisition. Within any growth form, plants growing on nutrient rich sites generally have lower nutrient-use efficiencies (the inverse of the weighted mean nutrient concentration of NPP) than plants growing on nutrient poor sites.

At the opposite extreme, low and intermediate nutrient environments are most successfully exploited by plants whose inherently low growth rates can be adequately maintained by their low capacities for photosynthesis and nutrient absorption. A higher absorption capacity would provide little advantage in infertile soils, where diffusion of nutrients from bulk soil to the root surface is the step that most strongly limits absorption. These plants maximize nutrient acquistion primarily by maintaining a large root biomass, and associated mycorrhizae, achieved in large part through slow root turnover. The long-lived nature of roots may in turn by partially responsible for their low root absorption capacity. The inherently low growth rates and the relatively small growth response to flushes

Figure 2. Comparison of physiological characteristics of plants in high nutrient environments (such as crop plants) with those in low to intermediate nutrient environments (plants dominating most natural ecosystems) from Chapin (1980).



of high nutrient availability enable the plant to acquire and maintain nutrient reserves and in this way survive periods of exceptionally low availability in soil. The annual nutrient requirements of these species are low because of (a) slow rates of tissue production and (b) low nutrient loss rates through both senesence and leaching. The litter produced by these plants generally has a wider C / N ratio and a higher lignin concentration than the litter produced by plants adapted to fertile sites. Litter of plants from sites of moderate to low fertility decompose more slowly and this perpetuates the low fertility condition. Finally, within a growth form, plants growing on nutrient poor sites have higher nutrient use efficiencies than plants growing on nutrient rich sites.

The Relationship Between Natural and Agricultural Production

It is our opinion that it will be difficult to predict agricultural production from the rate of organic production of the site's natural vegetation for two reasons. First, the conversion of a natural ecosystem to an agricultural ecosystem causes basic changes in resource availability. The availability of nitrogen, a critical resource for crop plants, is initially increased above the availability apparent in the natural ecosystem just prior to disturbance. In time, as the labile nitrogen pool of the site is diminished under the cropping, nitrogen availability decreases until it is below the availability in the natural system just prior to disturbance.

Second, the resource demands and resource use efficiencies of crop plants differ from those of most plants found in natural ecosystems. Crop plants generally have higher resource demands and higher rates of tissue turnover. In addition, crop plants have lower nutrient use efficiencies; where nutrient use efficiency is defined as the inverse of the weighted mean nutrient concentration of NPP.

While we do not believe it will be possible to predict the agricultural production from the rate of organic production of the sites natural vegetation, it may be possible to link the rate of organic production of the site's natural vegetation with nitrogen availability in the system and in turn to link nitrogen availability in the system to nitrogen demand of the proposed crop system.

In the sections that follow we suggest that the NPP of a natural ecosystem can be used to predict NMIN of the natural system. We can then use our understanding of the way NMIN of a natural site will change following clearing to predict NMIN in the agricultural site through time. For any year following conversion, the prediction of NMIN can be combined with information on the yield of a desired crop per unit of available nitrogen. The decision can then be made as to whether or not the site can supply the nitrogen required to achieve the desired crop yield. If the answer is no, a fertilizer application level can be determined to achieve the desired yield.

Linking Net Primary Production and Net Nitrogen Mineralization

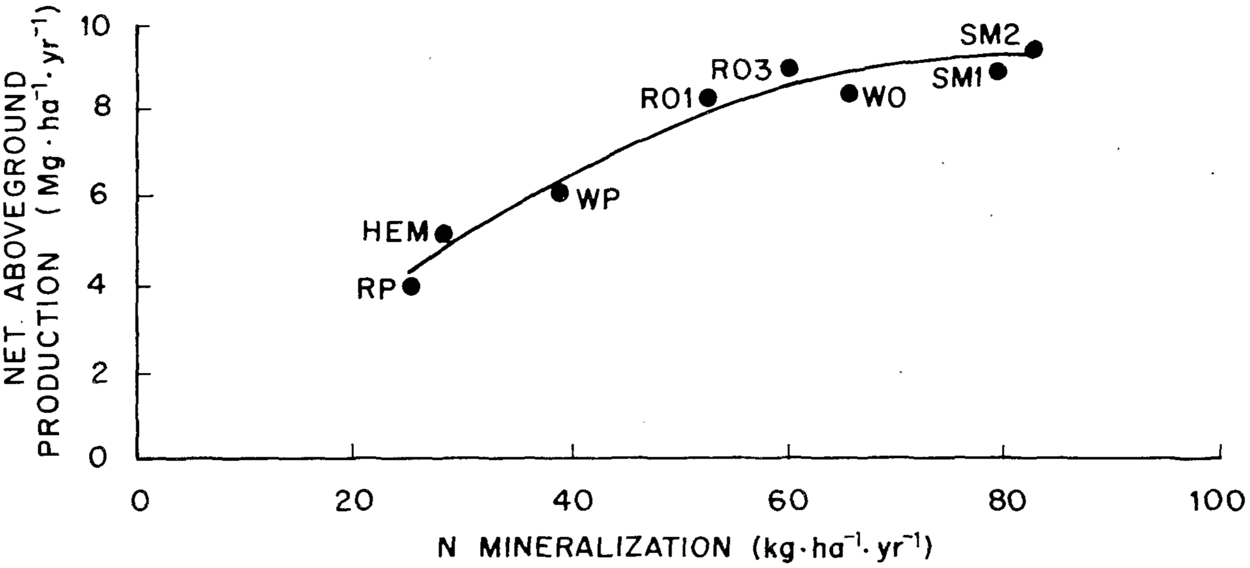
To review, net nitrogen mineralization (NMIN) is defined as that fraction of the inorganic nitrogen produced in soils that exceeds the microbial demand for nitrogen. This nitrogen represents the amount that can be taken up by plants or that can be lost from the system via leaching or gaseous flux.

During the past two decades, *in situ* studies of NMIN have frequently involved the incubation of soil in closed polyethylene bags or in boxes open on one side. When either method is used, soil samples are stored in containers (polyethylene bags or boxes) for a specified period (usually one month) at the depth in the soil from which they were taken. The difference between the content of inorganic nitrogen at the beginning and at the end of the incubation period gives an estimate of net mineralization.

The technique has been applied in a number of forest ecosystems and is also now being used in agricultural systems. The technique certainly provides a good relative measure of nitrogen availability to plants. In a recent application of the technique in an agricultural system, Westermann and Crothers (1981) reported a close correlation between N uptake as predicted by NMIN measurements and as measured in harvested above and below-ground biomass ($r = 0.98$, $n = 23$, $P < 0.01$). Evidence from the Westermann and Crothers study and preliminary results from our own research suggests that the *in situ* technique also provides a reliable quantitative index of nitrogen availability in soil.

We have recently developed a relationship between NMIN and aboveground NPP for a series of forest sites in the northeastern and northcentral parts of the United States. Figure 3 shows this relationship for a set of eight stands in Wisconsin.

Figure 3. Aboveground NPP, plotted as a function of NMIN for eight forest stands in Wisconsin. From Pastor et al. *(1984).*



Changes in Net Nitrogen Mineralization Following Conversion

As we noted earlier (see Figure 1), the rate of NMIN in the soil is related to the time since the last disturbance and how the site is being used. When a forest is converted to cropland we would expect a rapid increase in NMIN that may be described initially by a Q_{10} function. After a specified period, we would expect the rate of NMIN to decline according to an exponential decay function. This nitrogen mineralization "response function" may have to be specified according to climate and soil type. Nonetheless it will allow the prediction of changes NMIN during any growing season following conversion.

Net nitrogen mineralization and crop yield

The crop physiology literature contains many functions that describe the relationship between crop yield and nitrogen fertilizer demand for specific crops. For example, Figure 4 describes just such a relationship for cabbage. With knowledge of the N supplying power of the site and with a crop yield / unit nitrogen relationship, crop yield or NPP of the agricultural crop can be predicted. As is shown in Figure 5, the amount of additional nitrogen needed at a site to achieve a specific crop yield can also be calculated.

Summary

Our approach for linking the NPP of natural ecosystems with the NPP of agricultural ecosystems is summarized in Figure 6. First we suggest that the NPP of a natural ecosystem (NPP_{ns}) can be used to predict NMIN of that system ($NMIN_{ns}$). Next we use our understanding of the way NMIN of a natural site will change following clearing to predict NMIN in the agricultural site ($NMIN_{as}$) through time (from first year after clearing t_1, to the nth year after clearing t_n). Finally, for any year following conversion (t_i) the prediction of NMIN in the agricultural site ($NMIN_{as}$ (t_i)), can be combined with information on the yield of a desired crop per unit of available nitrogen (crop yield/unit Nmin). As noted earlier, the decision can then be made as to whether or not the site can supply the nitrogen required to achieve the desired crop yield. If the answer is no, a fertilizer application can be determined to achieve the desired yield. The approach of Van Keulen (1982, this volume) should prove very useful in predicting fertilizer N demands of crops at numerous sites around the world.

ECOSYSTEM MAINTENANCE AND AGRICULTURAL SYSTEMS

Ecosystem maintenance involves two tasks: keep-

Figure 4. *Yield of cabbage grown in Midlands region of England plotted as a function of N fertilizer applied at two levels of P and K fertilizer application. Modified from Milthorpe and Moorby (1974).*

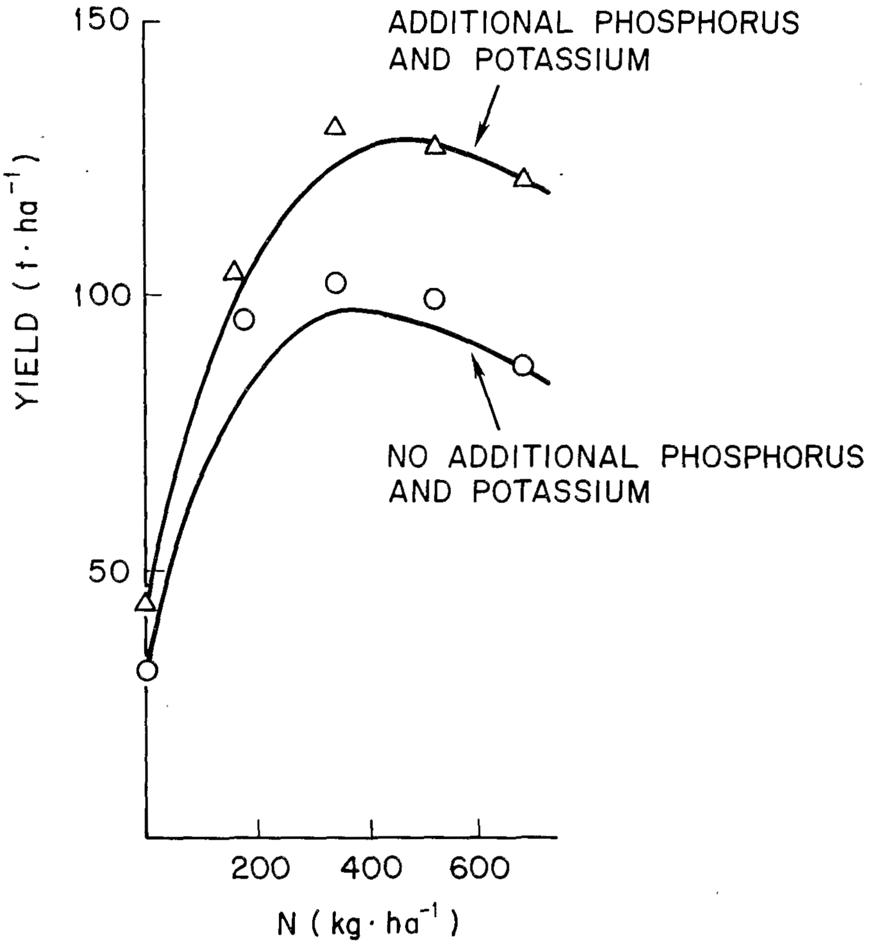


Figure 5. *NMIN of site converted from forest to cropland as a function of time. Dashed line describes N required for desired crop yield. Distance between solid and dashed lines represents amount of fertilizer that must be applied to achieve desired crop yield.*

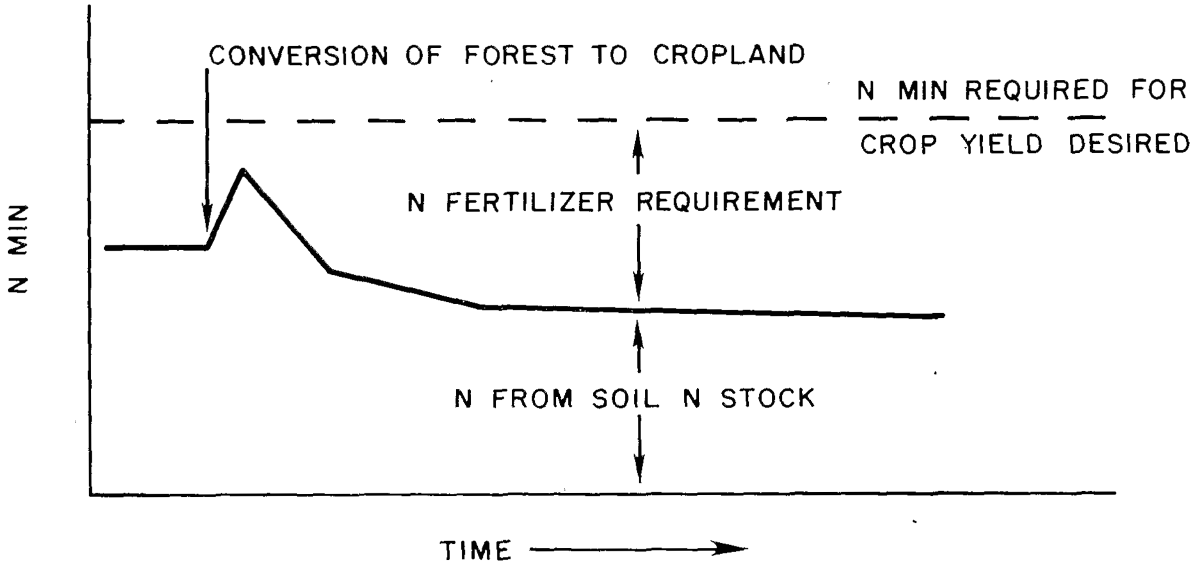


Figure 6. Summary of proposed approach for linking NPP of a natural ecosystem (NPP_{ns}) with NPP of an agricultural ecosystem (NPP_{as}). See text for further explanation.

$$NPP_{ns}(t_0) \not\longrightarrow NPP_{as}(t_1 \ldots t_n)$$

$$NPP_{ns}(t_0) \longrightarrow NMIN_{ns}(t_0)$$

$$NMIN_{ns}(t_0) + \text{Ecological Information} \longrightarrow NMIN_{as}(t_1 \ldots t_n)$$

$$NMIN_{as}(t_i) * (\text{Crop Yield / Unit NMIN}) \longrightarrow \text{Crop Yield}_{as}(t_i)$$

ing the system's carbon and nutrient stocks organized; and minimizing net losses of carbon and nutrients from the system. Both of these tasks require energy investments in the system.

A useful relative index of the magnitude of this investment in maintenance appears to be its net ecosystem production.

Net Ecosystem Production and Its Relationship to Net Primary Production

Net ecosystem production (NEP) refers to the rate of change in the carbon stocks of an ecosystem. Ecologists have developed a formal definition of NEP that can be stated as follows:

$$NEP = NPP - R_H \qquad \text{Equation 1}$$

where NPP is net primary production and R_H is the respiration of the heterotrophic component of the ecosystem. Net ecosystem production as defined in equation 1 was developed for natural ecosystems where inputs and outputs of carbon are small and thus can be ignored. For agricultural systems, however, inputs of "particulate" or "fixed" carbon such as those associated with manuring may be large. And outputs of "particulate" or "fixed" carbon associated with harvest and erosion may also be large. Thus, we must redefine NEP when we consider agricultural ecosystems. The following definition is proposed:

$$NEP = NPP + PI - R_H - PO. \qquad \text{Equation 2}$$

where PI is "particulate" carbon input and PO is "particulate" carbon output.

Net Ecosystem Production in Natural Ecosystems

Metabolic parameters for nine natural ecosystems appear in Table 1. For all of these systems NEP is positive; that is, all of the systems are accreting carbon. But not all natural ecosystems are carbon accumulators with NEP values greater than zero. Net ecosystem production in natural ecosystems can also be zero or even less than zero.

Ecological theory suggests that net ecosystem production of forest ecosystems is related to the time since the last disturbance (Figure 7). Immediately following disturbance NPP is less than R_H and NEP is negative. In time, the living vegetation exerts its control over the site and NPP exceeds R_H and NEP is positive. Numerous measures of NEP in carbon accreting forests have been made and some appear in Table 1. "Mature" ecosystems are thought to have a NEP that approaches zero.

Relationship Between Net Ecosystem Production and Nutrient Cycling

Ecosystems with a positive NEP are generally ecosystems which exhibit a net accumulation of nutrients. Similarly, ecosystems with a negative NEP are generally ecosystems which exhibit a net loss of nutrients.

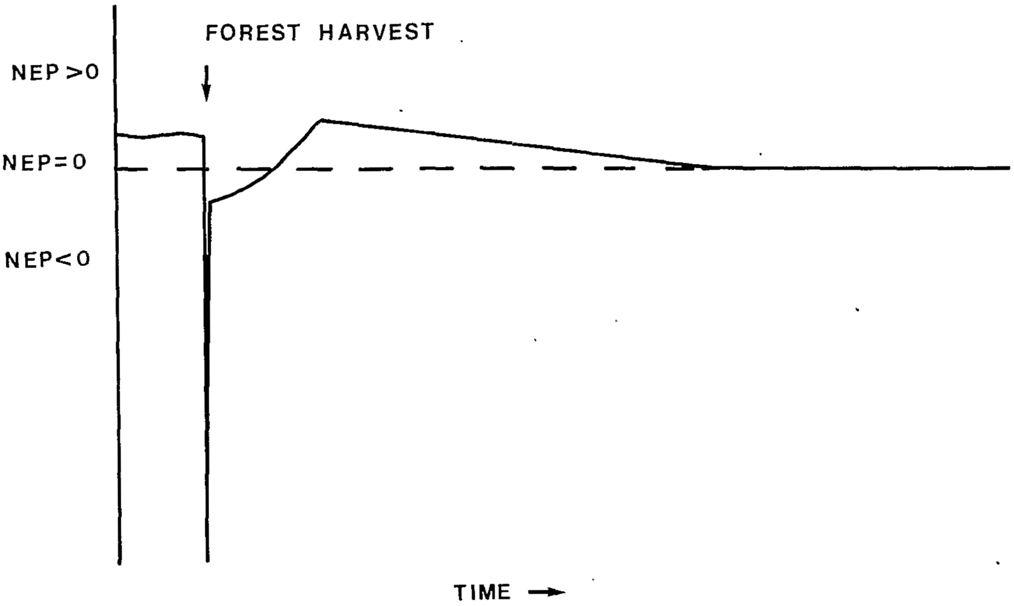
A complex set of interacting factors results in net losses of nutrients from forest sites immediately following disturbance (Vitousek, 1983); a time when NEP is negative. Shading of the soil

Table 1. *Comparative parameters of nine different natural ecosystems using indices from Reichle (1975). All values above the dotted line are in grams of carbon* m^{-2} *and grams of carbon* $m^{-2}\ yr^{-1}$ *except values in parentheses; values below the dotted line are dimensionless indices. All conversions from author's biomass values assume carbon content of biomass to be 50 %. TSC = total standing crop. GPP = gross primary production. NPP = net primary production.* R_A *= autotrophic respiration.* R_H *= heterotrophic respiration.* R_I *= ecosystem respiration. NEP = net ecosystem production.*

	FORESTS TYPES AND LOCATIONS								
Parameters	**Mixed deciduous Tenn., USA$_a$**	**Pine plantation N. Carolina, USA$_b$**	**Oak-Pine New York, USA$_c$**	**Subalpine coniferous Japan$_d$**	**Douglas fir Oregon, USA$_e$**	**Oak Britain$_f$**	**Mixed deciduous New Hampshire, USA$_g$**	**Shortgrass Prairie$_h$**	**Tundra$_i$**
TSC	8760	7062	5096	15905	41899	7466	8085		
GPP	2162	4124	1231	1910	8044	2330	1274	641	240
NPP	726	2056	542	535	544	1918	564	423	120
R_A	1436	2068	690	1375	7500	1412	700	218	120
R_H	670	694	282	331	378	564	356	294	108
R_I	2106	2762	966	1706	7878	1976	1056	512	228
NEP	56	1362	265	204	166	354	218	129	12
R_A/GPP	0.66	0.50	0.56	0.72	0.93	0.61	0.55	0.34	0.50
NPP/GPP	0.34	0.50	0.44	0.28	0.07	0.39	0.44	0.66	0.50
R_A/NPP	1.98	1.00	1.27	2.57	13.79	1.54	1.24	0.52	1.00
R_H/R_A	0.47	0.34	0.41	0.24	0.05	0.40	0.51	1.34	0.90
NEP/GPP	0.03	0.33	0.22	0.11	0.02	0.15	0.17	0.21	0.01

a From Harris *et al.* (1975).
b From Kinerson *et al.* (1977).
c From Woodwell & Botkin (1970) which report all values as biomass. They assumed that 1 g carbon dioxide represents 0.614 of dry matter. We back-calculated to obtain a value for carbon dioxide, then multiplied 0.27 to convert dioxide to carbon for all parameters except TSC.
d From Kitazawa (1977).
e Grier and Logan (1977).
f From Satchell (1973).
g Whittaker *et al.* (1974).
h Andrews *et al.* (1974).
i Reichle (1975).

Figure 7. Net ecosystem production as a function of time for a mid-successional forest that is cut and regrows to an old age forest.



surface is decreased, and soil temperature increases (Stone, 1973; Harcombe, 1977). Additionally, plant uptake and transpiration of soil water and mineral nutrient uptake are usually decreased for at least 2-3 years even in sites that rapidly regrow to forests (Marks and Bormann, 1972; Gholz, 1980; Boring *et al.*, 1981). With reduced evapotranspiration, water flux through the soil is increased, and so losses of nutrients through leaching to ground water and streams can be increased.

A major consequence of these changes in temperature and moisture is an increase in rates of decomposition and nutrient mineralization in deforested sites (Dominski, 1971; Stone, 1973; Stone *et al.*, 1979; Bormann and Likens, 1975). The forest floor decomposes rapidly (Covington, 1976; Bormann and Likens, 1979); and without forest regeneration will eventually disappear. The combination of increased decomposition (which consumes oxygen) and wetter soils (which slow oxygen diffusion) may also increase the occurrence of anaerobic microsites within the soil. Anaerobic conditions can lead to gaseous losses of nitrogen (Melillo *et al.*, 1983) and sulfur (Steudler and Melillo, unpublished data).

In hilly sites, another consequence of deforestation is an increase in soil erosion and particulate transport in streams. Delivery of soil to streams is increased because: (1) the wetter soil after deforestation is heavier and less cohesive, and thus more subject to soil creep and rapid slope failure; (2) the decay of tree roots reduces the cohesiveness of soil and increases soil creep and the probability of debris avalanches (Swanson *et al.*, 1981), and (3) the decrease and eventual disappearance of the forest floor alters the infiltration rate of the soil, allows raindrop impact on the mineral soil, and can thus increase surface run-off. Once material reaches streams, the increased stream flows in deforested sites are able to transport more and larger particulates downstream (Bormann *et al.*, 1974). The relationship between stream flow particulate transport often has an increasing exponential form, so the capacity to transport particles increases more rapidly than increases in peak stream flows. Where deforestation leads to agricultural land use, higher rates of erosion will be maintained indefinitely (Ritchie *et al.*, 1974; Rapp, 1975) unless practices such as no-till agriculture are adopted (Doran, 1980).

Net Ecosystem Production in Agricultural Ecosystems

We know of only one detailed study of net ecosystem production in agricultural ecosystems. The work was done by Dr. L. Ryszkowski on two agricultural ecosystems, a potato field and a rye field in Poland (Table 2). The potato field had a positive NEP of 103g C m^{-2} while the rye field had a negative NEP of 111g C m^{-2}. The positive NEP in the potato field was achieved by a particulate input of 263g C m^{-2}. Without this carbon input the potato field would have exhibited a negative NEP of 160g C m^{-2}.

Negative net ecosystem production is apparently common in agricultural ecosystems (Dr. D.

Table 2. Comparative metabolic parameters of two agricultural ecosystems. All values are in grams of carbon m^{-2} yr^{-1}. Data of Ryszkowski (personal communication). NEP calculated acoording to equation 2.

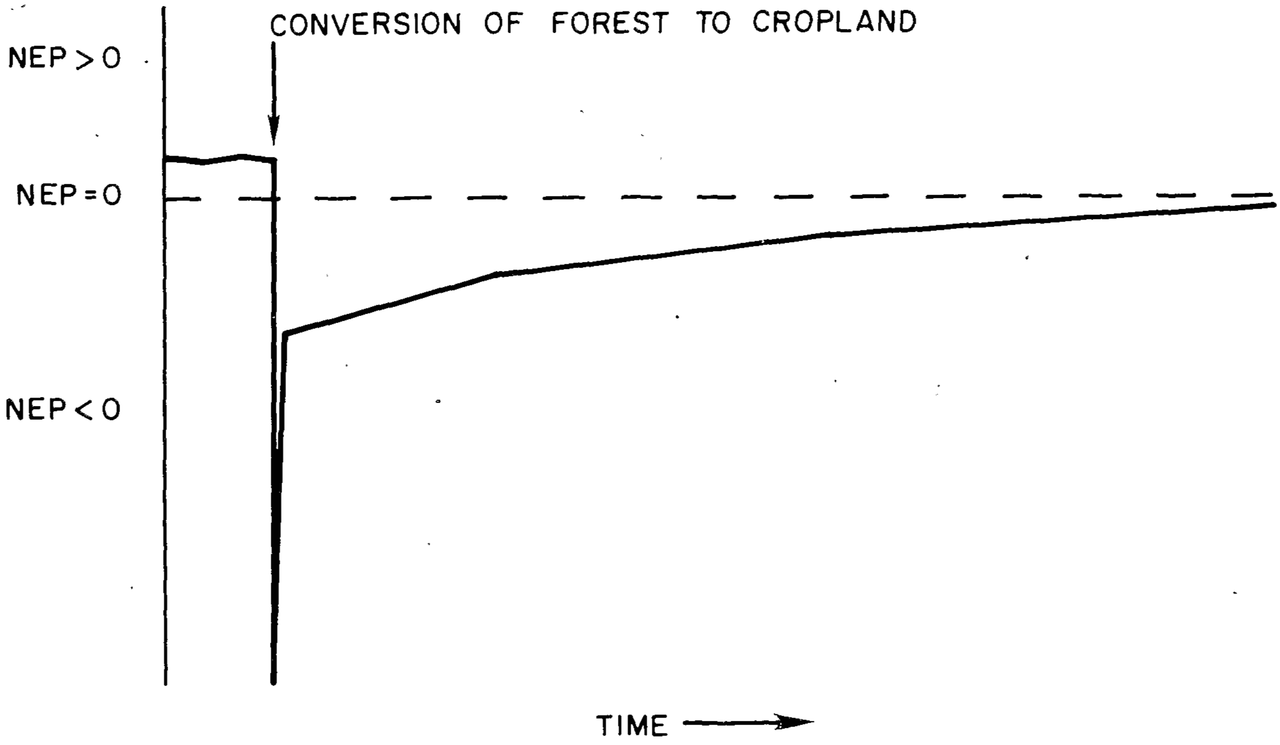
Comparative metabolic parameters	**Potato field**	**Rye field**
Gross primary production (GPP)	1286	1006
Autotrophic respiration (R_A)	431	342
Net primary production (NPP)	849	664
Particulate (PI) input	263	0
Heterotrophic respiration (R_H)	500	310
Particulate (PO) output	509	465
Net ecosystem production (NEP)	103	-111

Schimel, personal communication). This results because there is no net year-to-year accumulation of carbon in the vegetation on the site and because cultivation of soil causes a net reduction of the site's soil carbon stock.

The rate of soil carbon loss is variable and is related to the time since conversion of the site to cropland, the quantity of the carbon stocks of the natural systems prior to conversion, and the type of agriculture practiced. Based on the work of a number of researchers in Africa, Young (1975) has proposed the use of an exponential decay model to simulate carbon loss following conversion of natural ecosystems to cropland. For the soils of the tropics, Young suggested a range of decay constants "from over 10 percent in the first year after vegetation clearance to less than 1 percent after long periods of cultivation". This soil carbon loss is apparent in a simplified representation of the pattern of NEP change following conversion of a secondary forest to cropland which appears in Figure 8. The rate of NEP is most negative immediately following clearing as the labile component of the soil carbon stock is reduced through catabolic activity of microbes and soil erosion. After a prolonged period of cultivation and the depletion of a large fraction of the labile carbon stock of the soil, erosion may become the major mechanism responsible for the reduction of the soil's carbon stocks. The implications of negative NEP for nutrient cycling in agricultural systems are the same as those for natural systems; that is a negative NEP generally results in nutrient losses.

To minimize the net loss of nutrients from an agricultural ecosystem it appears to be necessary to have a high enough rate of agricultural NPP so that a sufficient fraction of it can be invested in maintaining the site's NEP equal to or greater than zero. While the investment of some fraction of the NPP in site maintenance appears to be desirable for long-term site productivity, such an investment can have negative consequences for crop production in the short term. If the fraction of the NPP left on site is carbon-rich and nutrient-poor, nutrients will be immobilized through microbial activity during the early stages of decay of the plant debris. Nutrients

Figure 8. Net ecosystem production plotted as a function of time for a mid-successional forest that is converted to cropland.



required to meet the immobilization demand can therefore reduce the amount of nutrients available to support plant growth. Tha amount of nutrients involved in the immobilization process can be predicted accurately and thus factored into a crop management regime (Melillo and Aber 1984).

Finally, it must be recognized that agricultural harvest is a process designed to remove nitrogen, in the form of protein, from the land. The nitrogen lost from the site through harvest must be replaced. Replacement can occur by adding nitrogen-rich materials such as occurs in certain manuring practices, or by promoting nitrogen fixation on the site. The "return" of nitrogen to the land by either mechanism is accompanied by organic matter inputs and therefore leads to a positive NEP.

Biomass as the Keeper of Organization in an Ecosystem.

An ecosystem is a basic functional unit of nature comprising both organisms and their non-living environment, intimately linked by a variety of biological, chemical and physical processes. According to Margalef (1963), biomass is the *keeper of organization* in such a system. The amount of biomass is viewed as being proportional to the influence that an ecosystem exerts over future events occurring within its boundaries. In other words, in an ecosystem with a relatively large amount of biomass, the structure and function of the system in the future are more dependent on the present intrasystem conditions than on inputs to the system. Such a situation, then, is one in which homeostasis is high. On the other hand, future structure and function of an ecosystem with relatively less biomass are more heavily influenced by inputs.

From the above argument it follows that an ecosystem's sensitivity to inputs will increase if the amount of biomass of the system is reduced significantly and then maintained at a relatively low level. The homeostasis of a system that has undergone this type of change will be much reduced in comparison to its former state.

Agricultural ecosystems tend to be of the "input sensitive" type. Inputs to such a system have to be quantitatively related to system demands (crop demands) and synchronous with those demands, otherwise the inputs will pass through the system. Natural systems, with their large organic matter stocks (living and non-living biomass), have mechanisms such as nutrient immobilization in decaying plant litter (which is related to both the quantity and quality of the organic matter stocks) that allow the system to be less "input sensitive". These mechanisms reduce the need for the synchrony of (nutrient) supply to the system and demand of the plant component of the system.

SUMMARY

In summary, we urge that agricultural plots be managed as whole ecosystems. Of course we should be concerned about crop yield. But we should also be concerned about ecosystem maintenance. Maintenance of a site's organic matter and nutrient stocks will assure long-term productivity. Agriculturalists should be "caretakers" or "builders" and not "miners".

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